The evolution of partner specificity in mutualisms

Christopher Carlson[1,2], , Erol Akçay[1], , Bryce Morsky[1],

[1]Department of Biology, University of Pennsylvania, Philadelphia, PA, United States
[2]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada
Corresponding author: Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks St, Toronto, ON, Canada, M5S3B2. Email: cachris@sas.upenn.edu; chris.carlson@mail.utoronto.ca

Abstract

Mutualistic species vary in their level of partner specificity, which has important evolutionary, ecological, and management implications. Yet, the evolutionary mechanisms which underpin partner specificity are not fully understood. Most work on specialization focuses on the trade-off between generalism and specialism, where specialists receive more benefits from preferred partners at the expense of benefits from non-preferred partners, while generalists receive similar benefits from all partners. Because all mutualisms involve some degree of both cooperation and conflict between partners, we highlight that specialization to a mutualistic partner can be cooperative, increasing benefit to a focal species and a partner, or antagonistic, increasing resource extraction by a focal species from a partner. We devise an evolutionary game theoretic model to assess the evolutionary dynamics of cooperative specialization, antagonistic specialization, and generalism. Our model shows that cooperative specialization leads to bistability: stable equilibria with a specialist host and its preferred partner excluding all others. We also show that under cooperative specialization with spatial effects, generalists can thrive at the boundaries between differing specialist patches. Under antagonistic specialization, generalism is evolutionarily stable. We provide predictions for how a cooperation-antagonism continuum may determine the patterns of partner specificity that develop within mutualistic relationships.

Keywords: mutualisms, symbiosis, cooperation, partner specificity, generalism, dispersal

Introduction

Mutualisms enhance the biodiversity in global ecosystems (Bascompte, 2019); therefore, understanding the evolutionary underpinnings of such associations is crucial to conservation and or promotion of biodiversity at the local, regional, and global scale (Bronstein et al., 2004). One important factor in the development of complex mutualism is partner specificity, the degree to which one organism preferentially interacts with a single partner species (Chomicki et al., 2020), which has been examined in numerous systems in which partners are acquired horizontally from the surrounding environment including legume-Rhizobium, fig-wasp, and damselfish-sea anemone mutualisms (Bronstein, 1987; Wang et al., 2012). The prevalence of partner specificity within horizontally transmitted interactions is difficult to explain given that there is a fitness cost associated with a mismatch between a host and its symbiont (Batstone et al., 2020; Uchiumi & Sasaki, 2020). Because specificity plays a pivotal role in shaping the stability, niche, and coevolutionary dynamics of mutualisms (Chomicki et al., 2020; Harrison et al., 2018; Uchiumi & Sasaki, 2020), variation in partner specificity may be explained by incorporating partner cooperation into a theoretical framework to examine how specificity and cooperation co-evolve in horizontally transmitted partnerships.

There is significant variability in the degree to which partners cooperate across both general and specific horizontally transmitted mutualisms such as plant-pollinator, coral-algae, and seed dispersal mutualisms (Bogdziewicz et al., 2019; Gomulkiewicz et al., 2003; Hoeksema & Bruna, 2000; Stat et al., 2008) which likely shapes the evolutionary stability of generalism vs. specialism. Some symbiotic species display little partner preference, forming partnerships with a wide variety of partner species (e.g., ant-plant and plant-mycorrhizal mutualisms involve generalist partners [Chomicki & Renner, 2017; Peay et al., 2015]) indicating that in the absence of one partner, another may serve as a substitute. Others are highly specific and only interact with as few as one other mutualistic partner species (e.g., moth-yucca plant, wasp-fig) (Gomulkiewicz et al., 2003; Machado et al., 2005). In such interactions, absence of a preferred partner could result in death. It is likely that specific mutualisms involve a high degree of pairwise coevolution, maximizing benefits when preferred partners interact, while reducing the benefits derived from associating with other partners. This trade-off makes specialism an apparently risky strategy relative to generalism, as absence/low abundance of a preferred partner may be highly detrimental to the fitness of the specialist (Thrall et al., 2007).

There is another and relatively less explored dimension to the generalist–specialist conundrum. Many mutualisms involve exchange of benefits that are costly to produce, and therefore even when the net outcome is mutually beneficial, there is an underlying conflict of interest. This conflict of interest may be resolved through behavioral mechanisms such as negotiation (Akçay & Roughgarden, 2007), or evolutionarily through adaptations and counter adaptations (as in nectar robbing, Irwin et al., 2010). The resolution mechanisms determine the division of benefits from an interaction,

and may cause one partner benefit more at the expense of the other. At the same time, mutualisms often also involve intricate behavioral adaptations and physiological adaptations to produce the benefits that both partners benefit from. Mutual specialization in these adaptations can lead to production of more benefits for both partners. This mutual specialization is reinforced by partner fidelity feedback given that the partners that cooperate the most receive the greatest benefit from mutualism (Bull & Rice, 1991; Friesen, 2012; Sachs et al., 2004). Physiological and behavioral adaptations mediate this cooperation in ant-plant mutualisms in which host plant capacity to house ants in domatia is linked to ant colony protection from herbivory (Archetti et al., 2011; Mayer et al., 2014). Thus, from the perspective of one of the partner species we can envision two kinds of specialism: cooperative specialism where both the focal species and its preferred partner enjoy higher benefits relative to non-preferred partners, and antagonistic specialists, where the focal species gets more benefits from its preferred partner, but the preferred partner gets less. These two kinds of specialisms will generate different kinds of ecological feedback (Bever et al., 1997), which will affect the evolutionary conditions under which specialism or generalism prevails.

An example of a system where such dynamics are expected is coral-algal symbioses, which are crucial to marine biodiversity. Within this symbiosis there exists significant variation in partner specificity; some coral hosts specialize, associating closely with a small range of Symbiodinaceae, while other hosts generalize, associating with many diverse symbionts (Thompson & Pellmyr, 1992). There is significant variability in how specific coral-algal associations are (Baker, 2003), yet theoretical models of coral symbiosis have not yet attempted to explain this variation (Cunning et al., 2017; Raharinirina et al., 2017; Roughgarden, 1975). Furthermore, while coral symbioses have been traditionally viewed as cooperative (Muscatine & Porter, 1977), there are also elements of Cnidarian symbiosis that showcase the regulation of conflict in the interaction, such as the coral host limiting the resource availability, reproductive capability, and resource extraction capability of their symbionts (Sutton & Hoegh-Guldberg, 1990; Wooldridge, 2010; Xiang et al., 2020).

Another example system is mycorrhizal symbioses, where generalism is common (Peay et al., 2015; Toju et al., 2013). It is possible that this trend toward generalism is dictated by the fact that dispersal is more difficult in this terrestrial system relative to aquatic symbiosis (Kinlan & Gaines, 2003a, b). In plant-mycorrhizal symbiosis, long distance dispersal of terrestrial spores must frequently rely on animal intermediaries (Paz et al., 2021), while aquatic propagules are dispersed vast distances by currents (Kinlan & Gaines, 2003b). Thus, in plant-mycorrhizal symbiosis, the likelihood of repeatedly partnering with a symbiont is greater. Yet, a few taxa form highly specific associations (Bruns et al., 2002; Sepp et al., 2019) in which hosts and symbionts associate together in strict, pairwise partnerships. Bever (2002) experimentally demonstrated the potential for antagonistic specialization in our sense using plant species *Plantago lanceolata* and *Panicum sphaerocarpon*, where the arbuscular mycorrhizal species growing best with one plant result in poor growth of that plant, and vice versa. And some plants appear to employ strategies to reduce mycorrhizal benefit and maximize host benefit (van der Heijden et al., 2015), especially when soils are replete with carbon (Kiers & Heijden, 2006). At the same

time, plant-mycorrhizal symbiosis also presents scope for cooperative specialization in which greater host capability to create a hospitable root environment for particular fungi and greater fungal ability to inhabit this environment likely increases symbiotic benefit for both partners (Hoeksema, 2010).

Antagonistic or cooperative specialization may also underlie mutualisms that resemble domestication. Such interactions often resemble a monopoly in which a host controls a resource, and specializes in a partner that provides an exchange rate favorable to the host, with examples including fungus-growing ants (Formicidae: Attini) and decomposing fungi (family Lepiotaceae) (Villesen et al., 2004), or between damselfish *Tegastes nigricans* and filamentous algae (Hata et al., 2010). In fungus farming ants, e.g., increased ant capability to harvest fungi does not necessarily benefit fungal fitness in certain lineages (Shik et al., 2016), representing a potential case of antagonistic specialization. Yet it is also plausible that in many of these interactions mutual behavioral and physiological integration of the partners represent coordinated ways of producing higher mutual benefits.

Here we consider the evolution of specificity using a model in which one partner species can exhibit cooperative or antagonistic specificity on different strains of the other partner species. Specialists in both cases receive an added benefit from a preferred symbiont type at the expense of less benefit with the opposite type. We also consider generalists who receive equal and intermediate benefit from either partner strain. When interacting with their preferred partners, specialists either enhance their partner's fitness (cooperative specialization), or reduce it (antagonistic specialization) relative to the partner's interaction with a generalist. We consider the ecological dynamics of these systems in well mixed and spatially structured populations as well as the evolution of both kinds of specialism as continuous traits, and derive conditions for the evolutionary stability of each given the ecological dynamics they produce. Finally, we analyze how incorporation of population spatial structure may impact the stability of specificity vs. generalism in an evolving population.

Model

We consider a population of two partner species, which we call "Hosts" and "Symbionts," for ease of referral to each side, although our model construction applies equally well to non-symbiotic mutualisms such as plant-pollination mutualisms. We assume a simple interaction structure that can represent many different kinds of mutualisms based on the exchange of resources (e.g., coral-algal mutualism) or services (e.g., plant-pollinator mutualism) (see Figure 1 for a view of the interaction from the host perspective, and Figure 2 for the symbiont perspective). Specifically, we assume that hosts translocate some proportion x of a resource, such as inorganic carbon in coral-algal symbiosis or nectar in plant-pollinator mutualism, to their symbiont partner. This partner produces a good or a service, such as organic carbon, which is γ times as useful as the original good. For example, symbiotic algae produce organic carbon using the inorganic carbon they receive from coral hosts. The organic carbon is more useful than the original inorganic carbon for both partners. The degree of phenotypic matching between hosts and symbionts improves this benefit of symbiosis for both partners as the match between host coral and symbiont might lead to
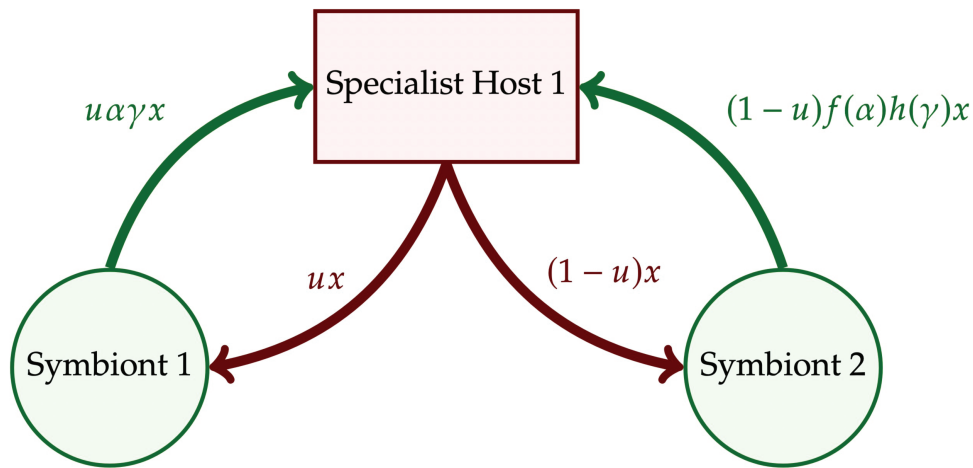
Figure 1. Associations for specialist host 1. Red arrows denote the amount of the resource given to each symbiont by a focal specialist host 1 with $0 \leq u \leq 1$. The symbionts each produce a good or service with value γx or $h(\gamma) x$. Green arrows denote the translocation of proportion α or $f(\alpha)$ of this resource back to the host. Parameters α and γ are associated with phenotypes specialized to one another, i.e., those that are "matched." $f(\alpha)$ and $h(\gamma)$ are for mismatched mutualisms.
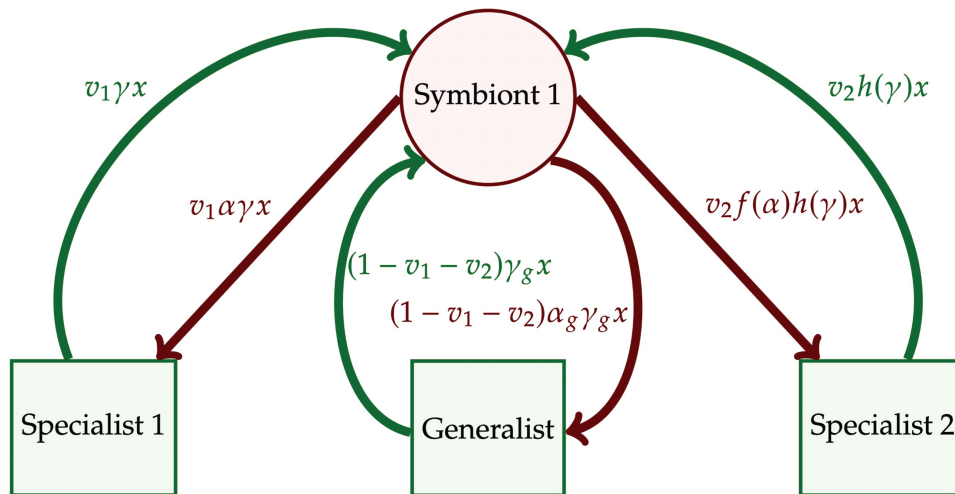

Figure 2. Associations for symbiont 1. Green arrows denote the value of the resource shared to symbionts by hosts with $0 \leq (v_1 + v_2) \leq 1$. Symbionts produce a good with value γx, $\gamma_g x$, or $h(\gamma) x$. The red arrows indicate the value of the good shared by symbionts to hosts with parameters γ_g and α_g associated with the generalist host phenotype.

the production of more organic carbon in coral-algal mutualism or the match between flower and proboscis morphology improves mutual benefit in plant-pollinator mutualisms. Symbionts then translocate a proportion α of the good they have produced back to their host at the expense of their own resource pool, as zooxanthellic algae translocate a proportion of their organic carbon back to a host at a cost to themselves, and pollinators perform a service for plants. However, there is no direct cost to the host resource pool as this proportion changes, e.g., there is no direct cost to a coral host from receiving more of its algal partner's organic carbon, and there is no direct cost to a pollinator from receiving more nectar from a plant. In this model, hosts and symbionts are in conflict over the evolvable variable α, signifying the division of benefits, but have mutual interest over increasing the similarly evolvable variable γ, which increases total benefit from the interaction.

To allow for the possibility of specialization, we assume that there are two types that make up the symbiont population. Conversely, the host population is made up of three

types: hosts that specialize on type 1 or 2 symbionts, and a generalist host. The potential associations for a focal type 1 specialist host are shown in Figure 1, where u and $1 - u$ are the frequencies of symbionts 1 and 2, respectively. All symbionts can associate with all host types, but experience and provide different costs and benefits from these associations. Specifically, we assume that all hosts translocate the resource indiscriminately at a cost x^2 to themselves (meaning that the resource is more valuable to the host the less it keeps). How much the hosts get in return from each symbiont depend on the parameters α and γ. Associations between matching host and symbiont types (e.g., symbiont 1 associates with specialist host 1) correspond to parameters α and γ, while host and symbiont mismatches (e.g., symbiont 2 associates with specialist host 1) correspond to $f(\alpha)$ and $h(\gamma)$. $f(\alpha)$ and $h(\gamma)$ are trade-off functions in which increasing the value with a preferred type reduces the mismatched value (i.e., $f'(\alpha) < 0$ and $h'(\gamma) < 0$). We consider concave up, concave down, and linear trade-off functions. Finally, both symbionts associating with generalist hosts exhibit parameters α_g and γ_g. The host

payoffs from exclusively interacting with a single symbiont type are:

Matched specialist host	$\pi = \alpha \gamma x - x^2,$
Generalist host	$\pi_g = \alpha_g \gamma_g x - x^2,$
Mismatched specialist host	$\pi' = f(\alpha) h(\gamma) x - x^2,$ (1)

where π and π' are the payoffs to specialist hosts matched and mismatched to their preferred symbiont, respectively. (In our symmetric setup, payoffs for specialist host depend only one whether they are matched or mismatched, and not on the identity of the strain they specialize in.) π_g is the generalist host's payoff, which they earn regardless of which symbiont they are with. We define our payoffs such that matched specialist payoff is greater than generalist–specialist payoff, which is greater than the mismatched specialist payoff π', i.e., $\pi > \pi_g > \pi'$.

Symbionts associate with one of the three host types where v_1 is the frequency of host 1, v_2 is the frequency of host 2, and $1 - v_1 - v_2$ is the frequency of the generalist host. The payoffs associated with these interactions for one symbiont type are shown in Figure 2. The symbiont payoffs are:

Matched to specialist host	$\psi = \gamma (1 - \alpha) x,$
With generalist host	$\psi_g = \gamma_g (1 - \alpha_g) x,$
Mismatched to specialist host	$\psi' = h(\gamma)(1 - f(\alpha)) x. (2)$

Here, ψ and ψ' are the payoffs to symbionts matched and mismatched to the host that prefers them, respectively, and ψ_g is the payoff to either symbiont when matched with the generalist host. By our assumptions, $\psi > \psi_g > \psi'$.

We average these payoffs over the distribution of partners in the population to determine the expected payoffs, w_j^i. Superscript $i = h, s$ denotes a host or symbiont, respectively, and subscript $j = 1, 2$ denotes type 1 or type 2, respectively. For example, the average payoff for a type 1 host is

$$w_1^h = u\pi + (1 - u)\pi' = ux(\alpha\gamma - x)$$
$$+ (1 - u)x(f(\alpha)h(\gamma) - x). \quad (3)$$

To study the dynamics of the frequencies of hosts and symbionts, we use the replicator equation (Taylor & Jonker, 1978) with two populations, where the change in frequency of a host or symbiont type is determined by the difference between its fitness and the mean fitness of its competitors. Our dynamical equations are thus:

$$\dot{u} = u(w_1^s - (uw_1^s + (1 - u)w_2^s)), \quad (4a)$$

$$\dot{v}_1 = v_1(w_1^h - (v_1w_1^h + v_2w_2^h + (1 - v_1 - v_2)\pi_g)), \quad (4b)$$

$$\dot{v}_2 = v_2(w_2^h - (v_1w_1^h + v_2w_2^h + (1 - v_1 - v_2)\pi_g)). \quad (4c)$$

Cooperative and antagonistic specialization

We consider two variations of this general model where the payoffs from specialism are determined in either a cooperative or antagonistic fashion. In the cooperative case, specialist hosts have greater efficiency in their association when they match with their preferred symbiont. We model this as the fraction of benefits returned α being the same for all host types ($\alpha = f(\alpha) = \alpha_g$), but $\gamma > \gamma_g = 1 > h(\gamma)$ such that a symbiont strain's effectiveness in returning host investment is greatest when matched to the host specializing on it. Generalists have the same efficiency with both symbiont types. Thus, under cooperative specialization, more benefit

is produced, but the relative division of it remains the same, such that both the specialist and its preferred symbiont benefit relative to the generalist and specialist with non-preferred symbiont.

In the antagonistic case, in contrast, specialist hosts have a higher α when paired with their preferred symbiont, specifically, $1 > \alpha > \alpha_g > f(\alpha) > 0$. We assume in this case all pairings have the same γ ($\gamma = h(\gamma) = \gamma_g$), such that there is no additional benefit being produced from specialization; specialist hosts are simply better at extracting a higher portion of the benefits from their preferred symbionts at no additional cost to themselves. This leaves symbionts that associate with matched specialist hosts with a lower fitness compared to interacting with generalist hosts or mismatched specialist hosts. We consider the term γ to be monotypic, meaning that there is no difference between phenotypes in the value of the benefit produced from symbiosis.

Spatial model

To understand the impact of spatial dynamics and heterogeneity, we extend these models by considering change in frequency of each type while diffusing across space. We model the diffusion process across the xy-plane by the following set of reaction-diffusion equations:

$$\dot{u} = D\Delta u + u(1 - u)(w_1^s - w_2^s), \quad (5a)$$

$$\dot{v}_1 = D\Delta v_1 + v_1\left(w_1^h - \left(v_1 w_1^h + v_2 w_2^h + (1 - v_1 - v_2) w_g^h\right)\right) \text{(5b)}$$

$$\dot{v}_2 = D\Delta v_2 + v_2\left(w_2^h - \left(v_1 w_1^h + v_2 w_2^h + (1 - v_1 - v_2) w_g^h\right)\right) \text{(5c)}$$

where D is the diffusion constant and $\Delta = \partial_{xx} + \partial_{yy}$ is the Laplace operator. See our Mathematica notebooks for the details of the numerical methods.

Invasion analysis

Finally, we consider how the traits α, γ, and x will evolve using adaptive dynamics and numerical simulations. We examined the outcome of invasion of a rare mutant whose trait values (i.e., values of α, γ, or x) differed from those of residents (Brännström et al., 2013). Trait values favored by natural selection were those that allowed an initially rare mutant to increase in frequency. When specialization was cooperative, we determined the invasion exponent, the fitness of these rare invading mutant hosts or symbionts strategist relative to a resident population. We assumed that the changes in strategist frequency from our dynamical equations (4a–c) and spatial model (5c) (ecological dynamics) occur rapidly relative to parameter changes (evolutionary dynamics). Thus, resident populations are the stable populations that emerge from the ecological dynamics. Next, we found the selection gradients, the change in the invasion exponent with respect to a change in a trait value γ, α, or x. The sign and stability of these selection gradients determined the pattern of selection that acted upon trait values. For mathematical details see Supplementary Material S1.3. When hosts specialized antagonistically, invasion exponents were intractable because there was no stable resident population. Therefore, we employed numerical simulations to determine whether a rare mutant host or symbiont would successfully invade. See the our Mathematica notebooks and Supplementary Material S2.2 for details.
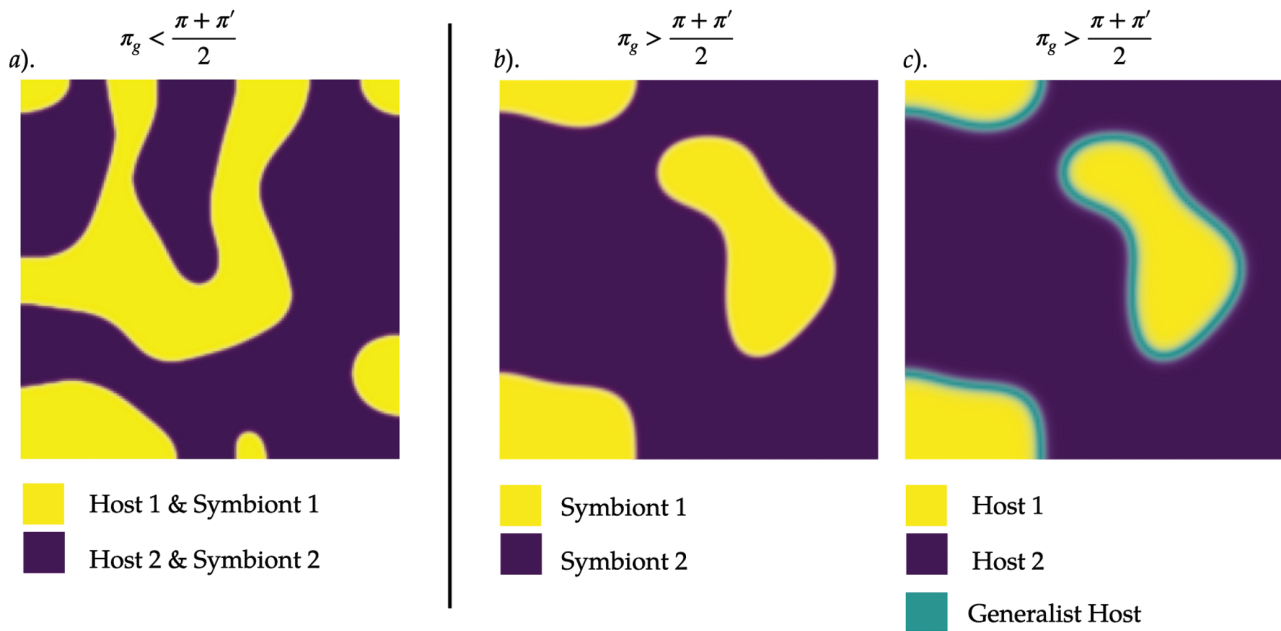
Figure 3. When diffusion is low cooperative specialization leads matched symbiont-host pairings to fix in distinct patches across space. This figure depicts the results numerical simulations using the system of partial differential equations in (5c) from initially random conditions. In panel *a* specialist hosts exclude generalists because their average payoff exceeds that of the generalist hosts. Panels *b* and *c* are meant to overlay one another. They depict the result of the same simulation beginning from random initial conditions. Panel *b* depicts patches of either symbiont type, and shows that there are borders with intermediate symbiont frequency between these patches when generalist payoff exceeds the average payoff of a specialist. Panel *c* shows the dynamics of the host population, and shows that generalists are dominant at these borders between matched specialist patches (approximately 85% of hosts are generalists at borders this simulation). In *a*, *b*, and *c* $D = 2.0 \times 10^{-6}$, $\alpha = 0.5$, and $x = 0.5$. In panels *a* and *b* $\gamma = 0.1$, $h(\gamma) = 0.4$, and $\gamma_g = 0.6$. In panels *c* and *d* $\gamma = 1.1$, $h(\gamma) = 0.1$, and $\gamma_g = 1$.

Results

Cooperative specialization

Ecological dynamics

The cooperative specialization model has two stable equilibria with matched host-symbiont pairs, i.e., all hosts are specialists of one type and all symbionts are their preferred symbiont. The system also features a continuous line of generalist host equilibria, which excludes specialist hosts, and has an intermediate symbiont frequency. The frequency of specialist symbiont 1 along this line, u^*, is determined by the difference between matched host payoff (π) and mismatched payoff (π'):

$$\frac{\pi - \pi_g}{\pi - \pi'} \leq u^* \leq \frac{\pi_g - \pi'}{\pi - \pi'}. \tag{6}$$

When this inequality is satisfied, generalists receive a greater fitness benefit from mutualism than specialists do on average. If the generalist payoff is less than the average specialist payoff (i.e., $\pi_g < (\pi + \pi')/2$), then this line of equilibria is unstable. If, however, generalist payoff is greater than the average specialist payoff, then it behaves as a type of saddle. It is attracting with respect to changes in the frequencies of hosts. However, symbiont frequencies may change by perturbations of the population. The endpoints of the line of equilibria are unstable. Thus, if the symbiont frequencies are perturbed beyond the endpoints, the system moves to one of the matching equilibria. Therefore, cooperative specialization is bistable in the long-run resulting in specialization in a well-mixed population (see Supplementary Material S1.1 for the mathematical details and see Supplementary Table S1 for relevant terminology). However, there can be long transients, depending on the frequency/intensity of mutations or invasions, during which nearly all hosts are generalists.

In the spatially explicit model, on the other hand, we observe spatial polymorphisms. When hosts specialize cooperatively and spread across space from a distribution which is initially random, host, and symbiont populations assort into monomorphic patches. The patches become stable over time when diffusion is sufficiently low as depicted in Figure 3. When diffusion is relatively high there is no stable patchy distribution, rather one specialist host and their preferred symbiont dominate the entire space (not depicted here). Which host-symbiont pair comes to dominate is determined by the initial abundances of all types.

When generalists receive a lower fitness benefit from mutualism than specialists do on average, as depicted in of Figure 3a, generalists are excluded. However, when generalists receive a higher fitness benefit from mutualism than specialists do on average and diffusion remains low, generalists can survive at the border of patches as depicted in Figure 3c. This phenomenon occurs because generalists are stable when symbiont frequencies lie within an intermediate range (given by the inequalities (6)), which is found at the boundaries between patches of different specialists. Increasing diffusion rates from an extremely low minimum reduces the size of these boundaries, decreasing generalist frequency. However, if only symbiont diffusion increases relative to host diffusion, specialist hosts do not diffuse into borders as quickly as their preferred symbionts and thus the width of these regions is maintained. Furthermore, as the mix of symbiont types homogenizes, hosts are more likely to encounter the intermediate range of symbiont frequencies given the inequalities (6), which favors the generalist equilibria over the specialist equilibria. Because of this, generalists become more frequent as symbiont diffusion increases as depicted in Supplementary Figure S1.

Invasion analysis

As shown above, in a well-mixed population, the long-term ecological equilibrium under cooperative specialization is the fixation of one type of specialist host and their preferred symbiont. In the spatial model, too, each specialist and their corresponding symbiont is fixed locally, except for boundary regions. Because these ecological dynamics result in fixed, matching patches, we examine how host and symbiont traits evolve in populations with a single matched host and symbiont pair. We consider how shared traits evolve when under host control or when under symbiont control. We first consider the evolution of shared traits under this monomorphic scenario and then consider the boundaries in the spatial model where both symbionts might be present. The mathematical details of the analyses are given in Supplementary Material S1.3.

First, our invasion analysis assumes that shared traits only evolve according to their effects on host fitness not symbiont fitness (i.e., they are under host control). When a single host and its preferred symbiont are fixed, we find that selection gradients for resource extraction α and efficiency γ are both positive, which means that mutant hosts with higher α or γ can always invade. This result is intuitive since γ increases host fitness, and because the symbiont population is monomorphic, the hosts do not experience the trade-off from increasing γ at the expense of $h(\gamma)$. A higher α will similarly increase the amount of good provisioned for the host, and thus is also selected for in hosts. Finally, the host resource provision x evolves to the evolutionarily stable intermediate value of $\alpha\gamma/2$, reflecting the balance of investment into symbionts vs. the cost of this investment to hosts.

Next, for the uniform population comprised of a specialist and its preferred symbiont, we consider the parameters under symbiont control so that the fitness of invading symbiont mutants determines their evolution. The selection gradient for mutual efficiency, γ, and resource allocation to trade, x, are both positive, indicating that mutant symbionts with larger values of these traits can successfully invade and replace residents with lower values. However, the selection gradient for host resource extraction, α, is negative, indicating that mutants with smaller values are favored by selection. This result is not surprising, as a symbiont is better off the more of the resource it keeps to itself. Further, hosts no longer experience a trade-off between the value of α and $f(\alpha)$ when increasing the value of α, since the host population is monomorphic and matching.

We also consider how shared traits may evolve in populations with a mix of symbiont types. Such local populations arise in our spatial ecological dynamics at the borders of the monomorphic, matching host-symbiont patches. At these borders a mix of both symbiont types will be maintained by migration from the interiors of the patches (Figure 3a). If the size of matching patches is large relative to borders, and diffusion of the non-evolving species is large relative to the mutating one, we can assume that the frequency of the non-evolving species is constant. This strong assumption was necessary to simplify the invasion analysis for the evolving species. In this scenario, the patches act as a source of the non-evolving species at the borders: the frequencies of the non-evolving species at the border are determined primarily by diffusion from monomorphic patches. Thus, their frequencies will not change at the borders as the evolving border resident population evolves. First, we find that as in the monomorphic case larger values of resource extraction

α will evolve and resource provisioning x will evolve to an intermediate value of $\alpha\gamma/2$. However, the resource efficiency γ is subject to a trade-off between matching and mismatching such that if γ increases (a host becomes more efficient with the preferred symbiont), $h(\gamma)$ decreases (the host becomes less efficient with the non-preferred symbiont). We considered a variety of trade-offs (Supplemental Figure S2) to conduct a partial analysis for this case that assumes a fixed intermediate frequency of each specialist (see details in Supplementary Material S1.3). We find that a concave up trade-off leads to invasion of ever larger values of γ. This, or the absence of any singular strategy, leads specialists to evolve to become even more cooperative with one symbiont or the other. A concave down trade-off, on the other hand, leads specialists to evolve to become a novel variety of generalist that receives approximately equal marginal benefit from interaction with either symbiont at the borders of fixed host patches. Finally, when the trade-off is linear, any value of γ may invade. These evolutionary analyses hold regardless of whether or not the evolving trait is under selection by the hosts or symbionts. Mathematical details are included in Supplementary Material S1.3.

Antagonistic specialization
Ecological dynamics

The antagonistic specialization model has two potential dynamical regimes. First, when generalist payoff exceeds average specialist payoff, specialist hosts are excluded and only generalist hosts remain at equilibrium. And, symbiont frequencies within the interval (6) form a stable line of equilibria. Within this interval, symbiont frequencies may drift from one value to another due to invasions or mutations. Conversely, when generalist payoff is less than the average specialist payoff, there are no stable equilibria: the frequencies of species oscillate. The oscillations do not include the generalist hosts, as generalist hosts are always less fit than at least one specialist host. For the mathematical details of these results see Supplementary Material S2.1.

Moving on to the spatial case, when generalist payoff exceeds average specialist payoff, generalists fix across space and both symbiont types coexist in each patch of the landscape, as symbiont diffusion leads their frequencies to homogenize across space after generalists fix. When generalist payoff is less that average specialist payoff, however, there is no stable distribution of hosts and symbionts throughout space. Rather, the size and position of types of hosts and symbionts oscillate over time. Cycling occurs within each individual patch, and hosts and symbionts of each type diffuse from each patch at rates proportion to their frequency and the diffusion rate D. Gradually, the oscillations synchronize in each patch across space. We depict this result in Figure 4.

The size of synchronous patches depends upon the value of the diffusion rate, D. When this rate is high, the entire plane cycles synchronously and its behavior matches the nonspatial case. When this rate is low, we observe patches cycling out of sync with one another. The lower the diffusion rate, the more distinct these patches become. When the diffusion rate differs between symbionts and hosts, the patch dynamics typically follow the partner with the higher diffusion rate. Greater symbiont mixing eventually results in greater host mixing, even when host diffusion is lower than that of symbionts. Similarly, host frequencies influence symbiont frequencies, thus greater
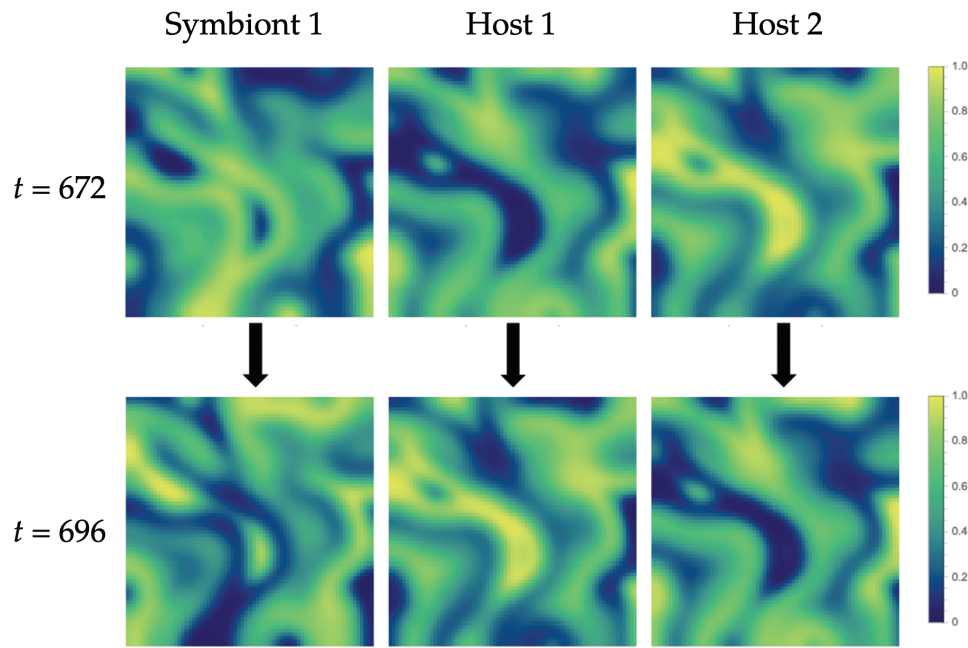
Figure 4. When specialization is antagonistic, hosts, and symbionts cycle from low to high frequency across space, if specialist average payoff exceeds generalist payoff. In these simulations, which begin from initially random conditions, the generalist host is driven to extinction. The frequency of symbiont 1, host 1, and host 2 is given from left to right. The population begins with the spatial distribution of phenotype frequencies in the top row at an arbitrary time ($t = 672$) and competing types eventually come to occupy the spaces occupied by their competitors at a later point in the cycle ($t = 696$). Here $D = 10^{-5}$, $\alpha = 0.9$, $f\alpha = 0.3$, $\alpha_g = 0.5$, and $x = 0.5$.

host diffusion similarly results in synchronization with the greatest diffusion rate.

Invasion analysis

For antagonistic specialization, our long-term ecological dynamics in a well-mixed population lead to a cycling population or to the generalist equilibria. First, we consider how the shared traits (i.e., α, γ and x) will evolve in the cycling case. Analytic adaptive dynamics are intractable in this cycling population because the timing of mutant invasion dictates the frequency of the strategists with which mutants compete, and thus influences the success of invasion. We therefore used numerical simulations to consider mutations that may occur anytime along the cycle for our invasion analyses. Additional details describing these methods are included in Supplementary Material S2.2.

In our first numerical simulations for the cycling population, we assume that α, γ, and x are under host control and only evolve according to their effect on host fitness. Because there is a mix of cycling symbionts, hosts experience a trade-off as mutations that increase the exchange rate (α) in matched symbiosis decrease $f(\alpha)$ in mismatched symbiosis. We considered linear, concave down, and concave up trade-off functions. For linear trade-offs, any value of α can invade a similar proportion of the cycle of a resident symbiont, indicating that α will evolve neutrally in this case (figure not shown). When $f(\alpha)$ is concave down there is a singular strategy $\alpha_{r*} \approx 1/\sqrt{2}$ that cannot be invaded by any other nearby value of α. Thus α_{r*} is an evolutionarily and convergence stable strategy (Figure 5a). In essence, hosts at α_{r*} are able to maximize average benefit from interactions with either symbiont type over the period of a cycle. On the other hand, when the trade-off is concave up greater values of extraction α will be always favored for hosts (Figure 5b).

With respect to evolving γ, greater cooperation allows mutants to invade the cycle of a resident, thus higher values will always be favored. Finally, when the proportion of traded resource (x) evolves under host control, there is an evolutionary stable value of investment $x_{r*} \approx (\alpha + f(\alpha))\gamma/4$ that balances the costs and benefits from trade with both matched and mismatched symbionts. See Supplementary Material S2.2 for relevant figures.

Next, we assume that shared traits (i.e., α, γ, and x) are under symbiont control in a cycling population. As with hosts, linear trade-offs between α and $f(\alpha)$ lead to neutral evolution of the exchange rate α. When the trade-off is concave down, there is an unstable singular strategy $\alpha_{r*} \approx 1/\sqrt{2}$ that can be invaded by nearby mutants (Figure 5c). This leads the symbiont exchange rate α to evolve away from the value of extraction that maximizes the fitness of the antagonistic hosts. A concave up trade-off will allow symbionts with reduced values of α to always invade the majority of a resident's cycle (Figure 5d). Essentially, selection pressure is on symbionts to escape the extraction of the host that specializes on them, at the expense of becoming more vulnerable to extraction from the opposite host type. Symbiont mutants with greater values of x and γ will always invade the majority of the cycle of a resident population. Greater resource investment (x) from hosts comes at no cost to symbionts, and there is no trade-off for increasing efficiency γ in the antagonistically specialized population. See Supplementary Material S2.2 for the pairwise invasibility plots.

Our ecological dynamics also result in a community that is composed entirely of generalist hosts, and a mix of symbiont types when generalist payoff exceeds average specialist payoff. Because hosts and symbionts do not cycle in this scenario, we were able to determine selection gradients for shared traits (α, γ, and x). In fact, because generalists traits do not vary
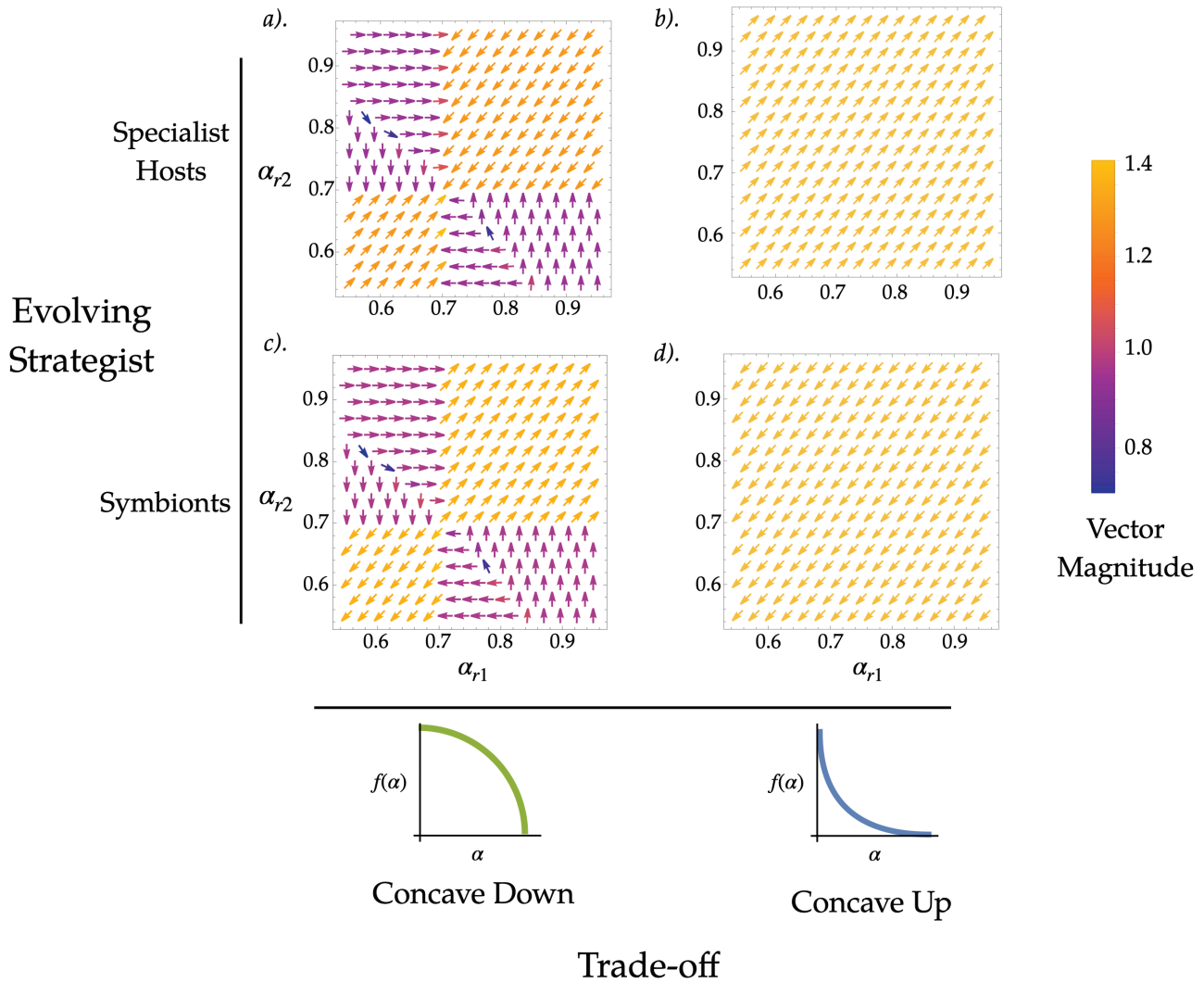
Figure 5. In the cycling population, the outcome of mutant invasion is determined by the trade-off between matched and mismatched antagonism. Each row of the figure corresponds to an evolving strategist: specialist hosts (top), or symbionts (bottom). While each column of the figure corresponds to a different trade-off function: concave down (left), or concave up (right). Because both type 1 and 2 hosts and symbionts are present in the cycle, we considered mutants of both types. Panels *a–d* show vector plots whose horizontal component is the proportion of a cycle an invading type 1 mutant is able to invade and whose vertical component is the proportion of a cycle an invading type 1 mutant is able to invade. The plots in the top row are for initially rare invading specialist hosts, and plots in the bottom row are for initially rare invading symbionts. Here, $x = 0.5$, and $\gamma = 1$. The trade-offs are: $f(\alpha) = \sqrt{1 - \alpha^2}$ (concave down), and $f(\alpha) = (1 - \sqrt{\alpha})^2$ (concave up). We used two sets of initial conditions: $v_1 = 0.34$, $v_2 = 0.66$, $v_1 = 0.66$, and $v_1 = 0.66$, $v_2 = 0.34$, $v_1 = 0.3$.

for either symbiont type, the selection gradients for all shared traits match those of the monomorphic case in 3.1.2. For mathematical details see Supplementary Material S2.2.1.

Discussion

Our model provides predictions about antagonistic and cooperative specialization that have important applications to biological systems. Cooperative specialization tends to lead to host and symbionts specialized to one another. However, generalists may prosper in the evolutionary short run or at spatial boundaries. Antagonistic specialization can lead to either generalist hosts or specialist hosts fixing, depending on the difference between the specialist host average payoff vs. the generalist host average payoff. Additionally, we consider the evolution of cooperative and antagonistic specialization. We find that increased cooperative specialization with a preferred partner evolves under cooperative specialization, while the

evolutionary trajectory of antagonistic specialization depends on the trade-off between matched and mismatched antagonism in a cycling population.

When specialization is cooperative, our model predicts that host-symbiont co-diversification will occur over long timescales. This is because under cooperative specialization, stable patches form in which only one specialist type is present (see Figure 3). The interior of these patches are isolated from gene flow from the conspecific specialist, thus there is reproductive isolation between strategists within each patch. Matched specialist partners will co-evolve to increase mutual benefit with their preferred partner at the expense of reduced benefit from mismatched symbiosis. This coevolution will further reduce the viability of mismatched specialists that enter from other patches, effectively limiting gene flow between patches. This evolution further isolates conspecific specialist strategists and promotes pairwise speciation of the fixed hosts and symbiont in each patch. Over longer timescales not explicitly examined

by our model, coevolution within patches, and reproductive isolation between patches, might lead hosts and symbionts to speciate. This dynamic will result in codiversified lineages of hosts and symbionts (Weiblen et al., 2015). By showing that cooperative specialization in mutualistic interactions may facilitate diversification, our model provides an important conceptual link between biodiversity and mutualism (Bascompte, 2019).

At the same time, specialization can also evolve to be antagonistic, with hosts or symbionts evolving to extract (or resist extraction of) more resources from each other. Such antagonistic specialization leads to cycling ecological dynamics in both well mixed and spatially structured populations (Figure 4). The behavior of these cycles is determined by the trade-off between matched and mismatched antagonistic specialization. When this trade-off is concave up, natural selection favors increased resource extraction from symbionts, increasing the amplitude of the population's cycle (Supplementary Figure S3). Greater amplitude will eventually lead to the extinction of a specialist host or symbiont at cycle peaks or troughs. Alternatively, in the case in which generalists initially out compete specialists, it is possible for specialists to invade the generalist population if natural selection leads specialist payoff average to exceed generalist payoff. Thus, in the antagonistic model, specialization allows for consistent turnover of strategists across both time and space.

Our model is especially applicable to coral symbiosis, and provides predictions that are particularly relevant to two aspects of this interaction: (a) the degree of cooperation vs. antagonism exhibited in coral symbiosis; and (b) the conditions that favor specialization and generalism. Researchers have found evidence for cooperative and antagonistic interaction between corals and their symbiotic algae (Xiang et al., 2020) without clear resolution as to which pattern is more prevalent at the population scale. Understanding the relationship between these partners is especially important as mass mortality events (bleaching events) caused by anthropogenic climate change occur in scleractinian corals when the costs of symbiosis outweigh associated host benefits (Baker et al., 2018). Our model incorporates interactions at the scale of individual hosts and symbionts and predicts distinct population dynamics associated with both the cooperative and antagonistic interpretations of coral symbiosis. It is possible that further empirical observations of coral population dynamics with our predictions in mind may shed light on the prevalence of each mode of association in this symbiosis. The prevalence of generalism vs. specialism is also a matter of contention in cnidarian symbiosis. While most corals appear to be symbiont specialists (Poland & Coffroth, 2016), much evidence suggests that associations with other symbiont types are also viable (Silverstein et al., 2012). Our results that favor generalist hosts, which evolved under both antagonistic and cooperative specialization, indicate that coexistence of these two strategists amongst coral hosts is quite possible. In the cooperative case, generalists persist at the borders between specialists even in the absence of environmental heterogeneity. Generalism is also stable in the antagonistic case when average generalist benefit exceeds that of specialist benefit. The relative prevalence of these strategies also has important implications for the conservation of corals and other symbiotic species. Heat tolerance in corals is often linked to algal partner species identity, thus increased flexibility of host association may allow hosts to associate with algal partners with more robust cellular physiology (Berkelmans & Van Oppen, 2006). Alternatively, specific partners may be more likely to have physiology that is optimized for symbiosis with a preferred partner (Matthews et al., 2017). These partnerships may be better able to mutually co-evolve to more effectively resist thermally stressful events.

Our model can also be applied to the symbiosis between plants and mycorrhizal fungi to explain the prevalence of generalism in this particular partnership. Increased abundance of fungal partner species has been found to increase overall plant community diversity (Van der Heijden et al., 1998), and researchers have found evidence of host-symbiont specificity in this mutualism (Hoeksema et al., 2009), though generalism seems more prevalent. Our model suggests that one reason for the prevalence of generalism could be low dispersal capability of plant and fungal partners. In our model, when dispersal rate is low (i.e., the diffusion constant D is low) ecosystems assort into a greater number of fixed host-symbiont patches, increasing the area of border regions in which an intermediate frequency of both symbiont partners occurs. In these border regions, generalism can evolve from specialism when specialization is cooperative. However, our model also predicts that extremely high levels of dispersal, especially in symbionts, should also favor generalism as ecosystems become very well mixed. Cooperative specialists do best relative to generalists when dispersal is intermediate (Supplementary Figure S1). This result may explain why host and symbiont partners with relatively large dispersive abilities such as corals and their zooxanthellic algae are often specialized (Poland & Coffroth, 2016), while plant-mycorrhizal partners tend toward generalism (Peay et al., 2015).

In our model, generalism persists in both antagonistic and cooperatively specialized mutualisms, indicating that this strategy may be adaptive even in the absence of ecological perturbation. Under antagonistic specialization, when generalist payoff is greater than the average specialist payoff, all hosts become generalists. In the case of cooperative specialization, mutually beneficial symbiosis means that increasing frequency of a specialist host simultaneously bolsters its preferred symbiont's frequency. Thus, generalism, outside of spatial conditions, is unstable in the long run due to invasions and mutations. However, in spatial simulations, generalists persist at the borders between monomorphic specialist patches when generalist payoff is greater than average specialist payoff (Figure 3). Furthermore, when the evolution of continuous host trait values are considered, it is possible for generalism to evolve from specialization at these borders Supplementary Material S2.2. These results show that generalists and specialists might co-coexist in ecological landscapes based on biotic interactions alone. In plant-microbial and plant-fungal mutualisms there is evidence that negative plant soil feedback promotes coexistence between a variety of plant, microbial, and fungal partner species, (Bever et al., 2010). This suggests precedent for coexistence between these strategies. In ecological communities, generalism could also be perpetuated by environmental disturbance. Events that reduce frequency of a preferred symbiont or host could create opportunities for generalist hosts to increase in frequency. In the case of mutualism, to be a generalist is to receive a benefit that is between the extremes that specialists receive from interacting with their preferred and not preferred partners. Generalists are therefore hedging their bets against the possibility that disturbance might make a preferred partner species

unavailable. Interestingly, our model shows that generalism can be evolutionarily stable even in an undisturbed environment. Incorporating ecological feedback into later iterations of this model could provide interesting insights into the adaptive benefits of generalism.

We also considered how fitness feedbacks, which align the fitness interests of interacting species, shape patterns of specificity. One form of fitness feedback is limited dispersal, in which antagonizing a mutualistic partner reduces the fitness of the antagonist (Sachs et al., 2004). When specialization is cooperative in our model, reduced dispersal leads host and symbiont phenotypes to coexist in monomorphic patches across space. Similarly, under antagonistic specialization, low dispersal leads to patches of cycling hosts that are more distinct from one another. These results indicate that this form of fitness feedback tends to promote coexistence across space of specialized partners. The term fitness feedback has also been applied to phenotypic traits that align the fitness optima of mutualistic partners (Akçay, 2015; Sachs et al., 2004). We reason that incorporating additional phenotypic feedbacks would not change the dynamics of cooperatively specialized mutualism, given that cooperative specialization already aligns the fitness of both partners. However, we found that phenotypic feedbacks made antagonistic specialization less profitable relative to generalism. In supplemental analysis, phenotypic feedbacks still lead to cycling population dynamics, but increasing feedback leads the generalist average payoff to exceed the specialist payoff Supplementary Material S2.2.3. This indicates that fitness feedbacks reduce the scope of antagonistic specialization by aligning host and symbiont fitnesses (Friesen, 2012).

The results of our model examining the evolution of shared mutualistic traits recapitulate the findings of evolutionary genetic models via a game theoretic lens. We show that a shared trait that represents high mutual fitness benefit with a preferred partner (γ) evolves similarly in two interacting species. The shared trait that represents the host's ability to improve its fitness at the expense of its symbiont's fitness (α) is subject to opposite selection gradients in each species, indicating a coevolutionary arms race. Evolutionary genetic models for joint trait evolution similarly highlight that shared traits experience similar selection when fitness optima are shared between species, or opposing selection when fitness optima are distinct between species (O'Brien et al., 2021; Queller, 2014). These patterns of selection lead to mutualistic coevolution, or a coevolutionary arms race each of which each is tied to distinct genomic signatures (O'Brien et al., 2021) that could be used to examine patterns of conflict and cooperation between species.

In mutualistic interactions in which specificity and generalism have complex benefits and costs, it is difficult to determine how these strategies will evolve. Our model provides critical insights into how specialization and generalism will evolve in both cooperative and antagonistically specialized mutualisms involving the exchange of a good. Our results showing that these strategies can coexist in cooperative mutualism, and that the frequency of each strategist cycles in antagonistic mutualism, reveal how different modes of species interaction have distinct outcomes. Because our model did not explicitly consider the effect of stochasticity or finite population size, future study examining how these factors interact with patterns of specificity, cooperation, and conflict could help to generate more refined ecological and evolutionary outcomes. Tying together the degree of specificity and cooperation in a species interaction has important implications for numerous mutualisms that are critical to both biodiversity (e.g., coral-algal mutualism) and agricultural productivity (e.g., legume-rhizobia mutualism). Further study examining the implications of our model may continue to enhance understanding of these systems.

Supplementary material

Supplementary material is available online at Evolution (https://academic.oup.com/evolut/qpac056).

Data availability

The code for the stability analysis and numerical simulations were written in Mathematica and can be found at https://github.com/christopheriancarlson/SpecificMutualism.

Author contributions

All authors contributed to the conception of the study and the final manuscript. C.C. developed the code for and analyzed the numerical simulations. C.C. and B.M. carried out the mathematical analysis and wrote the first draft.

Conflict of interest: The authors declare no conflict of interest.

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