# Thinking inside the box: community-level consequences of stage-structured populations

**Tom E.X. Miller and Volker H.W. Rudolf**

Department of Ecology and Evolutionary Biology, Rice University, MS-170, Houston, TX 77005, USA

**Ecologists have historically represented consumer–resource interactions with boxes and arrows. A key assumption of this conceptualization is that all individuals inside a box are functionally equivalent. Demographic stage structure, however, is a widespread source of heterogeneity inside the boxes. Synthesizing recent studies, we show that stage structure can modify the dynamics of consumer–resource communities owing to stage-related shifts in the nature and strength of interactions that occur within and between populations. As a consequence, stage structure can stabilize consumer–resource dynamics, create possibilities for alternative community states, modify conditions for coexistence of competitors, and alter the strength and direction of trophic cascades. Consideration of stage structure can thus lead to outcomes that are not expected based on unstructured approaches.**

## Ecological communities as boxes and arrows

Consumer–resource interactions are ubiquitous in nature and are a fundamental aspect of ecological communities. Understanding and predicting the dynamics of these interactions are central goals of community ecology, with implications for the preservation and management of biodiversity. Historically, community ecologists have represented consumer–resource interactions with boxes (indicating populations or species) connected by arrows that direct energy from resource to consumer. A key assumption of this conceptualization (and of most corresponding mathematical models and empirical studies) is that all individuals inside a box are functionally equivalent. In natural communities, however, no population is homogenous. Numerous factors can introduce heterogeneity within consumer or resource populations. Demographic stage structure (see Glossary) is arguably one of the largest sources of heterogeneity inside the boxes and has the potential to modify consumer–resource interactions.

## What is stage structure and when does it matter?

Demographic structure refers to the occurrence of different sizes, ages, or ontogenetic stages within a population. For convenience, we use 'stage' to include all of these dimensions of demographic structure, although we recognize biological differences among them (e.g. transitions among sizes are more flexible than among ages). Most multicellular organisms exhibit some form of stage structure. For organisms with overlapping generations, multiple stages of the life cycle can co-occur in time and space (e.g. most perennial plants and vertebrate animals). For others, stages might be separated temporally (many insects) or spatially (insects and amphibians that transition from aquatic to terrestrial habitats). In some organisms, morphological and ecological differences among stages are dramatic (amphibians, holometabolous insects and many marine invertebrates), whereas in others (many plants, fish and arachnids), differences might be more gradual. Each stage of the life cycle of an organism is dynamically linked to the other through demographic processes of growth, survival and reproduction.

It is widely recognized that demographic processes are stage dependent for many types of organism. This observation motivated major developments in quantitative population ecology during the 20th century, including

### Glossary

**Alternative stable state (ASS)**: a system (community) can persist indefinitely in two contrasting states under the same environmental conditions.

**Cannibalism**: killing and at least partial consumption of smaller conspecifics by larger (older) stages.

**Cohort competition**: competition between different life stages of the same species, including direct interference, or resource- or predator-mediated interactions.

**Complex life cycle**: here used for species with a life history that is characterized by an abrupt ontogenetic change of the morphology, physiology, or behavior of individuals.

**Interference competition**: aggressive interactions between members of the same species (e.g. contests over mates, space, or food); often occurs in a density-dependent manner.

**Intraguild predation (IGP)**: a system where competing species are also engaged in predator–prey interactions.

**Ontogeny**: course of development of an organism.

**Overcompensatory density dependence**: a form of density dependence in which increasing input leads to decreasing output; in stage-structured populations, increasing the density of one stage decreases the abundance of downstream stages.

**Ontogenetic niche shift**: a change in resource use, competitive ability, or vulnerability to predation during development that modifies intra- or interspecific interactions.

**Stage structure**: the occurrence of different sizes, ages, or ontogenetic stages within a population.

**Stage distribution**: the relative abundances of co-occurring life stages.

**Stage refuge**: shift in the vulnerability of individuals during their development from being vulnerable to predation to not being vulnerable to predation, or vice versa.

**Stage partitioning**: incomplete overlap in the use of life stages of a single resource species by different consumer species.

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*Corresponding author:* Rudolf, V.H.W. (volker.rudolf@rice.edu)

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life-table analysis and stage-based matrix projection models. In sharp contrast to its prominent role in the study of single-species dynamics, stage structure has received relatively little attention in the context of ecological communities. We are just beginning to understand the ways in which stage-related heterogeneity 'inside the box' can transcend the population level to influence the structure and dynamics of multi-species assemblages.

Here, we synthesize recent advances in understanding of how stage structure can influence communities consisting of consumers (or predators) and resources (or prey). We identify the features of stage-structured populations that lead to opportunities for community-level effects and then describe these effects at multiple levels of community organization: (i) the stability of pair-wise consumer–resource systems; (ii) the structure of multi-species communities (how many and which species persist at equilibrium); and (iii) the dynamics of multi-species communities (spatiotemporal variation in densities and responses to perturbation). Because theory has greatly outpaced empirical work in this area, we focus on recent advances in theory, but highlight related empirical work when possible.

## How does stage structure affect communities?

Stage structure *per se* does not necessarily modify expectations for community dynamics. Stage-structured populations often equilibrate at stable stage distributions determined by intrinsic demographic rates. If this distribution is invariant, then little information might be gained by explicitly accounting for multiple stages. For example, if a predator forages randomly on stages of a structured prey population, then it does not modify the prey stage distribution and its effect on total prey density might be sufficient to characterize the interaction. We argue that the strongest (and most interesting) community-level effects of stage structure are manifested when the stage distribution responds dynamically to perturbations imposed by ecological interactions within and between species and with the abiotic environment. Such dynamic responses are probable when interactions occur non-randomly with respect to stage.

The ecology of individuals typically changes over the course of ontogeny, including changes in resource use, competitive ability, or vulnerability to consumption. These changes can be classified more generally as ontogenetic niche shifts. We consider two main classes of ontogenetic niche shifts. First, shifts in intraspecific interactions, such as asymmetric competition between life stages (e.g. shift from inferior competitor to superior competitor) or cannibalism (shift from conspecific prey to conspecific predator), can indirectly influence interspecific interactions. Competition between stages, or cohort competition, could involve direct interference or cases where the ability to exploit a shared resource varies with size or stage (e.g. light competition in plants or competition for food in many animals) [1,2]. However, most studies of the consequences of ontogenetic shifts in intraspecific interactions for community dynamics have focused on cannibalism. Cannibalism is a widespread feature of size-structured animal populations and ubiquitous in both aquatic and terrestrial systems [3–7]. Cannibalism has long been known to influence the dynamics of natural populations (reviewed in [8]), but ecologists have increasingly recognized that it can also fundamentally alter the dynamics of species interactions [5,9–14], community structure [5,13] and even entire ecosystems [15]. Although cannibalism does not necessarily require stage structure, it is more likely to occur when there is strong size disparity among co-occurring conspecifics [16].

Second, ontogenetic niche shifts can also involve interspecific interactions. There are many possible types of ontogenetic shift in interspecific interactions, including stage-related changes in use of resources and/or vulnerability to consumers (Figure 1) [1,17]. For example, recent estimates suggest that species with complete metamorphosis (such as amphibians, holometabolous insects, many aquatic invertebrates and many parasites) share on average only 0–8% of their resources between stages [18]. Even in species without metamorphosis, stage transitions often lead to concurrent changes in diet [3,18].

Just as resource use can change over consumer ontogeny, interactions with consumers can also vary across stages of a resource. Life cycles of many species include stage refugia that are invulnerable to consumers. Often it is the older, larger, and/or reproductive stage of the resource life cycle that gains protection from consumers, as in many insects [19,20] and fish [21]. However, some predators exhibit a preference for larger prey, which might be more profitable (e.g. [12,22,23]). Stage refugia (and ontogenetic diet shifts) modify the 'interactive population size', or the number of individuals within a population that participate in an

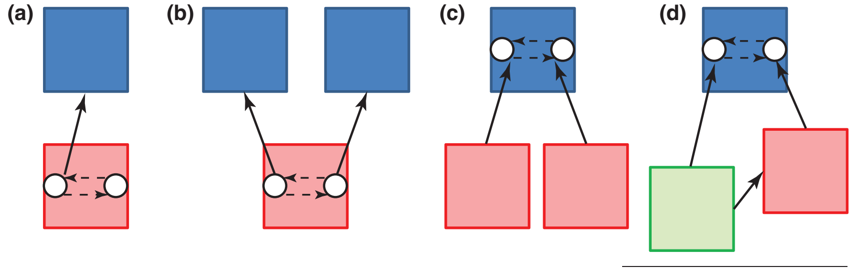

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**Figure 1**. Examples of ontogenetic niche shifts in interspecific interactions. Boxes represent consumer (blue) or resource (red or green) populations and circles within boxes represent stages within populations. For clarity, only two stages are represented (e.g. juveniles and adults). Solid arrows indicate trophic interactions and direct energy from resource to consumer. Dashed arrows indicate demographic transitions between stages (e.g. maturation and reproduction). **(a)** Shift in the vulnerability of a resource species to consumers (the later resource stage is a refuge from predation); **(b)** shift in consumer identity between resource life stages (e.g. each stage is consumed by a different species); **(c)** shift in resource or habitat use between consumer life stages (each stage uses a different resource or habitat); and **(d)** shift in interaction type from competition to predation (early consumer stage competes with its future prey).

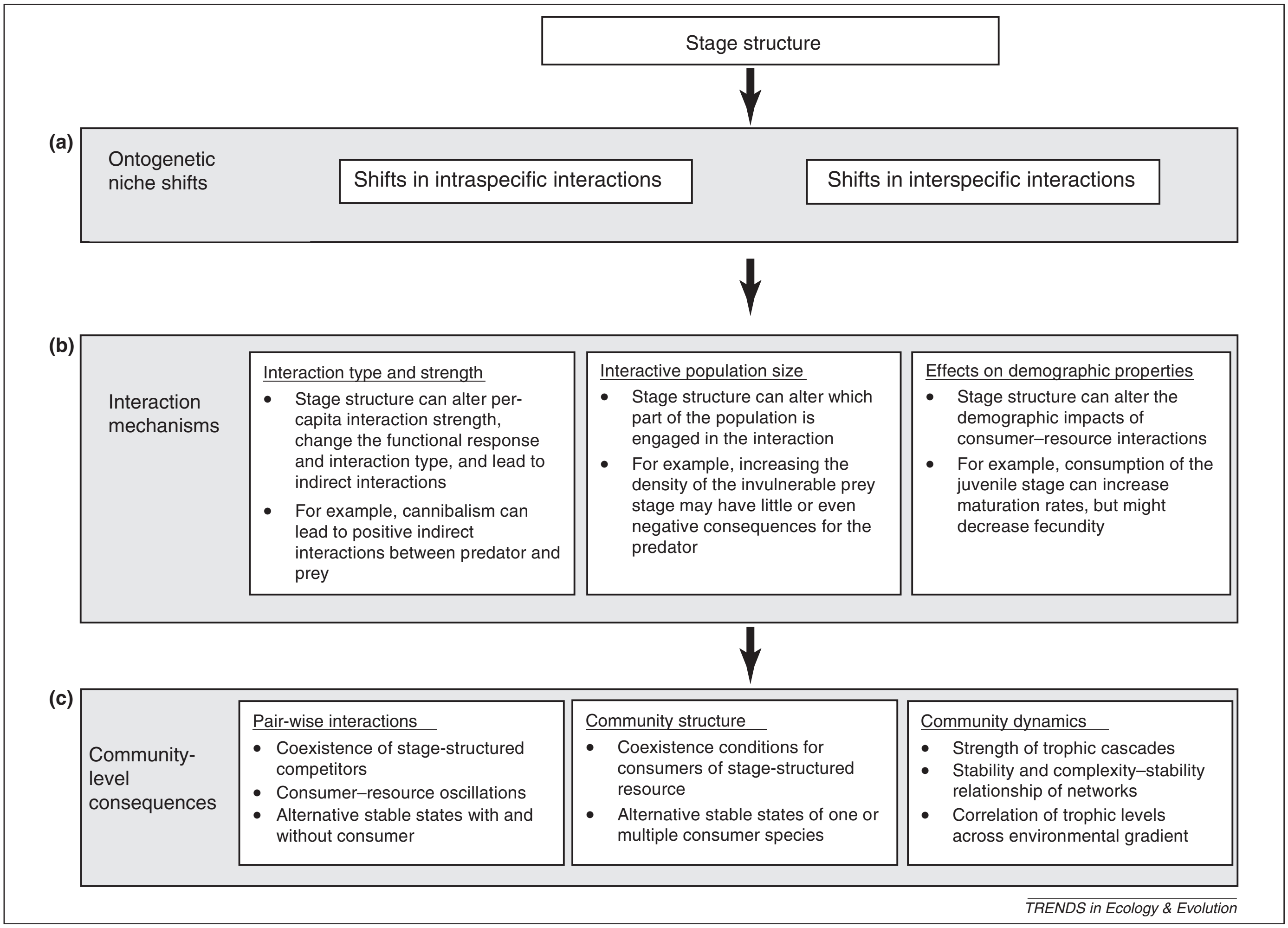

**Figure 2**. Pathway of stage-structure effects from population properties to interaction mechanisms to community level. **(a)** Stage structure within populations creates the potential for ontogenetic niche shifts that affect intra- and/or interspecific interactions. **(b)** These properties of stage-structured populations modify interaction mechanisms, including three main components: (i) the functional relationship between species (e.g. per capita consumption rate); (ii) the 'interactive population size' of species (how many and which individuals within a population are involved in an interaction); and (iii) the demographic impacts of interacting species (which feed back to influence densities). For instance, cannibalism can lead to a predator-dependent functional response (thereby altering the functional relationship), stage refugia can reduce the density of prey influenced by predation (altering the effective density) and consumption of juvenile stages can increase maturation rates. In many instances, all three components are interconnected through feedbacks (e.g. between density and demographic rates). **(c)** Consequently, stage structure can fundamentally alter pairwise interactions and community structure and dynamics (see main text for detailed examples). If all stages are ecologically equivalent, then there are no ontogenetic niche shifts **(a)**, interaction modifications **(b)**, or community-level consequences of stage structure (c); unstructured approaches would be appropriate in this case.

interaction (Figure 2). Furthermore, among stages that are vulnerable to consumption, different stages might interact with different subsets of consumer species. For example, as plants undergo transition from seeds to adults, their resistance traits and the identities of their herbivores and mutualists often change systematically [24–27]. Such stage-specific interactions can alter transition rates among resource stages, leading to indirect interactions among consumers that attack different stages of a shared resource. Thus, ontogenetic niche shifts are common and important conduits linking the dynamics of different resources, consumers, habitats and ecosystems [28,29].

Through these ontogenetic niche shifts, stage structure can alter the three main components that determine the dynamics of species interactions (the type and strength of interaction, the density of interacting individuals, and the demographic impacts of the interaction) and thereby influence the dynamics and structure of consumer–resource communities in ways that cannot be predicted with unstructured approaches (Figure 2). Here, we examine the types of effect that stage structure commonly has on communities and highlight the specific underlying mechanisms.

## What types of effect can stage structure have on ecological communities?

### *Effects on consumer–resource coexistence and dynamics in two species systems*

#### *Alternative stable states in consumer–resource systems*

In classic one consumer–one resource models, the persistence of a consumer is always guaranteed once a threshold resource density is achieved [30]. However, recent theory [31,32] indicates that the presence of a stage refuge in the resource population (Figure 1a) creates potential for alternative stable community states with and without consumers, even at high resource densities. This discrepancy between structured and unstructured models arises because of how resource individuals are distributed between vulnerable and invulnerable stages. If density dependence is concentrated in one life stage (e.g. because the stage is competitively inferior to other stages [33]) and

### Box 1. Emergent Allee effects and emergent facilitation

For a given population density of a resource, consumer persistence requires sufficiently high relative abundance of vulnerable resource individuals and consumer extinction might occur if the resource population becomes dominated by an invulnerable stage (e.g. [31]). The resource stage distribution is determined by intrinsic, density-independent rates of demographic transition as well as the degree to which those rates are sensitive to density (or food availability). For example, strong density dependence at the juvenile stage leads to slow maturation rates and a juvenile-dominated, 'maturation-regulated' population, whereas strong density dependence at the adult stage leads to low reproductive rates and an adult-dominated, 'reproduction-regulated' population [33]. Stage-specific density dependence can occur when both stages compete for shared resources and one is competitively inferior, highlighting an additional role for interstage interactions (e.g. [82]). Alternatively, stage-specific density dependence could reflect competitive interactions concentrated among individuals within the same stage (e.g. when stages are temporally or spatially separated), with the strength of competition varying across stages.

If density dependence is overcompensatory (Figure I), then consumer-induced mortality relaxes competition among survivors, accelerates demographic transitions and shifts the stage distribution, potentially in favor of the consumers (if it shifts toward the vulnerable stage). Theoretical work and some empirical data suggest that, through these dynamic feedbacks, consumers can facilitate their own persistence [31,32]. A threshold density of consumers is required to invade a consumer-free resource population and trigger a switch to a stage distribution that can support consumers. This has been termed an 'emergent Allee effect' because there is no cooperation among consumer individuals and consumption is purely exploitative; positive effects of consumer density operate via the dynamics of the stage-structured resource [32]. The direction and magnitude of response to stage-specific consumption depends on whether density dependence acts most strongly on the juvenile or adult stage, and on which stage is subject to consumer attack [83,84,33].

The same mechanism of emergent Allee effects for a single consumer can also lead to indirect positive effects between consumers that specialize on different stages of the same resource species. A consumer that feeds on a strongly density-regulated stage can increase rates of demographic transition among survivors, leading to an increase in the availability of other stages. Stage-specific consumers might therefore rely on consumption by a 'competitor' at other points in the resource life cycle for their persistence. This positive indirect interaction has been called 'emergent facilitation' because, as above, it arises via the stage-structured life cycle of the resource [63].

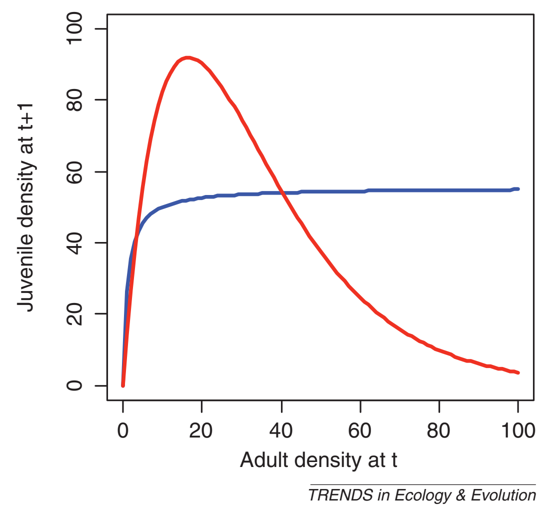

**Figure I**. A hypothetical example of overcompensatory density dependence in the recruitment of juvenile offspring in relation to adult density at different time points (*t*; red line). Beyond the recruitment peak (at approximately 20 adults), mortality in the adult stage would have a positive effect on juvenile density. By contrast, the blue curve shows a saturating form of density dependence, where adult mortality can only reduce juvenile density. This example shows classic Ricker (overcompensatory) and Beverton-Holt (saturating) recruitment functions.

overcompensatory (meaning that mortality in one stage has positive effects on the density or biomass of itself or a subsequent stage), then consumer-induced mortality can shift the stage distribution, potentially in favor of the consumers (Box 1). Through these feedbacks, consumers can facilitate their own persistence and cannot easily invade the stable, consumer-free community state (Box 1) [31,32]. Competition between stages has an important role in these dynamics, highlighting how ontogenetic shifts in both intra- and interspecific interactions can operate simultaneously.

Empirical evidence that overcompensatory responses to mortality can shift the stage distribution comes from arthropod [34,35], zooplankton [36] and fish [37] populations studied in the laboratory. There is also evidence that this mechanism operates in nature: in one Norwegian lake, culling invulnerable fish from the strongly density-regulated adult stage led to an increase in the relative abundance of small, vulnerable fish and facilitated re-establishment of a top predator [31].

Overcompensatory responses to mortality can have important implications for the management of invasive stage-structured populations (Box 2). For example, Pardini *et al.* [38,39] estimated demographic rates for invasive garlic mustard (*Alliaria petiolata*), including the influence of density dependence on particular transitions. Their model revealed complex dynamics in which harvesting of the rosette (juvenile) stage could have a positive effect on the mean population size for low harvesting rates, suggesting that weak or incomplete management actions could increase weed density. The model of Buckley *et al.* [40] made similar predictions for a positive effect of harvesting on densities of the invasive scentless chamomile (*Tripleurospermum perforatum*). Thus, with incomplete knowledge of stage-structured, density-dependent demography, management actions might backfire [41]. These results highlight the importance of considering the occurrence, strength, functional form and stage specificity of density dependence in structured populations of management concern.

*Stability of consumer–resource dynamics* Consumer–resource interactions are prone to instability because consumers can overexploit their resource, leading to strong oscillations and possibly extinction of both species. In single-species dynamics, stage-structured cannibalism can either increase or decrease oscillations, depending on the occurrence of other density-dependent processes [8], which in turn might indirectly drive predator–prey dynamics [15]. However, cannibalism can have stabilizing effects on consumer–resource dynamics in a community context. For example, recent evidence suggests that stage-structured cannibalism in a predator stabilizes predator–prey

### Box 2. Stage-structured harvesting

We use ‘harvesting’ to refer to any intended, human-induced mortality in natural populations, including collection of commodities as well as management activities intended to reduce the densities of undesirable species. For commodity harvesting, often only one or a few stages of the resource life cycle have significant nutritional, economic, or cultural value. For pest control, management activities often target specific life stages, such as the juvenile or reproductive stages of plants. Thus, consideration of stage structure is relevant for understanding the dynamics of natural populations subject to human harvesting.

If density dependence is overcompensatory (Box 1), harvesting can increase population density [33]. This increase is more likely in stage-structured populations because stage structure can result in a temporal separation of mortality and density dependence [33]. Furthermore, stage-structured harvesting can lead to redistribution of the biomass across stages when density dependence affects maturation and reproduction rates unevenly [33]. Laboratory studies provide evidence that stage-structured harvesting can indeed lead to overcompensatory responses and biomass redistribution, including Nicholson’s classic blowfly experiments [85]. More recently, similar effects have been observed in mites [34], poeciliid fish [37] and zooplankton [86]. Given that stages can differ in their ecology (e.g. [87]), such shifts in stage distribution can alter the functional role of a species in the ecosystem, with dramatic consequences for ecosystem processes, even if the biomass remains constant. This might explain why changes in the stage-structured harvesting of predatory fish in the Scotian Shelf altered the density of lower trophic levels dramatically, even though the total biomass of the predatory fish remained constant [88].

dynamics (i.e. decrease or prevent predator–prey population oscillations and promote coexistence) [13]. Indeed, such a stabilizing effect has been observed in experimental studies with protists, where systems with a cannibalistic top predator showed decreased variation in population size and were the only systems that persisted for the entire duration of the experiment [42]. Cannibalism tends to stabilize predator–prey systems because it causes a reduction in predator population growth (through mortality or nonlethal behavioral modification) that is positively related to predator density but negatively related to prey density [10].

Stage refugia (Figure 1a) can also stabilize consumer–resource dynamics because the invulnerable stage can prevent overexploitation of the resource, bounding consumer density and providing a continuous source of vulnerable individuals. The stabilizing effect of stage refugia appears to be a general result [43,44], but is particularly well studied in the context of insect biological control [19,45–47]. The presence or absence of an invulnerable host stage could explain why some biological control programs result in stable pest suppression whereas others (in which hosts lack a stage refuge) lead to unstable densities and sometimes local extinctions of predator, prey, or both [47].

*Coexistence of stage-structured competitors* When individuals change in size during their development, this also typically alters their competitive abilities. For example, in many systems, larger individuals are competitively dominant, either because of increased abilities in exploiting a resource or owing to interference competition. Alternatively, small individuals might be more efficient in converting resources into body mass, thus outcompeting larger individuals. As a consequence, competitive dominance between species might shift during ontogeny (reviewed in [1]). Theory suggests that these shifts can alter competitive outcomes in several ways. In systems where coexistence is impossible with unstructured competitors, stage structure can promote coexistence, given that each species is competitively dominant at a different stage, and is mainly limited by (i.e. has a population bottleneck in) the stage that is competitively inferior [48–50]. The mechanism is related to a general competition principle: if each species is limited by a different stage, this is comparable to assuming that each species is limited by a different resource. Thus, stage structure can create niche space separation between competitors if their stage-dependent demographic rates are sufficiently different. Recent work indicates that stage structure can also promote coexistence even if only one species exhibits an ontogenetic niche shift through a similar mechanism, but this requires that adults are more food limited than are the juvenile stages [51].

## Effects on the structure of multi-species communities

*Species coexistence in communities with intra-guild predation* In natural communities, predators often feed at multiple trophic levels and, thus, might also compete with their prey for shared resources, resulting in intraguild predation (IGP) [52]. Understanding the coexistence of IG predator and prey species is a long-standing puzzle in community ecology. In many instances, IGP arises owing to ontogenetic shifts in the type of interactions (i.e. life history omnivory: early IG predator stages compete for resources with their future prey) [52,53] (Figure 1d). Recent work indicates that such ontogenetic shifts can facilitate or impede coexistence compared with unstructured models, depending on what resources are used by the late IG predator stage. If the large predator stage can only persist by consuming the IG prey (i.e. the predator shows a complete ontogenetic diet shift), coexistence is promoted because the IG predator is unlikely to invade the system and exclude the IG prey. However, a recent model suggests that coexistence is unlikely if the large IG predator stage also consumes the shared resource [54]. Competition with the IG prey can prevent successful recruitment of small IG predators into the adult stage at low resource productivity, and the IG predator cannot persist. However, once the resource productivity exceeds a certain threshold, the predator can reach the large size class, reduce prey density and thereby increase resource availability for small predators, ultimately leading to the extinction of the prey [54]. These theoretical predictions are consistent with a study on size-specific invasion success in an experimental fish system [55].

Recent theory also indicates that the introduction of stage-structured cannibalism increases opportunities for coexistence in IGP systems. First, contrary to classic predictions, cannibalism in a predator can allow IG predator and prey to coexist even when the predator is more efficient in exploiting the shared resource. Second, if cannibalism is strong enough, it can even prevent the predator-mediated extinction of the prey predicted by unstructured models [5]. Given that cannibalism is very frequent in systems with IGP [3,5,52], these results could explain why IGP is so common in natural communities [56] contrary to predictions from classic unstructured models [57,58].

### Consumer partitioning of resource stages and indirect interactions

Thus far, we have discussed consequences of ontogenetic shifts in interspecific interactions in terms of vulnerable and invulnerable resource stages. In many resource species, different life stages are equally vulnerable to consumption but by different consumer species (Figure 1b). For example, resource stage partitioning is common in communities of parasitoids that share insect hosts [19], herbivores (e.g. [59]) and mutualists (e.g. [26]) that share plant hosts, and parasites that share vertebrate or invertebrate hosts [60,61]. Thus, consumers that appear to have high or complete overlap in use of resource species might partition the resource life cycle, leading to niche separation and opportunities for coexistence that are not expected based on unstructured models. However, one important complication that distinguishes stage partitioning from other forms of niche partitioning is that life stages of the resource population are dynamically linked by growth, survival and reproduction. These demographic processes provide a pathway of indirect interaction among stage-specific consumers leading to surprising competitive outcomes.

In the absence of overcompensatory density dependence (Box 1), consumption of an early resource stage (e.g. eggs) reduces availability of a later stage (e.g. larvae). This creates a competitive advantage for consumers that act early in the resource life cycle and makes stable coexistence of early and late consumers impossible or possible only under restrictive conditions [46,62]. However, with overcompensatory density dependence in the resource population, consumption might relax competition among survivors and lead to increased availability of a subsequent stage (Box 1). Consumers of different resource life stages might not only coexist in this case, but also depend on their ‘competitors’ to maintain a flux of resource individuals out of strongly density-regulated life stages [63] (Box 2).

Depletion of a strongly density-regulated life stage is not the only way that consumers can modify the resource stage distribution. Some consumers, such as many herbivores and mutualists of plants, directly alter demographic rates through their effects on host performance without actively depleting host density. This can result in either positive or negative indirect interactions between stage-specific consumers, depending on the directions in which each modifies the resource stage distribution [64,65]. Interestingly, coexistence is possible even when consumers have complete overlap in their use of resource stages, and competitive exclusion is possible even when the consumers have no overlap in resource use, contrary to classic expectations based on independent resources [65]. These competitive outcomes depend sensitively on the nutritional benefits that different consumers receive from different life stages; a phenomenon that has received little empirical attention.

Finally, empirical evidence indicates that consumers can not only shift the relative abundances of resource stages (density-mediated effects), but also modify the traits of resource stages. Vonesh and Osenberg [66] showed that a predator of treefrog eggs (*Hyperolius spinigularis*) reduced egg densities and caused surviving eggs to hatch earlier and at smaller sizes, which negatively affected a larval predator. This is the first study to consider both density- and trait-mediated indirect effects among stage-specific consumers. Additional studies are needed to determine whether there are general trends in the relative importance of these interaction pathways.

### Ontogenetic niche shifts and alternative stable community states

Just as ontogenetic shifts in consumer identity can lead to indirect interactions between different consumer species, ontogenetic shifts in resource use (Figure 1c) can lead to indirect interactions between seemingly different resources, habitats, or ecosystems [28,29,67]. For instance, when two stages of a consumer use different resources (or habitats), a gradual shift in productivity of one resource can lead to a dramatic shift in the consumer stage distribution and counterintuitive changes in abundance (e.g. increasing a resource can decrease the abundance of the respective consumer stage) [28,68], even under more complex food web scenarios [69]. This suggests, for example, that a small increase in the productivity of pond environments dramatically reduces the abundance of larval amphibians or aquatic insects and increases abundance of their adult counterparts in terrestrial environments [28]. Comparable models with unstructured consumers (e.g. [70]) or shared resources [33] do not predict these abrupt shifts between alternative stable states. Dramatic differences across ponds in the stage structure of pumpkinseed sunfish and their stage-specific resources provide some empirical support for the model predictions [71].

### Effects on the dynamics of multi-species communities

*Trophic cascades* Individuals within stage-structured populations often occupy different trophic levels, thus creating ‘trophic heterogeneity’ within food chains [72], which fundamentally alters trophic cascades and leads to dynamics that cannot be predicted from classic unstructured models. For instance, size-structured cannibalism creates trophic structure within populations with at least two distinct functional groups: cannibals and conspecific victims. This difference in trophic position between stages can result in positive density- and trait-mediated indirect interactions (DMII and TMII, respectively), even in a single predator–prey system [13]. Depending on the trophic level at which cannibalism occurs, this can alter the strength of trophic cascades and correlations of abundances among trophic levels (Box 3). For instance, if cannibalism in a prey species is strong relative to predation rates and predators prefer cannibalistic stages, increasing the predator density can increase the prey density (owing to a reduction in cannibalism), which can decrease the density of the basal resource [5] (Figure 3). This theory was recently supported experimentally in an insect–cotton system in which the addition of a top IG predator reduced cannibalism within the IG prey, enhanced herbivore suppression and improved plant performance [73].

Finally, ontogenetic niche shifts between vulnerable and invulnerable stages (Figure 1a) provide an additional

### Box 3. Indirect interactions with stage-structured cannibalism

With stage-structured cannibalism, there are at least two trophic levels within a population: cannibals and conspecific victims. As a consequence, cannibalism can lead to positive indirect interactions between predator and prey stages, altering top-down and bottom-up effects across trophic levels (Figure 2, main text). The effects and underlying mechanisms, however, depend on the trophic level at which cannibalism occurs.

- Cannibalism in the predator can: (i) reduce the strength of top-down trophic cascades; and (ii) create a positive correlation between predator and prey density across a productivity gradient that is not predicted by classical Lotka-Volterra-type models [13]. The underlying mechanism for both patterns is that cannibalism can reduce the per-capita predation rate (on heterospecifics) of the predator with increased predator density. This reduction in heterospecific predation rate typically arises through both density- and trait-mediated mechanisms that often occur concurrently [13]. First, when large cannibalistic predator stages show a saturating functional response (e.g. Holling type II), fewer heterospecifics are consumed as more small conspecifics are cannibalized, resulting in a positive indirect interaction between small predator stages and heterospecific prey [10]. Second, small predators commonly reduce their foraging activity in the presence of cannibalistic stages to avoid being cannibalized, resulting in a positive indirect interaction between large cannibalistic predator stages and heterospecific prey [9,89]. As a consequence, the negative effect of increasing predator density on prey survival is reduced by the concurrent decrease in its per-capita predation owing to stage-structured cannibalism. Both indirect interaction types could explain why stage-structured predators are 10–45% less efficient in suppressing their prey than are predators with only one stage [9,14,90,91].
- Cannibalism in the prey can also reduce the strength of trophic cascades; however, here the underlying mechanism is a compensatory response in the prey, not a change in the per-capita attack rate of the predator. By consuming cannibalistic stages, the predator also reduces cannibalism rates in the prey population. In addition, cannibalistic prey stages often reduce their foraging rate (including cannibalism) as an antipredator response to the presence of a heterospecific predator. In both scenarios, the reduction in cannibalism rates counteracts the additional mortality imposed by the predator, thereby reducing the net impact of the predator on the prey population [12]. This compensatory response can alter the trophic cascades expected from unstructured models (Figure 2, main text).

way in which stage structure can modify the strength of trophic cascades. Increasing the productivity of a habitat can accelerate development from a vulnerable juvenile stage to an invulnerable adult stage. Thus, high productivity can lead to increased relative abundance of the refuge stage, a weaker impact of consumers and lower consumer density [74]. These productivity-related shifts in stage distribution, consumer density and consumer impact provide a possible explanation for differences in the strength of trophic cascades among systems in which resource species do and do not achieve a stage refuge from consumption, a hypothesis with some empirical support [75]. In general, this suggests that differences in the presence and type of stage-structured interactions explain why the strength of trophic cascades varies so widely among systems [76].

*The stability of ecological networks* Most studies on stage-structured species interactions have looked at simple community modules with only a few species, but

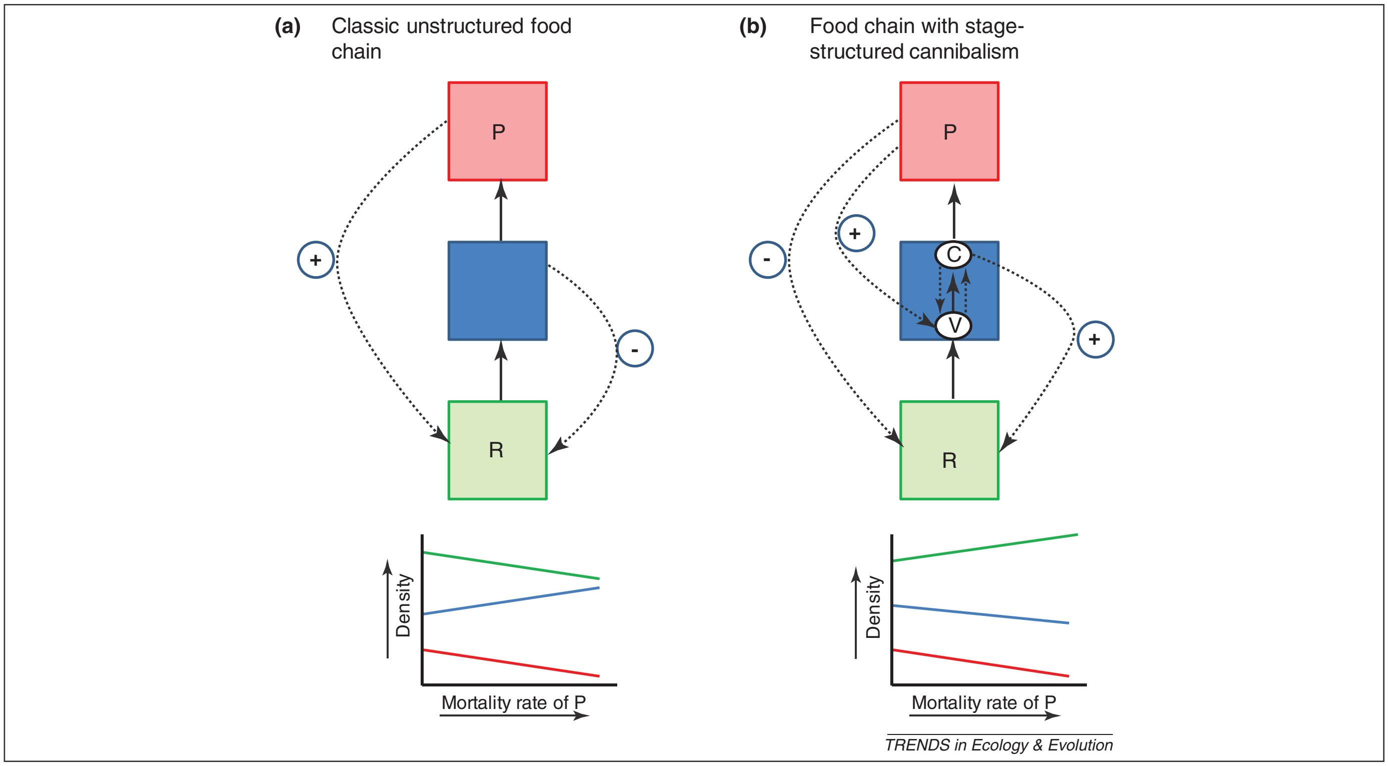

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**Figure 3**. Example of trophic cascades in food chains with and without stage-structured cannibalism. **(a)** Without cannibalism, increasing the top predator (P; red) density decreases the intermediate consumer (blue box), which has an indirect positive effect on the resource (R; green). Thus, increasing the mortality of the predator (e.g. owing to harvesting) decreases resource density (R). **(b)** However, with cannibalism (C, cannibals; V, conspecific victims) in the intermediate consumer, increasing the predator density can have a negative effect on the resource, given that cannibalism is strong relative to consumption rate of the predator (P; Box 3). Consequently, increasing the mortality of the predator can lead to an increase in resource density (R).

### Box 4. Outstanding questions

- How important are stage-structured interactions in plant–herbivore, host–parasite and mutualistic systems?

  Coverage of interaction types and taxonomic groups is uneven. Existing theoretical and empirical work largely focuses on 'traditional' consumers (e.g. predators), especially in aquatic systems. The extent to which similar processes occur in plant–herbivore, host–pathogen and mutualistic communities is largely unknown.
- What are the effects of stage structure on complex ecological networks and functioning of ecosystems?

  There is a good understanding of the effects of stage structure in simple community modules, but researchers are only beginning to understand the effects in more complex interaction networks and how they influence ecosystem processes.
- How important are trait-mediated effects relative to density-mediated effects in stage-structured interactions?

  Most studies have focused on density-mediated effects of stage structure. There is some evidence for trait-mediated effects in ontogenetic shifts in both intra- and interspecific interactions. The relative importance of density- and trait-mediated effects is poorly understood.
- How will stage-specific harvesting impact the functioning of natural communities?

  Increasing evidence indicates that stages differ in their ecological role and that stage-specific harvesting alters the stage structure and population dynamics. These changes are likely to alter the structure of communities and ecosystem processes.
- How common is stage-specific overcompensatory density dependence and when is it important for communities?

  Although theory indicates a crucial role of stage-specific overcompensation for predator–prey interactions, its occurrence and importance are not well understood and probably depend on the natural histories of the species involved.
- How do the effects of cohort competition on community dynamics compare to interstage consumption (i.e. stage-structured cannibalism)?

  Most studies of interstage interactions have focused on cannibalism. The community dynamics that result from competition or facilitation between stages require further study.
- Are there systematic differences in the frequency of ontogenetic niche shifts across systems?

  Recent estimates indicate that ontogenetic niche shifts are more common than was previously thought. However, it is unclear whether the frequency and extent of ontogenetic niche shifts within species differ predictably across species, communities and ecosystems.

how does stage structure influence complex networks? Although understanding of the influence of stage structure is still limited, there is some evidence suggesting that ontogenetic niche shifts strongly influence the stability of complex networks. Recent analyses of empirical and model food webs indicate that ontogenetic shifts in resource use (Figure 1c) strongly reduce the structural stability (i.e. robustness) of complex ecological networks, and may even reverse the relationship between complexity and stability from positive to negative [18]. This pattern arises because species with several specialized stages appear to be generalists at the species level but, upon closer inspection, act as sequential specialists that are hypersensitive to resource loss. As a consequence, species that consume multiple resources typically have a higher extinction risk than is assumed in unstructured models, with this reducing network stability. This analysis, however, is restricted to qualitative networks, which do not include information on interaction strength. Stages within species often differ not only in their resource use, but also in their interaction strength. Given the importance of interaction strength for the stability of complex networks [77], accounting for such stage-specific differences probably has important implications for the dynamics of networks.

## Future directions

The progress synthesized in this review clearly demonstrates the importance of stage structure for community dynamics and opens several new and important avenues for further research (Box 4). The development of theory for community effects of stage structure has far outpaced empirical work. Armed with a solid theoretical foundation, there is now a need for experimental tests of model predictions and data-driven modifications of the theory. Most of the few empirical studies to date have elucidated particular mechanisms under laboratory conditions. Little is known about the importance of these mechanisms and their expected community-level effects in natural settings. Second, the general importance of stage structure for community structure and dynamics would be best assessed if future empirical work were conducted across a greater diversity of taxonomic groups, habitat types and interaction types than has been done thus far [e.g. aquatic systems (especially fish) and predator–prey interactions are particularly well represented in the existing literature]. For example, the scarcity of studies focusing on plants is surprising given the wealth of research on stage-structured demography of plants and plant–consumer interactions. Similarly, although this review has focused on antagonistic interactions, mutualistic interactions are also typically stage structured and often involve ontogenetic niche shifts (e.g. herbivory to pollination in many Lepidoptera [78,79] and facilitation to competition in plants [80] and marine invertebrates [81]); the community-level implications of these shifts are not well understood. Finally, future studies need to expand to move past simple, two- or three-species community modules to ask whether and how stage structure can influence the structure and functioning of complex food webs.

## Concluding remarks

Identifying the minimum level of resolution required for predicting population and community dynamics has been a persistent challenge in ecology. Our review of the effects of stage structure on consumer–resource communities indicates that explicit consideration of demographic heterogeneity 'inside the box' can lead to new understanding of community structure and dynamics, and highlights the ways in which unstructured approaches might lead us astray (Figure 2). Although the specifics of the underlying mechanisms might differ between systems, all of the mechanisms simply require that the ecology of an individual changes over ontogeny, which is arguably the case for most species. Models and experiments that explicitly consider stage structure are invariably more complex than their unstructured counterparts. However, given the ubiquity of stage structure in consumer–resource communities and the dramatic differences between unstructured and stage-structured approaches, we think that the potential gains in understanding warrant the additional effort.

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