Trends in Ecology & Evolution

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Opinion

Intraspecific Adaptation Load: A Mechanism for Species Coexistence

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Evolutionary ecological theory suggests that selection arising from interactions with conspecifics, such as sexual and kin selection, may result in evolution of intraspecific conflicts and evolutionary 'tragedy of the commons'. Here, we propose that such an evolution of conspecific conflicts may affect population dynamics in a way that enhances species coexistence. Empirical evidence and theoretical models suggest that more abundant species is more susceptible to invasion of 'selfish' individuals that increase their own reproductive success at the expense of population growth (intraspecific adaptation load). The density-dependent intraspecific adaptation load gives rise to a self-regulation mechanism at the population level, and stabilizes species coexistence at the community level by negative frequency-dependence.

Highlights

Community ecology has suggested that adaptation to environmental conditions (resources and other species) can affect species coexistence.

There has been little discussion on how adaptation to intraspecific interactions (sexual and social conflict) affects community dynamics despite its importance in evolutionary ecology.

We propose that adaptation to intraspecific conflicts, which often leads to evolution of selfish traits occurring at the expense of population growth (intraspecific adaptation load), can promote species coexistence.

It stems from the density-dependent nature of intraspecific adaptation load; it tends to be larger in a larger population and serves as a self-regulating mechanism, which results in negative frequency-dependent growth in community dynamics.

We discuss methods for empirically studying intraspecific adaptation load to better link community and evolutionary ecology.

Species Coexistence Promoted by Adaptation to Conspecifics

What promotes species coexistence in nature has been a central issue in community ecology [1,2], in which adaptation has been regarded as an essential process. Adaptation shapes the population's interactions with its abiotic and biotic environments, and drives population and community dynamics [3–5]. While most studies on the role of adaptation in ecological dynamics have focused on adaptation to interspecific interactions and/or abiotic environments (e.g., habitat selection [6], utilization of light environments [7], prey defense traits [8], and predator foraging traits [9,10]), there is an alternative, overlooked mode of adaptation that can affect ecological dynamics; that is, adaptation to conspecifics, including those to sexual and nonsexual (i.e., social) conflict [11,12]. There seems a gap left unfilled between evolutionary and community ecology, given that a large proportion of topics in evolutionary ecology is of intraspecific interactions (**sexual selection** and **social selection**, see Glossary). In fact, one of the most popular textbooks of behavioral ecology [13] has 15 chapters, of which nine are on intraspecific interactions whereas only three chapters concern interspecific interactions.

Does the gap imply that adaptation to conspecifics is less important for community dynamics? What, if any, is the general role of conspecific conflicts in ecological dynamics and species coexistence? Some studies have suggested that species coexistence can be influenced by adaptation to conspecifics, such as adaptation in sex allocation [14–18] and sexual conflict [19–21] as well as **eco-evolutionary feedbacks** of **social dilemma**, including allelotoxin production by plants and siderophore production by bacteria [22–27]. However, these studies have been conducted independently and few attempts have been made to synthesize them. Here, we provide a more comprehensive and general view to how adaptation to conspecifics may affect community dynamics by considering **absolute fitness** (Box 1) and introducing a new concept, **intraspecific adaptation load**, which measures the negative effect of intraspecific adaptation on population growth. We show that intraspecific adaptation load can be density-dependent in many cases, resulting in

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Box 1. Two Indices of Reproduction for Evolutionary and Community Ecology

Evolutionary and community ecology both focus on reproductive processes of organisms, but they have used separate indices for reproductive outputs because of their different biological levels. Evolutionary ecologists are interested in heterogeneity within species to predict genotype dynamics [13]. Evolutionary biologists, especially population geneticists, tended to focus on relative fitness and ignore demography (but see studies on life-history evolution). On the other hand, community ecologists are interested in heterogeneity between species, and they have investigated the population growth rate for predicting demography with limited interests in intraspecific variation [2,58].

For synthesizing evolutionary and community ecology, we need a unified index: evolutionary ecologists need to examine absolute fecundity [45], whereas community ecologists need to consider heterogeneity within populations [58]. Studies on eco-evolutionary dynamics have tackled the challenge by considering genetic and species diversity simultaneously [3–5], but they tended to concentrate on the situations where phenotypic optima for individual reproductive success and population growth coincide. We point out the importance of considering mismatches between individual- and population-level fitness due to intraspecific conflicts, which can be expressed by frequency-dependent selection (i.e., individual fitness depends on its own trait as well as the population mean trait) of quantitative genetic models [59]. When fitness is frequency-dependent, some singular points with the locally minimum population growth rate can be ESSs [59].

Consider a situation where individual-level selection favors the selfish trait that maximizes the proportion of their offspring in a local population but reduces the total number of offspring of the population (i.e., population growth). A population without selfish individuals can enjoy the largest population growth rate but are invaded by selfish mutants [31]. Previous empirical studies demonstrated that selfishness (cheaters and male mating harassment) can reduce population growth around 25% and 50% in subsocial ants [60] and damselflies [47], respectively. We show how the negative frequency-dependent growth arising from the evolution of selfishness promotes species coexistence by equalizing growth rates in Box 2.

negative frequency-dependent growth at the community level, and thereby enhances species coexistence.

When Sexual and Social Interactions Lead to Intraspecific Adaptation Load

Adaptations that affect individual performance (i.e., the reproductive outputs of individuals) should affect population performance (i.e., population growth). For example, adaptation that improves resource use efficiency may not only increase the individual reproductive success, but also lower the minimum resource level required for a population to increase and make the species superior in interspecific resource competition. While adaptations to interspecific interactions and/or abiotic environments improve competitive superiority of the species, intraspecific adaptations can have qualitatively different consequences for population dynamics in two ways.

First, intraspecific adaptation often reduces population growth when an intraspecific conflict occurs over the distribution of reproductive opportunities of conspecifics. In this case, higher per-capita reproductive outputs are selected for at the expense of those of other individuals. We call this population-level expense of intraspecific adaptation intraspecific adaptation load. A good example is longer genitalia of male ground beetles, which can be advantageous in sperm competition and would be favored in male intrasexual competition. However, longer genitalia decrease female reproductive success by increasing egg dumping [28] and thus can have negative effects on population growth (intraspecific adaptation load). Indeed, Takami and colleagues [28] found that a small effective population size was associated with longer male genitalia (i.e., more selfish males), implying the possibility that adaptation to intrasexual competition may take place at the expense of population growth.

Second, while intraspecific adaptation increases the intensity of intraspecific competition, it may only have a minor effect on, or even weaken, interspecific competition. This is because the limiting resources in intraspecific conflicts such as mating partners are usually valuable only in the intraspecific sexual or social context and not valuable for heterospecifics. For example, the long male genitalia of ground beetles may not affect mate availability for other species. This is in contrast with the 'normal' competition over food or space, in which evolutionarily improved

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performance of a species reduces the resource availability for other competing species and thus causes a negative effect to its competitors.

Magnitude of intraspecific adaptation load is measured by the amount of the decrease in the population growth rate attributable to intraspecific adaptation. An imaginary population with no intraspecific conflict would help providing a conceptual benchmark; suppose that all the individuals in the population behave cooperatively to increase the population performance. Such a population will be more efficient in gaining resources and transforming the acquired resources to population growth and therefore have a substantial competitive advantage over heterospecific populations. However, this does not occur in the real world, because no population is free from the invasion by conspecific cheaters, who exploit the contributions of other conspecifics. This is due to the unavoidable mismatch of interests between the individual-level reproductive success and population-level growth (as **Nash equilibrium** is not always **Pareto optimum** from game theoretical perspective [29]). This, together with the rich body of theory and empirical data from evolutionary ecology, strongly suggests that virtually all organisms are likely to show intraspecific adaptation load, although its magnitude may vary across taxa. The negative effects of intraspecific conflicts to population growth may be regarded as the **tragedy of the commons** at the population level caused by adaptive evolution [30,31], and may take various forms such as production of male offspring, male-male competition over mating, sexual conflict, and invasion of **selfish individuals** [31]. In the following, we demonstrate that intraspecific adaptation load can be density-dependent in examples of social dilemma and sex allocation. Density-dependence of intraspecific adaptation load is key for integrating ecology and evolutionary biology.

Intraspecific Competition and Density-Dependent Load

Consider a case where the selfish trait confers benefit to the focal individual but incurs cost to other individuals. The best-known evolutionary games, such as the snowdrift and hawk–dove [29], are good examples. Those game theoretical situations are often found in nature: for example, in a subsocial ant species (*Pristomyrmex punctatus*) in which all workers reproduce asexually, selfish individuals preferentially invest their resources to the production of their own eggs instead of carrying out group tasks (Figure 1A) [32]. In laboratory yeast (*Saccharomyces cerevisiae*) populations, selfish cells take advantage of an extracellular enzyme produced by cooperative cells but do not contribute to its production [33].

Individuals with lower selfishness contribute more to the population-level performance (e.g., group tasks of ants and extracellular enzymes of yeasts), which is exploitable for any individuals in a local population. In addition, individuals with higher selfishness may have a greater chance of obtaining the benefits from the cooperative individuals, assuming that the individual reproductive success is determined by the relative selfishness of the focal individual compared with the local population mean as well as the population-level performance, which decreases with increasing population-level selfishness [34]. A simple analysis (Box 2) indicates that the evolutionarily stable strategy (ESS) level of selfishness is an increasing function of the number of individuals in the local population, meaning that larger populations favor higher selfishness and suffer from larger intraspecific adaptation load (Figure 1C) [35].

A similar argument holds for the classic theory of sex allocation. Theory predicts that, if a single female exclusively utilizes a local resource, organisms are selected to invest almost all resources to production of female offspring to minimize competition among male siblings [36]. However, production of more male offspring is favored when two or more females share the local resource [37], although production of male offspring does not contribute to population growth. The ESS

Glossary

Absolute fitness: a genotype's unnormalized fitness, and the genotype abundance increases (decreases) if it is larger (smaller) than one.

Density-dependent selection: selection, whose direction and strength depend on the focal population's density.

Eco-evolutionary feedbacks: feedbacks between ecological (e.g., population density, community composition, and ecosystem functions) and evolutionary (i.e., gene frequency changes) processes.

Equalizing force: a mechanism that promotes species coexistence by equalizing average growth rates of populations.

Intraspecific adaptation load: reduction of population growth rates due to adaptive evolution driven by intraspecific interactions.

Modern coexistence theory: a framework of community ecology to understand species coexistence by examining reciprocal invasibility of species when rare.

Nash equilibrium: an equilibrium solution for a non-cooperative game, where no individual has anything to gain by changing their own strategy.

Pareto optimum: a state of resource allocation from which it is impossible to reallocate to make any one individual better off without making (at least) one individual worse off.

Reproductive interference: interspecific reproductive interactions that reduce the reproductive success of individuals involved.

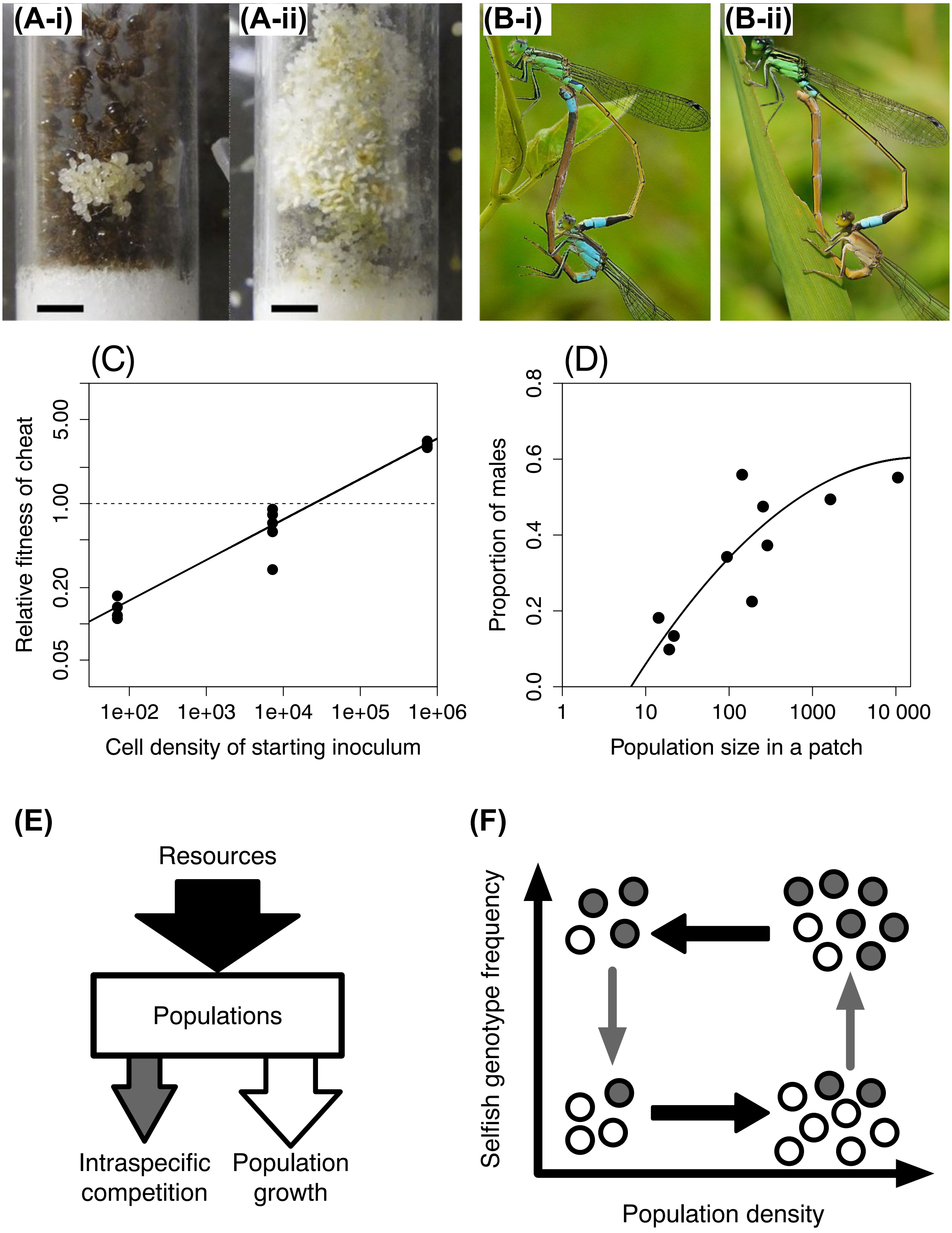
Selfish individual: an individual that increases its own relative reproductive success by reducing the common resource.

Sexual selection: selection arising from sexual reproduction through intrasexual (e.g., male-male) competition and intersexual interactions (e.g., female mate choice).

Social dilemma: a situation where pursuing an individual-level benefit results in the loss of a population-level performance.

Social selection: selection arising from intraspecific individual interactions in non-sexual contexts.

Stabilizing force: a mechanism that promotes species coexistence through negative frequency-dependence in community dynamics (e.g., resource partitioning).



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proportion of male production is $(n - 1)/(2n)$ [36] (see the supplemental information online), suggesting that the population growth rate with the ESS trait decreases with the local population size (Figure 1D). Thus, the production of male offspring is also regarded as density-dependent intraspecific adaptation load. See the supplemental information online for a more general modeling framework and Box 3 for other examples of intraspecific adaptation load.

Intraspecific adaptation load arises because organisms allocate obtained resources to intraspecific competition and population growth (Figure 1E). By focusing on specific types of intraspecific adaptation and comparing population growth rates with and without intraspecific adaptation, we can quantify intraspecific adaptation load, L, as follows:

$$L = \frac{W_{\mathrm{noIA}} - W_{\mathrm{IA}}}{W_{\mathrm{noIA}}}, \qquad [1]$$

where W is the absolute fitness (i.e., the per-capita finite rate of increase), noIA indicates no intraspecific adaptation (i.e., the least selfish situations), and IA represents the presence of intraspecific adaptation. In the examples of ants and yeasts [32,33], it is possible to estimate empirically the absolute fitness with and without cheaters by manipulating population densities and genotype frequencies. In the example of sex allocation, it may be possible to estimate the absolute fitness with and without male production if there is a genotype that does not produce male offspring.

Tragedy of the commons: a situation where individual competition results in reduced resource abundance and overall fecundity of a population.

Intraspecific Conflicts Stabilize Species Coexistence through Negative Density-Dependence

Evolutionary ecological theory predicts that the intraspecific adaptation load tends to be higher in larger populations [38,39]. There are supporting empirical evidence in microbial experiments (Figure 1C) [33,35]. The finding that more males (i.e., a ‘free-riding’ sex) are produced in denser populations (Figure 1D) due to less localized mate competition [14–18] supports the theory that relates population density to intraspecific adaptation load. Although there is a variety of mechanisms for density-dependent adaptation that reduces population growth rates due to sexual and social selection [40], all of them show the same pattern: small population sizes tend to reduce the tragedy of the commons [30,31]. The density-dependent intraspecific adaptation load is explained by more severe intraspecific competition when the density of a focal species is higher and intraspecific interactions are frequent. Since the social resources competed over in intraspecific competition have basically no value to heterospecific individuals, selection pressure to intraspecific adaptation should depend on conspecific population density alone (i.e., **density-dependent selection**).

The density-dependent nature of intraspecific adaptation load, combined with rapid adaptation or phenotypic plasticity, results in negatively density-dependent population growth rates: abundant species becomes more selfish and reduces its growth rate by increasing intraspecific

Figure 1. Eco-evolutionary Dynamics Driven by Intraspecific Adaptation. (A) The presence of selfish genotypes can cause the public goods dilemma in the nest of the subsocial ant (*Pristomyrmex punctatus*) [32,60], where more eggs were produced but they were neglected and began to decay due to poor hygiene (A-i) in contrast to the nest without cheaters (A-ii, scale bars are 2 mm). (B) Female color polymorphism (B-i, andromorph, B-ii, gynomorph) in damselfly (*Ischnura senegalensis*) can weaken male mating harassment, thereby enhancing population performance [47]. (C) Density-dependent fitness of cheats that produce less iron-scavenging siderophore molecules of bacteria (*Pseudomonas aeruginosa*) [35]. (D) Density-dependent sex ratio of a parasitic wasp (*Nasonia vitripennis*) [37]. (E) Resources or energy obtained by populations (a black arrow) are allocated to intraspecific competition (a gray arrow; intraspecific adaptation load) and population growth (a white arrow). (F) A population with selfish genotypes decreases its density (a top black arrow), whereas that with less selfish genotypes increases its density (a bottom black arrow). Due to density-dependent selection, a dense population favor increasing a frequency of selfish genotypes (a right gray arrow), whereas a sparse population decreases a frequency of selfish genotypes (a left gray arrow). X and Y axes are population density and selfish genotype frequency, respectively. Selfish and non-selfish (cooperative) genotypes are represented by gray and white circles, respectively [33].

adaptation load, whereas rare species can enjoy higher growth rate due to low selfishness (Figure 1F). As the energy input to the competing community is finite, the negative density-dependence in population growth (i.e., self-regulation) becomes negative frequency-dependence at the community level, promoting species coexistence (Box 2), as predicted by community network theory and classical competition theory [41]. The advantage of rare species due to negative frequency-dependent growth is often called **stabilizing force** in **modern coexistence theory**, and species coexistence is possible when both stabilizing and **equalizing forces** are strong enough [3]. Simulations demonstrate that adaptation of selfishness can stabilize dynamics and enhance species coexistence with negative frequency-dependence (Box 2 and Figure S1 in the supplemental information online), which is consistent with the previous studies [14–18]. In the natural communities, we predict that intraspecific adaption load is more likely to contribute to coexistence by increasing stabilizing niche differences when intraspecific adaptation load has a strong impact on population growth (Box 1) and when it can rapidly change via evolution or plasticity [23]. These conditions should be explored in more detail in future studies.

Box 2. Intraspecific Adaptation Load with Social Dilemma

Here, we outline how intraspecific adaptation load with density-dependence emerges with social dilemma and how it promotes species coexistence using a metapopulation model. Consider that the individual-level absolute fitness, W, is affected by its own selfishness, z ($0 \le z \le 1$), and the population mean selfishness, $\bar{z}$, as follows:

$$W(z,\bar{z}) = F(z,\bar{z})G(z,\bar{z}) + H(z,\bar{z}), \qquad \text{[I]}$$

where F (≥ 0) is the proportion of common resources distributed to the focal individual, G (≥ 0) is the total common resources shared by individuals in a local population [34]. For some types of adaptation (e.g., sex allocation), we may need H (≥ 0), a fitness gained not through the intraspecific competition. The selfishness, $\bar{z}$, evolves along the fitness gradient,

$$\left.\frac{\partial W}{\partial z}\right|_{z=\bar{z}} = \underbrace{G\left.\frac{\partial F}{\partial z}\right|_{z=\bar{z}}}_{\text{positive}} + \underbrace{F\left.\frac{\partial G}{\partial z}\right|_{z=\bar{z}}}_{\text{negative}} + \left.\frac{\partial H}{\partial z}\right|_{z=\bar{z}}. \qquad \text{[II]}$$

If fitness gain through improved intraspecific competition (the first term of the right-hand side of Equation II) is larger than the fitness loss due to decreased population absolute fitness (the sum of second and third terms), then selection favors increased selfishness.

The fitness of a variant strategy of selfishness z in social dilemma can be given by:

$$W(z,\bar{z}) = \underbrace{\frac{z}{z + (n-1)\bar{z}}}_{\text{intraspecific comp.}} \underbrace{\lambda[1-z + (n-1)(1-\bar{z})]^a}_{\text{common resource}}, \qquad \text{[III]}$$

where $\bar{z}$ is the population mean selfishness (excluding the focal), n is the population size ($n \geq 1$), λ is the maximum fecundity, and a is a nonlinearity coefficient ($0 < a \leq 1$): the hawk–dove evolutionary game (or, more generally, the avoidance of competition) is represented by setting $a = 1$, whereas the cooperator-defector game is represented by setting $a < 1$, which causes a synergistic increase in the population growth. The ESS selfishness, $z_{\mathrm{ESS}} = (n - 1)/(n + a - 1)$, is obtained by the fitness gradient based on Equation III, and is an increasing function of n. The population growth evaluated at the ESS trait, $W(z_{\mathrm{ESS}}, \bar{z}_{\mathrm{ESS}})$, is a decreasing function of n. Therefore, the population growth is maximized ($W = \lambda$) without social conflict ($n = 1$) and larger populations will be more selfish and grow more slowly, and intraspecific adaptation load, $L = 1 - [a/(n + a - 1)]^a$, is increased with population size.

The frequency dynamics of species i in the community, p_i ($0 \le p_i \le 1$), can be represented by the replicator equation, which is equivalent to the Lotka-Volterra competition model [61]:

$$\frac{dp_i}{dt} = p_i\left.\left[r_i(z_i,\bar{z}_i) - \sum_{j=1}^{S} r_j(z_j,\bar{z}_j)p_j\right]\right|_{z_i=\bar{z}_i}, \quad \frac{d\bar{z}_i}{dt} = v_i\left.\frac{\partial r_i(z_i,\bar{z}_i)}{\partial z_i}\right|_{z_i=\bar{z}_i}, \qquad \text{[IV]}$$

where $r_i = \log(W_i)$ is the per-capita growth rate of species i with no interspecific competition, v_i is additive genetic variance, and the trait value z_i changes along the fitness gradient [59]. Local population sizes are assumed to be correlated to species frequencies in a competing community as the energy input to the community is finite. As intraspecific interactions do not occur in vacant local habitats, we assumed a zero-truncated Poisson distribution to represent the local population size n_i as a function of the frequency p_i [18]: $n_i = k_i p_i/[1 - \exp(-k_i p_i)]$, where k_i is the scaling parameter. Species could not coexist without adaptation (i.e., fixed growth rates: data not shown), but rapid evolution of selfishness promoted coexistence (Figure I).

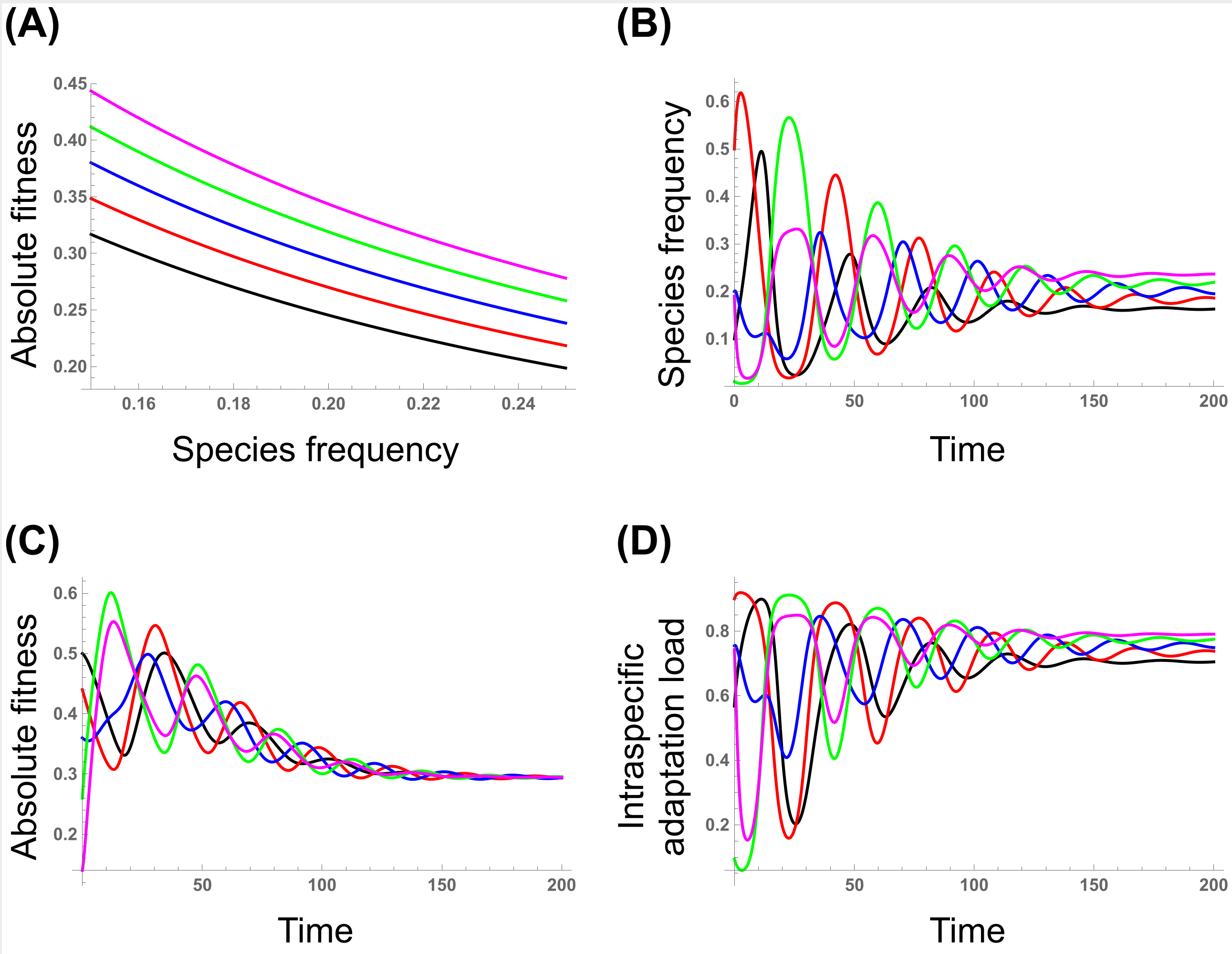

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Figure I. An Example of Eco-evolutionary Dynamics Simulations Driven by Intraspecific Adaptation (A) Absolute fitness with the ESS trait, $W_{ESS} = \lambda n^{a-1}(1 - z_{ESS})^a = \lambda n^{a-1}[a/(n + a - 1)]^a$, is a decreasing function of the species frequency in the community, p_i. Parameter values and corresponding colors are $a = 1$ and $k_i = 20$ for all five species and $\lambda_i = 1$ (black), 1.1 (red), 1.2 (blue), 1.3 (green), and 1.4 (magenta). Five competing species coexisted because intraspecific adaptation caused negative frequency-dependent growth (B). Intraspecific adaptation equalized the absolute fitness, W (C), as more abundant species had larger intraspecific adaptation load, L (D). The parameter value of additive genetic variance is $v_i = 0.01$ for all five species. We assume that genetic variance is constant, but it should decrease at low population size in reality. Therefore, evolution may be slow in small populations irrespective the slope of fitness gradient and coexistence may become difficult. Note that this is a toy model for a proof of concept, and further studies are needed for understanding the quantitative effects of intraspecific adaptation load on species coexistence.

Toward a Synthesis of Intraspecific Adaptation and Species Coexistence

Species Coexistence Promoted by Inter- and Intraspecific Adaptation

Previous studies about rapid evolution that enhances species coexistence usually made an *a priori* assumption of a trade-off between traits optimal for intra- and interspecific interactions [42–44]. For example, Vasseur and colleagues assumed a negative relationship between intra- and interspecific competition coefficients of the Lotka–Volterra competition model and proposed that neighbor-dependent selection may enhance species coexistence [22,23,25]. Wittmann and Fukami analyzed a metacommunity model assuming a trade-off between population growth and resistance to interspecific interference and hypothesized that regional species coexistence is promoted by rapid evolution (eco-evolutionary buffering) [27].

Box 3. Examples of Intraspecific Adaptation Load

In addition to social dilemma and sex allocation, we present three additional examples of intraspecific adaptation load. The first example is traits related to male–male competition over mating or fertilization success. Male–male competition can select for male traits that increase the reproductive success of the bearers at the costs of their mates [62]. Males can harm females and increase their mortality by coercing females into mating or manipulating female behavior to prevent multiple mating (Figure 1B) [63,64]. This can result in reduction of population sizes [48]. Similarly, in animals with parental care, males sometimes kill offspring to turn parenting, nonreceptive females into receptive (i.e., infanticides), which is also likely to reduce population growth rate [65]. If organisms do not 'waste' energy by harming females and offspring, population growth could be increased. Sexual conflict can be regarded as the tragedy of the commons [19,66] and a source of intraspecific adaptation load [20,21].

The second example is female mate choice: it can promote evolution of extraordinary signals of males (e.g., vivid color and costly dancing behavior). These traits are unnecessary for organisms to increase population growth, and may rather decrease population growth [56], for example, by attracting predators (i.e., sexually antagonistic pleiotropy). The balance between natural and sexual selection will determine the outcome of such conflicts [55]: for example, color of male guppies may be more vivid in habitats with less predation pressures [46].

The third example is begging competition between offspring for parental investment. Begging competition can attract predators [67] and converts a part of parental investment into the energy for begging behavior at the expense of its growth [68]. Sibling conflict is another cause of intraspecific adaptation load. It should be, however, noted that there could be a counter-evolution as pointed out in the main text: recent studies in plants demonstrated that this kind of intraspecific competition between relatives for space and soil resources is avoided [69], and plants competing with a clonal self plant produced more clonal individuals than plants competing with a non-self plant [70].

Our theory, in contrast, does not require any *a priori* assumptions of trade-offs between inter- and intraspecific interactions. Instead, we propose that the evolution of selfishness, with its density-dependent nature, is a potential, general stabilizing force promoting species coexistence. Avoidance of extinction of rare species caused by lowered intraspecific adaptation load can be viewed as a specific type of evolutionary rescue [45], where rapid evolution does not cause adaptation to environments, but reduces intrinsic disadvantage.

Factors Diminishing Intraspecific Adaptation Load

Nature presents many examples where intraspecific adaptation is strong. A sexual population is never free from invasion of male-producing females [36,37]; intrasexual competition leads to evolution of costly ornaments and aggression [46–48]; and even for clonal species, a group of cooperators suffers from invasion of cheaters [24,32,33,35]. This generality implies that intraspecific adaptation load can be ubiquitous and therefore serve as a general mechanism for promoting species coexistence. However, it should be noted that there are several possible mechanisms that may weaken the intraspecific adaptation load. For example, organisms may show little intraspecific conflict when population-level selection is stronger than individual-level selection or as a byproduct of kin selection [49,50]. When species extinction is common, population-level selection may become dominant and prevent evolution of selfishness [49,50], but the relative strength of population-level selection may be weaker than individual-level selection except for eusocial organisms [51].

Individual-level selection may reduce intraspecific adaptation load by selecting for counteradaptation to the selfish exploitation by conspecifics (e.g., byproduct cooperation) [52]. For example, the evolution of female color polymorphism in damselflies, *Ischnura senegalensis* (Figure 1B) may have evolved as a counteradaptation to male mating attempts that are costly for females, and it results in increased population density [47]. Male damselflies reduce female fecundity by mating attempts, and tend to be attracted to females with the more common phenotype, resulting in negative frequency-dependent selection. Takahashi and colleagues [47] found that populations with unbiased frequencies in female color polymorphism had higher population densities, probably due to weakened male mating harassment.

When Intraspecific Adaptation Does not Promote Species Coexistence

So far, we have focused on the cases where intraspecific conflicts are detrimental to interspecific competition and enhance species coexistence. However, if a trait has harmful effects both on conspecifics and heterospecifics, adaptation to increase individual reproductive success at the cost of other conspecifics may prohibit local species coexistence. For example, **reproductive interference** favors the more abundant species (i.e., positive frequency-dependence in community dynamics), and prohibits species coexistence [53]. Also, there is a heated debate about the potential effects of sexual selection on population growth and persistence; with evidence both for positive [54] and negative [55,56] effects. When sexual selection increases population growth rates, it may prohibit species coexistence.

Concluding Remarks and Future Perspectives

Based on empirical evidence and theoretical models, we provide a new perspective that intraspecific sexual and social interactions drive rapid evolution, cause negative density-dependence in population growth, and promote species coexistence. In community ecology, researchers have often posited trade-offs between traits for intra- and interspecific competition [23,27], but it was not clear how common they are in nature. We argue that negative density-dependence driven by rapid evolution may be more pervasive than previously thought because of an inherent zero- or negative-sum game in intraspecific competition (and the resultant tragedy of the commons) [31]. The phenotypic variations we observe in sexually reproducing organisms, such as visual, acoustic, or chemical signals, fancy ornaments, and eye-catching mating behaviors, are often treated as symbols of biodiversity. Yet, we would suggest that they are not only symbols, but also can contribute to the maintenance of biodiversity through their detrimental effects on population-level success. In the absence of evolutionary tragedy of the commons, organisms might have evolved to have higher population growth, but it might not be possible for us to observe the variety of species with those phenotypic variations.

The concept of intraspecific adaptation load suggests a new empirical direction for understanding how evolution to intraspecific conflicts promotes species coexistence (also see Outstanding Questions). In particular, invasive species offer unique opportunities because of their reduced genetic variation. In ants, for example, aggression toward conspecific aliens (i.e., unrelated individuals of the same species from different colonies) is controlled by genetically based chemical labels, and such aggression is considered as kin-selected adaptation [50]. The bottleneck reduces variation in the labels, making colony distinction difficult. This may reduce the intraspecific competition and promote the successful invasion of Argentine ants with supercolonies [50]. Furthermore, a recent development in time-series analysis [57] may allow us to examine feedback between community properties, population densities, and social traits in the wild.

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Outstanding Questions

How can mathematical analyses and numerical simulations that explicitly consider resource dynamics provide further insights to the effects of intraspecific adaptation load on intraspecific competition, interspecific competition, and species coexistence?

How can we quantify intraspecific adaptation load by manipulating genotype frequencies in experiments? Can we estimate the magnitude of intraspecific adaptation load from previous studies?

How can we quantify density-dependent selection and negative density-dependent population growth driven by sexual and social selection in the wild?

How general is intraspecific adaptation load and its density-dependence in the wild?

How can we quantify feedback between population dynamics and intraspecific adaptation load from, for example, time-series data of abundance, phenotypic traits, and genomic data?

How does intraspecific adaptation driven by density-independent selection (e.g., obligate sexual reproduction) affect species coexistence via the equalizing force?

How often does genetic bottleneck of invasive species reduce intraspecific adaptation load by (i) removing selfish genotypes and (ii) increasing the genetic similarity between individuals?

What kind of feedback is possible between intraspecific adaptation load, ecological processes, and evolutionary dynamics?

How can we explain patterns in trait evolution by considering population-level selection, population persistence, and intraspecific adaptation load?

How does kin selection based on genetic relatedness alter evolution of selfishness, intraspecific adaptation load, and species coexistence?

How can intraspecific adaptation load (including sexual conflict) promote species diversification?

Supplemental Information

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