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Ontogenetic antagonism–mutualism coupling: perspectives on resilience of stage-structured communities

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Organisms typically change their diets ontogenetically. Recent studies have shown that an ontogenetic diet shift undermines the resilience of stage-structured food webs. Here, we study the integration of stage-structured food-web theory into theory of hybrid community (i.e. mixture of different interaction types), considering that not only diet but also interaction type often changes because of ontogenetic niche shift (e.g. the metamorphosis of pollinating insects, in which juveniles and adults are herbivores and pollinators, respectively). We developed and mathematically analysed a one-consumer two-resource model in which juvenile and adult consumers utilise different resources as antagonists and mutualists, respectively. Model analyses illustrated that the consumer either goes extinct or coexists with the resources depending on the initial condition when the resources have low carrying capacities while their community dynamics always converge to a single steady state when the resources have high carrying capacities. These dynamic features are different from those of the corresponding purely antagonistic module in previous studies, in which the consumer always goes extinct for low resource carrying capacities while the dynamics converge to either juvenile-dominated or adult-dominated state depending on the initial conditions for high resource carrying capacities. Taken together, we can suggest that ontogenetic antagonism–mutualism coupling is stabilising in that it increases the potential for species coexistence in unproductive environments while improving community resilience in productive environments. Further, these effects are generally robust to interaction nonlinearity. Beyond the previous concern of the instability in stage-structured food-webs, our results suggest that antagonism–mutualism coupling can play a crucial role in stabilising stage-structured hybrid (e.g. plant–animal) communities under environmental changes. The present study represents an important first step in understanding how interaction type diversity can mediate the dynamics of stage-structured communities.

Introduction

Intraspecific variation is ubiquitous in nature because many organisms are multicellular and exhibit ontogenetic growth. During ontogenetic growth, the morphology, physiology, and behaviour of organisms can quantitatively and qualitatively vary

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(ontogenetic niche shifts) (Wilbur 1980, Werner and Gilliam 1984). Whereas ontogenetic niche shifts have long been studied in behavioural and evolutionary ecology, recent studies have shown that ontogenetic niche shifts can critically affect population stability and community structure (Miller and Rudolf 2011, de Roos and Persson 2013, Nakazawa 2015). These studies suggest that when juveniles and adults utilise different resources, their ontogenetic diet shift would generate alternative community states (ACSs) characterised by either juvenile or adult dominance (Schreiber and Rudolf 2008, Guill 2009, Nakazawa 2011a, b). Therefore, a sudden and irreversible regime shift may occur in community structure under environmental changes. In addition, ontogenetic niche shifts are predicted to increase the extinction risk of species in stage-structured food webs (Rudolf and Lafferty 2011). Overall, it is suggested that ontogenetic niche shifts can undermine the stability (resilience or species persistence) of ecological communities in many cases (but also see Hin et al. 2011, Nakazawa 2011a, b).

Previous studies have exclusively focused on purely antagonistic (i.e. predator–prey) food web systems. However, ecological communities are formed by different types of biotic interactions, including not only antagonism but also mutualism and competition (i.e. a hybrid community) (Melian et al. 2009, Allesina and Tang 2012). While antagonistic and mutualistic systems have traditionally been studied independently (McCann 2011, Bascompte and Jordano 2014), theoretical models have demonstrated the importance of antagonism–mutualism coupling in promoting species coexistence (Freedman et al. 1987, Ringel et al. 1996, Jang 2002, Wang 2013, Lee 2015). Recently, the stabilizing effect of antagonism–mutualism coupling has also been confirmed for large network models (Mougi and Kondoh 2012, Sauve et al. 2014, Kondoh and Mougi 2015, Lurgi et al. 2016): even if purely antagonistic or mutualistic systems are not persistent, their combination can allow numerous species to coexist therein. These predictions may solve the longstanding paradox: complex ecological communities with high biodiversity do not theoretically persist while numerous species do in fact coexist in nature (May 1972). Although the underlying mechanisms of the stabilisation due to antagonism–mutualism coupling are elusive and often controversial (Mougi and Kondoh 2014, Suweis et al. 2014), the idea of hybrid community is appealing because interactions among the most diverse groups of organisms (insects and plants) are actually a hybrid of antagonism and mutualism (herbivory and pollination, respectively), and their high biodiversity may no longer be paradoxical. Nevertheless, the previous studies of hybrid community models have not yet considered stage structure despite the ubiquity of ontogenetic niche shifts in nature. Therefore, it remains unclear how ontogenetic niche shifts mediate stage-structured communities when different interaction types are mixed (Revilla and Encinas-Viso 2015). In particular, it may be intriguing to address community

consequences of ontogenetic antagonism–mutualism coupling, since ontogenetic niche shifts can undermine the resilience of stage-structured food webs while antagonism–mutualism coupling generally facilitates species coexistence in non-structured communities.

To fill the knowledge gap, we propose a novel community view which we call 'stage-structured hybrid community'. In this community view, an ontogenetic niche shift changes not only diet but also interaction type. Here, we consider the typical case where the interaction type changes from antagonism to mutualism ontogenetically, although other scenarios are also possible (Miriti 2006). A well-known example is the metamorphosis of Lepidoptera (butterflies and moths), in which juveniles (larvae) are antagonistic herbivores whereas adults are mutualistic pollinators (Altermatt and Pearse 2011). Similar types of ontogenetic niche shifts (i.e. from antagonism to mutualism) are observed in other holometabolous insects, such as Hymenoptera (e.g. bees), Diptera (e.g. flies), and Coleoptera (e.g. beetles) (Wäckers et al. 2007). In addition, many frugivorous birds feed on insects at the juvenile stage, which indicates ontogenetic niche shifts from antagonistic insectivory to mutualistic seed dispersal (Drewe et al. 2004, Holland et al. 2006). As such, stage-structured hybrid communities are commonly observed in plant–animal interactions (also see Discussion for more general applicability of this view to other systems).

Here, we theoretically investigate the dynamic consequences of ontogenetic antagonistic–mutualistic coupling. We started with a community module approach rather than network modelling since dynamics of large complex models are generally difficult to understand mechanistically. A module approach can facilitate mechanistic understanding of how a focal factor operates in the reduced system (Murdoch et al. 2003, Kondoh 2008). This is important as our study is an initial attempt to integrate the two major theories (i.e. stage-structured community and hybrid community) that potentially have contrasting effects on community dynamics (i.e. destabilization of stage structure and stabilisation of hybrid community). In addition, the module approach has another advantage that it will fit well with small scale experiments to mechanistically understand systems. As a minimum module of stage-structure hybrid community, we develop and mathematically analyse a one-consumer two-resource system, in which juvenile and adult consumers utilise different resources as antagonists and mutualists, respectively. To highlight community consequences of ontogenetic antagonism–mutualism coupling, we comparatively discuss dynamic features of the present stage-structured hybrid module and those of the corresponding purely antagonistic module in previous studies that does not include any mutualistic interactions (Schreiber and Rudolf 2008, Nakazawa 2011a). Finally, we present future directions to extend the present community module for more realistically describing stage-structured hybrid (e.g. plant–animal) communities in nature.

Model

Schreiber and Rudolf (2008) developed a one-consumer two-resource model in which juvenile and adult consumers exploited different resources as antagonists. Here, their model is modified to incorporate mutualism into resource exploitation by adults (i.e. an ontogenetic niche shift from antagonism to mutualism). Importantly, mutualism not only yields benefits but also incurs costs, a perspective known as consumer–resource theory of mutualism (Bronstein 1994, 2015, Johnstone and Bshary 2002, Holland and DeAngelis 2009). This theory has recently been proposed to take into account the common fact that mutualistic organisms often exploit rewards provided by their partners while benefiting them (reviewed by Bronstein 2015). For example, pollinators consume nectar/pollen provided by plants, which can be costly for the plants and may affect their population dynamics or evolution in pollination mutualism. Based on this idea, Holland and DeAngelis (2010) modelled pollination mutualism without considering stage structure. In the present study, their modelling approach (i.e. consumer–resource theory) is applied to incorporate adult mutualism into the stage-structured antagonistic community module developed by Schreiber and Rudolf (2008). Consequently, our model is formulated as follows:

$$\frac{dR_J}{dt} = r_J \left(1 - \frac{R_J}{K_J}\right) R_J - F_J\left(R_J\right) C_J \tag{1a}$$

$$\frac{dR_A}{dt} = r_A \left(1 - \frac{R_A}{K_A}\right) R_A - F_A\left(R_A\right) C_A + B\left(C_A\right) R_A \tag{1b}$$

$$\frac{dC_J}{dt} = b_A F_A\left(R_A\right) C_A - b_J F_J\left(R_J\right) C_J - d_J C_J \tag{1c}$$

$$\frac{dC_A}{dt} = b_J F_J\left(R_J\right) C_J - d_A C_A \tag{1d}$$

Hereafter the terms 'consumer' and 'resource' are used to refer to the stage-structured species (e.g. pollinating insects) and its interacting partners (e.g. plants) according to consumer–resource theory of mutualism. In the model, R_i and C_i are resource and consumer abundances, respectively (i = J for juveniles or A for adults). Both resources exhibit a logistic growth, with intrinsic growth rate r_i and carrying capacity K_i. The consumer has a stage-specific death rate d_i. The juveniles and adults exploit different resources to mature to adulthood or reproduce offspring. The function $F_i(R_i)$ is the functional response of resource exploitation, and the parameter b_i is the conversion efficiency. The adults facilitate the population growth of their resource according to the function $B(C_A)$. Note that while the mutualistic interaction exists between the adults and their resource, it increases the juvenile abundance via increasing adult reproduction (see the first term of Eq. 1c). Our model simplifies to the model of Schreiber and Rudolf (2008) when all interactions are linear and the adults are antagonistic (i.e. $F_A(R_A) > B(C_A)$). When the dynamics

are not static (e.g. limit cycles and transient phase), the adults can be either antagonistic or mutualistic in time depending on the relative abundances of R_A and C_A. The functional forms of $F_i(R_i)$ and $B(C_A)$ are specified later.

Three approached were used to analyse the model. First, invasion analysis was used to examine the potential of the consumer coexisting with the resources. Second, the existence of ACSs (community resilience) was examined via zero-net-growth isocline (ZNGI) analysis. Finally, numerical analysis was applied to examine parameter sensitivity, effects of interaction nonlinearity, and effectiveness of mutualisms (robustness of predictions). Detailed descriptions of our numerical simulations are as follows. The fourth-order Runge–Kutta method was used for numerical analysis. Simulations were run for 1×10^5 time steps with a fixed time interval of 0.01, and the long-term average abundances were evaluated for the last 5000 time steps to remove transient dynamics. Local stability was assessed on the basis of whether the coefficient of variation was smaller than 1×10^{-6} for either juvenile or adult abundance. When the threshold was exceeded, the dynamics generally exhibited limit cycles (Supplementary material Appendix 1 Fig. A1e, A1g). The population was regarded as extinct if any variable was lower than 1×10^{-4}. For each given parameter setting, these processes were repeated for 100 different initial conditions: $R_i(0) = K_i$ whereas $C_J(0)$ and $C_A(0)$ were exhaustively selected from 2^{-1} to 2^8 with an exponent increment of 1. If the long-term averages of at least two of the 100 simulations differed by more than 1% for either juveniles or adults, the parameter setting was regarded to cause ACSs. All of the numerical analyses were programmed using C language.

Results

Consumer invasibility

With invasion analysis, the conditions for consumers to invade a consumer-free equilibrium and coexist with the resources were mathematically specified, which ensures the ability of the consumer to persist (i.e. exist in the system over a long time period) and have dynamics bounded from zero. First, suppose that the consumer is rare and the resource abundances are at the carrying capacity ($C_i = 0$ and $R_i = K_i$). The consumer can invade the consumer-free equilibrium when the number of consumer offspring surviving to adulthood (the basic reproductive number, R_0) is greater than one:

$$R_0 = \frac{b_A F_A\left(K_A\right)}{d_A} \times \frac{b_J F_J\left(K_J\right)}{d_J + b_J F_J\left(K_J\right)} > 1 \tag{2}$$

where the first term represents the expected number of juveniles produced by an adult individual during the adult stage and the second term represents the probability of a juvenile individual surviving to adulthood. This condition predicts that the consumer cannot invade the consumer-free

equilibrium when foraging gain $F_i(K_i)$ is low. However, the effects are not symmetric between stages and juvenile foraging gain is more crucial compared with adult foraging gain. In brief, the consumer cannot invade the consumer-free equilibrium at extremely low values of $F_A(K_A)$ even if $F_J(K_J)$ is very high because the second term is a saturating function of $F_J(K_J)$ (Eq. 2). These predictions are the same as those in the corresponding antagonistic module (Schreiber and Rudolf 2008). Importantly, however, in the present hybrid module, the consumer may not always go extinct (i.e. can maintain positive abundance) even if $R_0 < 1$, because the mutualism generates an alternative equilibrium for the consumer to exist.

Alternative community states

ZNGI analysis was conducted to investigate existence of ACSs under the assumption that the consumer coexists with the resources ($C_i^* > 0$ and $R_i^* > 0$). Following the previous invasion analysis, how stage-specific resource carrying capacity (K_i) can influence the occurrence of ACSs was examined. For analytical tractability and mechanistic understanding, all interactions in model 1 were assumed to be linear in the ZNGI analysis (see below for nonlinear cases):

$$F_i(R_i) = a_i R_i \quad (3a)$$

$$B(C_A) = \alpha C_A \quad (3b)$$

where a_i and α determine the efficiencies of resource exploitation and mutualism, respectively. When $a_A > \alpha$, the net

effect of the adult interaction is antagonistic. By contrast, when $\alpha > a_A$, the adults are mutualistic, which represents our primary interest. Consider the coexistence equilibrium state where the population growth rates of all variables are zero ($dR_i/dt = 0$ and $dC_i/dt = 0$). When dR_i/dt is $= 0$, the equilibrium resource abundances are solved as $R_J^* = K_J(1 - a_J C_J^*/r_J)$ and $R_A^* = K_A[1 - (a_A - \alpha)C_A^*/r_A]$, respectively. Using these relationships, the four equilibrium equations (1a–d) are reduced to the following two relations between the juvenile and adult equilibrium abundances (Schreiber and Rudolf 2008, Nakazawa 2011a, b):

$$C_A^* = \frac{b_J a_J K_J}{d_A}\left(1 - \frac{a_J}{r_J}C_J^*\right)C_J^* \quad (4a)$$

$$C_J^* = \left[\frac{b_A a_A K_A}{d_J}\left(1 + \frac{\alpha - a_A}{r_A}C_A^*\right) - \frac{d_A}{d_J}\right]C_A^* \quad (4b)$$

These are quadratic functions of each other (hereafter denoted as $ZNGI_A$ and $ZNGI_J$, respectively), and their intersections determine the equilibrium points. On the C_J^*–C_A^* plane, $ZNGI_A$ is always an upward convex with its vertex in the first quadrant (solid curves in Fig. 1). By contrast, the functional form of $ZNGI_J$ changes depending on whether $a_A > \alpha$ (adults are antagonists) or $a_A < \alpha$ (adults are mutualists). Specifically, $ZNGI_J$ is a rightward convex for $a_A > \alpha$ and leftward for $\alpha > a_A$ (dashed curves in top vs. bottom panels of Fig. 1). Consequently, the interaction type critically affects the dynamical consequences, which we examine separately below.
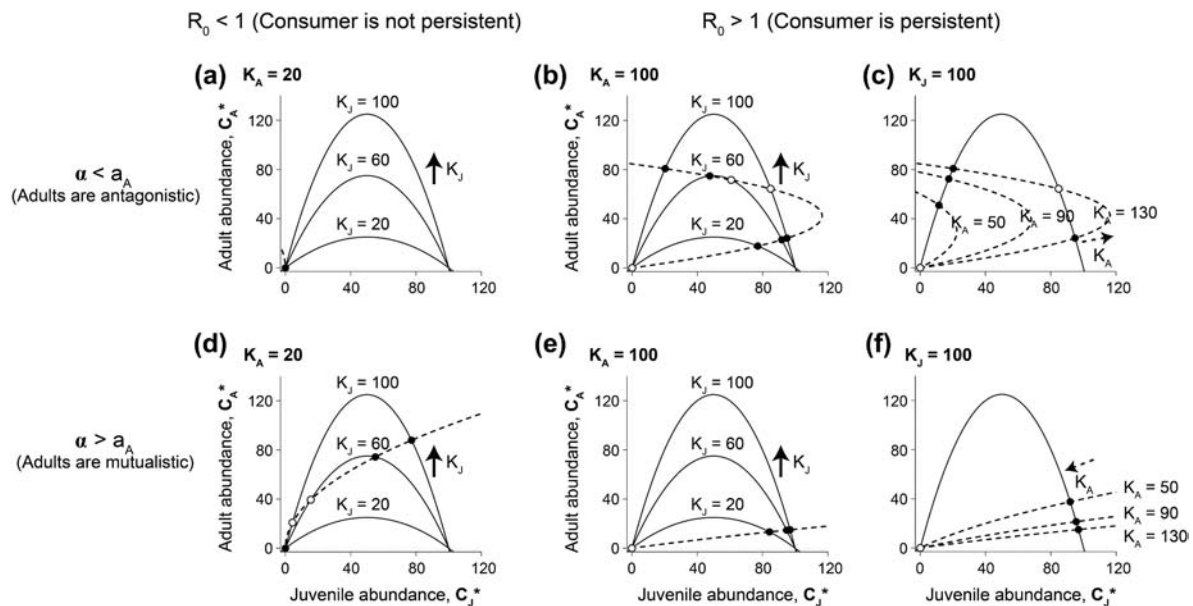

Figure 1. Parameter dependence of $ZNGI_A$ and $ZNGI_J$ on the C_J^*–C_A^* plane when the adults are (a–c) antagonists ($a_A > \alpha$) and (d–f) mutualists ($\alpha > a_A$). The solid and dashed lines represent $ZNGI_A$ and $ZNGI_J$, respectively, which shift in the directions indicated by the arrows with varying (a, b, d, e) K_J and (c, f) K_A. The consumer either (a, d) cannot or (b, c, e, f) can invade the consumer-free equilibrium. Solid and open circles represent stable and unstable equilibria, respectively. (a, d) $K_J = 20$, 60, and 100 while fixing $K_A = 20$; (b, e) $K_J = 20$, 60, and 100 while fixing $K_A = 130$; and (c, f) $K_A = 50$, 90, 130 while fixing $K_J = 100$. $\alpha = $ (a–c) 0 and (d-f) 0.02. Other parameters are $r_i = 1$, $a_i = 0.01$, $b_i = 0.5$, and $d_i = 0.1$.

First, suppose that the adults are antagonists ($a_A > \alpha$). When K_A is low such that $R_0 < 1$ (inequality 2), $ZNGI_A$ and $ZNGI_J$ intersect only at the origin. Therefore, the consumer cannot invade the consumer-free equilibrium and always goes extinct (Fig. 1a). When K_A becomes higher, $ZNGI_J$ shifts to the upper right, allowing the consumer to achieve positive abundance (Fig. 1b). In the situation with sufficiently high K_A, increasing K_J generates ACSs (Fig. 1b), where the dynamics converge to either juvenile-dominated or adult-dominated state depending on the initial conditions. Similarly, increasing K_A leads to juvenile-dominated and adult-dominated ACSs for high K_J (Fig. 1c). These results are the same as those of the corresponding antagonistic module (Schreiber and Rudolf 2008, see also Nakazawa, 2011a).

Next, suppose that the adults are mutualists ($\alpha > a_A$). When K_A is low, $ZNGI_A$ and $ZNGI_J$ intersect only at the origin (i.e. the consumer always goes extinct) if K_J is extremely low (Fig. 1d). However, as K_J increases, $ZNGI_A$ shifts upwards, generating ACSs with or without the consumer, despite $R_0 < 1$ (Fig. 1d) (hereafter denoted as consumer-associated and consumer-free ACSs, respectively). Here, an Allee effect emergences, because the consumer can maintain positive population size and coexist with the resources if the initial abundance is sufficiently high (see Supplementary material Appendix 1 Fig. A1b and A1c for different community dynamics depending on the initial consumer abundance). When K_A becomes higher, $ZNGI_J$ shifts to the lower left. As a result, the consumer-free equilibrium disappears, and the consumer always coexists with the resource (Fig. 1e). In this situation, the dynamics always converge to the consumer-associated state without any ACSs (Fig. 1e). The same pattern can be found at any value of K_A if K_J is sufficiently high (Fig. 1f).

Comparing the above two scenarios (i.e. the adults are antagonists and mutualists, respectively) reveals how ontogenetic antagonism–mutualism coupling influences the dynamics of stage-structured community. First, adult mutualism prevents consumer extinction that inevitably occurs in the antagonistic system in unproductive environments (Fig. 1a versus 1d). This is because, like Allee effects, the consumer–resource relationship in mutualism forms a minimum viable population threshold below which the consumer goes extinct due to insufficient benefits but above which it can maintain positive abundance (Holland and DeAngelis 2010). In addition, the mutualism can suppress the juvenile-dominated and adult-dominated ACSs that occur under productive conditions in the antagonistic system (Fig. 1b versus 1e or Fig. 1c versus 1f). This is explained as follows. The original mechanism underlying ACSs in stage-structured antagonistic system is the positive feedback caused by negative indirect effects between stage-specific resources (Schreiber and Rudolf 2008, Guill 2009, Nakazawa 2011a, b). Suppose that the juvenile resource becomes abundant. It promotes maturation of the juveniles and the adult resource is affected negatively (apparent competition), which in turn further increases the juvenile resource in the same manner because adult

reproduction is suppressed. Consequently, a positive feedback emerges, causing the dynamics to converge to either the juvenile-dominated or adult-dominated ACSs depending on the initial conditions. However, this mechanism is reversed if the adults are mutualists, and the positive feedback becomes a negative feedback. That is, if the juvenile resource becomes abundant, it promotes maturations of the juveniles and positively affects the adult resource (i.e. apparent mutualism), which in turn facilitates adult reproduction and decreases the juvenile resource. Taken together, it is suggested that ontogenetic antagonism–mutualism coupling is stabilising in that it increases the potential for species coexistence in unproductive environments by generating an alternative consumer-associated state while improving community resilience in productive environments by suppressing ACSs.

Parameter sensitivity, effects of interaction nonlinearity and effectiveness of mutualism

To assess the robustness of predictions made above, numerical simulations were performed and results were summarised in a parameter space of stage-specific resource carrying capacity (Fig. 2). Here, the adults were a priori assumed to be potential mutualists ($\alpha > a_A$). In the linear case, the consumer always goes extinct when K_J and K_A are extremely low (the black region with the label R in Fig. 2a). For low K_A, an increase in K_J leads to the consumer-free and consumer-associated ACSs (the green region with the label R/RC_{stable}). A further increase in K_J causes limit cycles around the consumer-associated equilibrium (the light green region with the label R/RC_{cycle}), and the consumer population eventually collapses (the black region at the lower right part) following large fluctuations (Supplementary material Appendix 1 Fig. A1a). When K_A is higher, the dynamics always converge to the consumer-associated equilibrium (the blue region with the label RC_{stable}). However, this also fluctuates in limit cycles with an increase in K_J (the light blue region with the label RC_{cycle}). These numerical results are generally supported by the invasibility criterion (Eq. 2) and ZNGI analysis (Fig. 1), and robust to changes in parameter values (Supplementary material Appendix 2 Fig. A2).

For the case of nonlinear interaction, the Holling type-II functional responses were used to model a saturation of foraging gain or mutualistic benefits:

$$F_i(R_i) = \frac{a_i R_i}{1 + h_i a_i R_i} \tag{5a}$$

$$B(C_A) = \frac{\alpha C_A}{1 + \beta \alpha C_A} \tag{5b}$$

where h_i and β represent handling times of resource exploitation and mutualism, respectively. When resource exploitation is nonlinear, the parameter region allowing consumer invasion becomes smaller (the red lines of Fig. 2a versus 2b or Fig. 2c versus 2d). This is because the invasibility criterion is violated owing to the reduced foraging gain
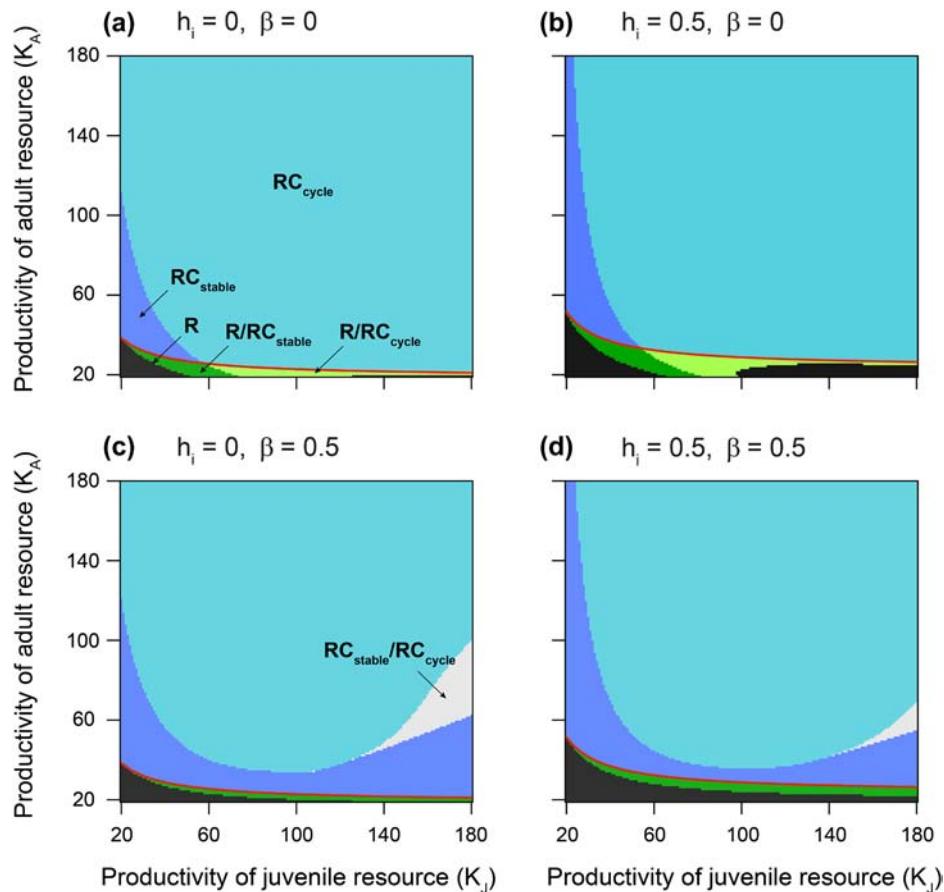
Figure 2. Effects of interaction nonlinearity on the community structure and the occurrence of ACSs in the K_J–K_A space. (a) Both resource exploitation and mutualism are linear ($h_i = 0$ and $\beta = 0$), (b) only resource exploitation is nonlinear ($h_i = 0.5$ and $\beta = 0$), (c) only mutualism is nonlinear ($h_i = 0$ and $\beta = 0.5$), and (d) both are nonlinear ($h_i = 0.5$ and $\beta = 0.5$). The domain labels indicate different community states in corresponding colour regions. For R, only the resource exists (black); for RC_{stable} and RC_{cycle}, the consumer and resources coexist at equilibrium (blue) or on limit cycles (light blue). Double labels indicate the occurrence of ACSs for R/RC_{stable} (green), R/RC_{cycle} (light green), and RC_{stable}/RC_{cycle} (white). Red curves indicate the boundary of consumer invasibility (Eq. 2). Other parameters are the same as in Fig. 1d–f (i.e. all scenarios include mutualism).

for low K_i (Eq. 2). When mutualism is nonlinear, the invasibility criterion remains unchanged (the red lines of Fig. 2a versus 2c or Fig. 2b versus 2d). However, the likelihood of consumer extinction increases (the black regions) because the mutualism benefit is reduced due to the increased handling time. Nonlinear mutualism generates another type of ACSs in productive environments where the consumer always exists but the dynamics converge to either of alternative coexistence states, which exhibit an equilibrium point or limit cycles depending on the initial conditions (the white region with the label RC_{stable}/RC_{cycle} in Fig. 2c–d). This is because the system becomes closer to the purely antagonistic system in which the juvenile-dominated and adult-dominated ACSs occur at high values of K_J and K_A (Fig. 1b–c) (Schreiber and Rudolf 2008, Nakazawa 2011a). Indeed, the static and cyclic ACSs correspond to the adult-dominated and juvenile-dominated states, respectively (Supplementary material Appendix 1 Fig. A1f–A1g). All the patterns were generally robust to changes in parameter values (Supplementary material Appendix 2 Fig. A3–A5).

In addition to the occurrence of ACSs, the effectiveness of mutualism was examined across the parameter space. This was assessed by determining whether the long-term average of the adult resource abundance was greater than its carrying capacity (Fig. 3). This analysis was desirable when the consumer–resource theory of mutualism was applied because the interaction may become antagonistic owing to reward exploitation by the adults (Holland and DeAngelis 2010). In the case of linear mutualism, the adults are always net mutualists if they coexist with the resources (the red and light red regions in Fig. 3a–b). By contrast, when mutualism is nonlinear, the adults can be net antagonists under some parameter conditions (the blue and light blue regions in Fig. 3c–d). Notably, the parameter region for the net antagonism is overlapped with that for the static consumer-associated state (the blue region or RC_{stable} of the white region in Fig. 2c–d) which corresponds to the adult-dominated state (Supplementary material Appendix 1 Fig. A1f, A1g). This implies that the net antagonism results from heavy reward exploitation by dominant adults. Overall,
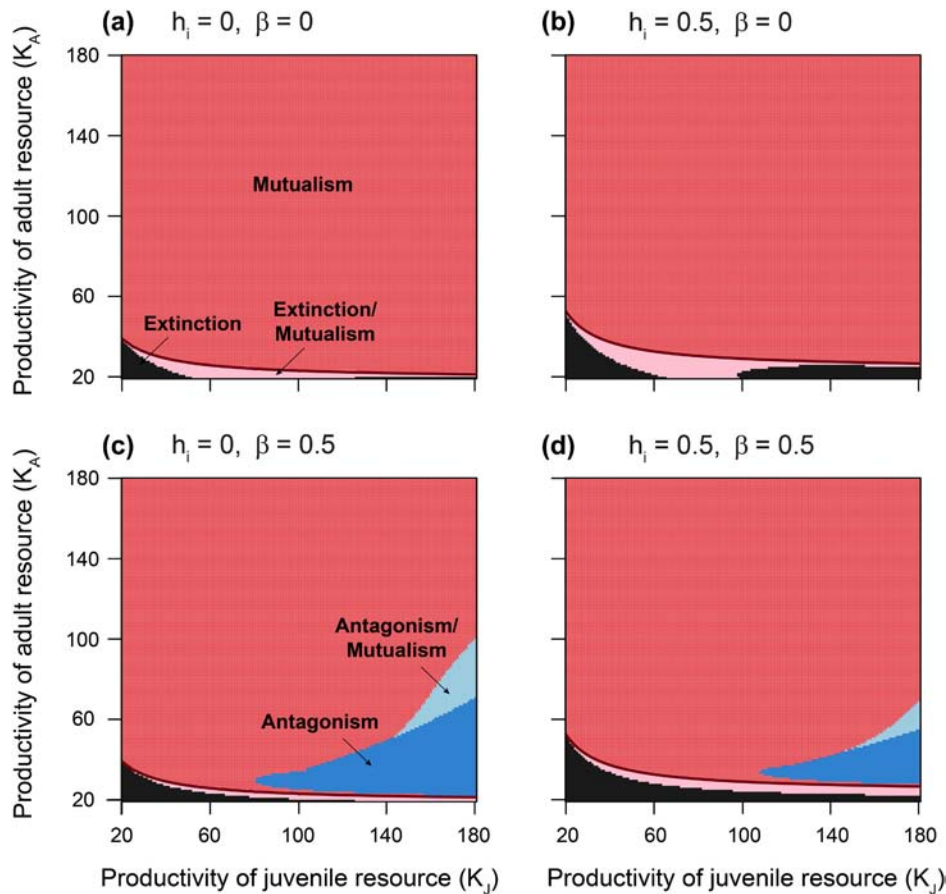
Figure 3. Effectiveness of mutualism in the K_J–K_A space. (a) Both resource exploitation and mutualism are linear ($h_i = 0$ and $\beta = 0$), (b) only resource exploitation is nonlinear ($h_i = 0.5$ and $\beta = 0$), (c) only mutualism is nonlinear ($h_i = 0$ and $\beta = 0.5$), and (d) both are nonlinear ($h_i = 0.5$ and $\beta = 0.5$). The effectiveness of mutualism was determined by whether the long-term average of the adult resource abundance was greater than the carrying capacity. Different colours indicate different community states: adults are absent (black), always net mutualists (red), net mutualists if present (light red), always net antagonists (blue), and either net mutualists or net antagonists (light blue). All parameters are the same as in Fig. 2 (i.e. all scenarios include mutualism).

although ACSs are observed when the mutualistic interaction is nonlinear (white regions in Fig. 2c–d), this bistability is ecologically irrelevant as long as adults are net mutualists (red region in Fig. 3).

Discussion

We developed a stage-structured hybrid community module in which the consumer species undergoes an ontogenetic niche shift from antagonistic to mutualistic interactions with different resources. Our model analyses illustrated that the consumer either goes extinct or coexists with the resources depending on the initial conditions when the resources have low carrying capacities while the community dynamics always converge to a single steady state (equilibrium point or limit cycles without ACSs) when the resources have high carrying capacities. Notably, these dynamic features are different from those of the corresponding antagonistic module, in which the consumer undergoes an ontogenetic diet shift without shifting to mutualism. Specifically, the antagonistic

module predicts that the consumer always goes extinct for low resource carrying capacities while the dynamics converge to either juvenile-dominated or adult-dominated state depending on the initial conditions for high resource carrying capacities (Schreiber and Rudolf 2008). For more detailed comparisons, see Fig. 2 of Nakazawa (2011a) in which ACSs occur when both K_J and K_A are high in the corresponding antagonistic module. Taken together, we can suggest that ontogenetic antagonism–mutualism coupling can play a stabilising role: it increases the potential for species coexistence by generating an alternative equilibrium for consumer invisibility (persistence) in unproductive environments while improving community resilience by suppressing ACSs in productive environments (Fig. 1). Further, these stabilising effects are generally robust to interaction nonlinearity (Fig. 2, 3), considering that unproductive and productive environments lead to consumer extinction and ACSs, respectively, irrespective of whether interactions are linear or nonlinear in the corresponding antagonistic module (Schreiber and Rudolf 2008, Nakazawa 2011a). Overall, we conclude that ontogenetic antagonism–mutualism coupling

have critical implications for stable species coexistence and resilience of stage-structured hybrid (e.g. plant–animal) communities under environmental changes.

General applicability of the stage-structured hybrid community view

The present stage-structured hybrid community module model has implications for the population dynamics of many pollinating insects that exhibit metamorphosis (e.g. Lepidoptera), in which larvae and adults are herbivores and pollinators, respectively (Altermatt and Pearse 2011). Recent studies have reported that adults of Lepidoptera play a more crucial role in pollination than previously thought (Hahn and Brühl 2016, Rader et al. 2016). Furthermore, their larvae are crucial herbivores of many plants and have been extensively used in the study of antagonistic plant–insect interactions (Crawley 1988). However, the regulatory mechanisms of their population dynamics remain controversial (Myers and Cory 2013). This is partly because few studies of their behaviours or demography have explicitly considered both larval and adult stages (Altermatt and Pearse 2011). Our results provide insights to this knowledge gap and is potentially applicable to any organisms that exhibit similar ontogenetic changes in the interaction type, such as other holometabolous pollinators (e.g. Hymenoptera, Diptera, and Coleoptera) (Wäckers et al. 2007) and seed-dispersing frugivorous birds (Holland et al. 2006).

It is important to note that the view of stage-structured hybrid community can be applied not only for plant–animal interactions but also for other mutualistic systems, although model modifications are necessary. This is because the relative costs and benefits of mutualism can change ontogenetically depending on the stage or body size, which may cause ontogenetic changes in the interaction type between antagonism and mutualism. This idea can be supported by consumer–resource theory of mutualism, which proposes that antagonism and mutualism are not binary alternatives but exist on a continuum (Bronstein 1994, 2015, Johnstone and Bshary 2002, Holland and DeAngelis 2009, 2010). Indeed, evidence have suggested that species relationships that were traditionally considered mutualistic could change ontogenetically. Examples of such relationship include: nutritional mutualism between plants and mychorrizal fungi (Johnson et al. 1997), defensive mutualism between aphids and ants (Breton and Addicott 1992, Stadler and Dixon 2005), and cleaning mutualism between hosts and cleaner fish (Grutter 2000, Cole 2010, Skelton et al. 2014). For example, ants protect aphids when the aphid colony size is small, but they sacrifice aphids when the colony size becomes too large (Breton and Addicott 1992, Stadler and Dixon 2005). Here, an aphid colony is considered an individual partner of the mutualism. Although roles of ontogenetic niche shifts in mutualism remain poorly discussed (Woodward et al. 2005), considering the ubiquity and importance of ontogenetic niche shifts (Miller and Rudolf 2011, de Roos and Persson 2013, Nakazawa 2015), we suggest that the view of stage-structured hybrid community would be widely applied to many ecological communities in nature.

Future perspectives on model development

Here we discuss how the present module can be extended to more realistically describing stage-structured hybrid communities. First, although the present study considered that the juveniles were antagonistic and the adults were mutualistic for describing pollination mutualism in plant–insect interactions, ontogenetic antagonism–mutualism coupling may occur from mutualistic juveniles to antagonistic adults. However, we can infer that this coupling would also be stabilising, because the positive feedback underlying ACSs in stage-structured antagonistic module can be reversed into a negative feedback when either the juveniles or the adults are mutualistic. Therefore, ontogenetic antagonism–mutualism coupling may generally increase community resilience.

Second, although the present study assumed that the consumer undergoes a complete ontogenetic diet shift, some species may partly share common resources between stages (interstage resource sharing; Fig 4a). For example, bee larvae and adults rely on common resources, but only the adults contribute to pollination. In an extreme case, larvae and adults of hawkmoths are specialist herbivores and pollinators, respectively, of the same plant species (Bronstein et al. 2009, Revilla and Encinas-Viso 2015). Hin et al. (2011) developed an intraguild predation module model by assuming a stage structure of the intraguild predator, the interaction topology of which is the same as that of ours, except that the intraguild prey utilises the basal resource. Their module model showed that an interstage resource sharing of the intraguild predator suppresses species coexistence. In another study, Nakazawa (2011b) showed that interstage resource sharing suppresses ACSs characterised by either juvenile or adult dominance in the corresponding antagonistic module. These predictions suggest that interstage resource sharing counteracts effects of stage structure, and thus it may suppress the stabilising effects of ontogenetic antagonism–mutualism coupling.

Third, future studies may consider ontogenetic antagonism–mutualism coupling caused by the stage structure of resource species. For example, plants are attacked by herbivores at the vegetative stage but often require animals for pollination or seed dispersal at the reproductive stage (Bronstein et al. 2007, Boege et al. 2011). To describe this situation, we propose another module, in which a stage-structured resource interacts with antagonists and mutualists at different developmental stages (Fig. 4b). de Roos et al. (2008) showed that ACSs can occur in the corresponding antagonistic module due to the positive feedback between stage-specific consumers. Therefore, if the interaction type of resource exploitation at either stage becomes mutualistic (i.e. stage-structured hybrid community), the positive feedback underlying ACSs could be reversed into a negative feedback (Nakazawa unpubl.). This means that ontogenetic antagonism–mutualism coupling mediated by the resource stage structure would also increase community resilience.
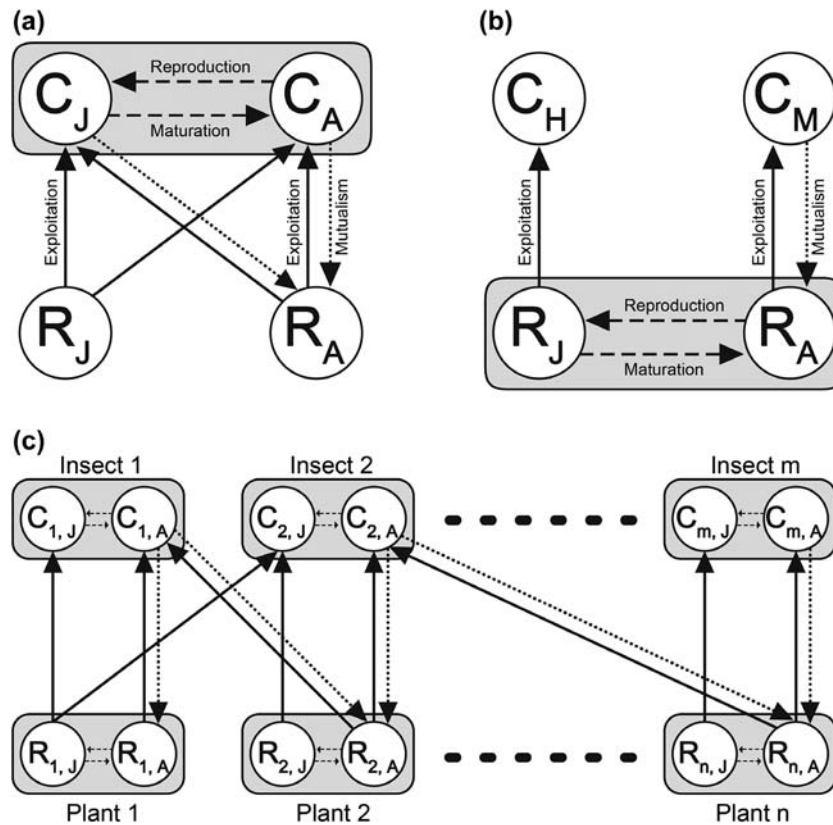
Figure 4. Extended conceptual models of the stage-structured hybrid community. (a) A one-consumer two-resource module in which antagonistic juveniles and mutualistic adults of the consumer partly share the resources; (b) a two-consumer one-resource module in which the resource interacts with antagonistic and mutualistic consumers at vegetative and reproductive stages, respectively; and (c) a stage-structured bipartite network with m consumers and n resources (interstage resource sharing omitted). Grey boxes represent different species in which maturation and reproduction couple juvenile (vegetative) and adult (reproductive) stages. Solid and dashed lines denote resource exploitation and mutualism, respectively.

Finally, it is necessary to develop network models for establishing of the stage-structured hybrid community view. Particularly, bipartite graphs comprising two trophic levels are desired to describe plant–animal interactions (Fig. 4c). Simulating dynamics for various structural properties is useful for determining stability conditions of the hybrid community network. Mougi and Kondoh (2012) reported that the relative proportion of antagonism and mutualisms critically affects species coexistence in non-structured hybrid networks. In stage-structured systems, this parameter must be manipulated in a stage-specific manner, which will be done by neutralising the strength of mutualism (i.e. $\alpha = 0$) for species that remain as antagonism after ontogenetic niche shifts. Meanwhile, Sauve et al. (2014) argued that connectance, rather than nestedness and modularity, is crucial for species coexistence in hybrid community networks. This parameter also needs to be manipulated in a stage-specific manner in stage-structured systems. According to Sauve et al. (2014), connectance within a stage may facilitate species coexistence. However, connectance across stages (associated with interstage resource sharing) may just decrease network resilience because at the species level connectance

does not change with degree of interstage resource sharing. Future studies will be required to explore these predictions. At the same time, field data on stage-specific interaction data are also important for realistically describing stage-structured hybrid communities (Altermatt and Pearse 2011, Nakazawa 2016).

Conclusions

Here, we proposed the integration of two crucial factors in community dynamics: ontogenetic niche shift (Miller and Rudolf 2011, de Roos and Persson 2013, Nakazawa 2015) and antagonism–mutualism coupling (Mougi and Kondoh 2012, Sauve et al. 2014, Kondoh and Mougi 2015, Lurgi et al. 2016). Considering that the benefits and costs of mutualism change dynamically according to the consumer–resource theory of mutualism (Bronstein 1994, 2015, Johnstone and Bshary 2002, Holland and DeAngelis 2009), the stage-structured hybrid community view is potentially applicable not only to pollination mutualism of holometabolous insects but also to many mutualistic relationships. To illustrate the importance of the present community view,

we analysed the minimum module model and showed that ontogenetic antagonism–mutualism coupling promotes stable species coexistence under environmental changes. However, we are still at the initial stage of establishing the novel community view. Given the ubiquity and importance of stage structure and mutualism, further research efforts are necessary to make both theoretical and empirical advances for a more comprehensive understanding of the mechanisms underlying the great biodiversity in stage-structured hybrid (e.g. plant–animal) communities in nature.

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Supplementary material (available online as Appendix oik-04702 at <www.oikosjournal.org/appendix/oik-04702>). Appendix 1–2.