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Individual interaction data are required in community ecology: a conceptual review of the predator–prey mass ratio and more

Abstract Community ecology is traditionally species-based and assumes that species comprise identical individuals. However, intraspecific variation is ubiquitous in nature because of ontogenetic growth and critical in food-we dynamics. To understand individual interaction-mediated food webs, researchers have recently focused on body size as the most fundamental biological aspect and assessed a parameter called the predator–prey mass ratio (PPMR). Herein, I review the conceptual development of the PPMR and suggest four major concerns regarding its measurement: (1) PPMR should be measured at the individual level because species-averaged values distort actual feeding relationships, (2) individual-level PPMR data on gape-unconstrained predators (e.g., terrestrial carnivores) are limited because previous studies have targeted gape-limited fish predators, (3) predators' prey size selectivity (preferred PPRM) is conceptually different from dietary prey size (realized PPMR) and should be distinguished by incorporating environmental prey abundance information, and (4) determinants of preferred PPMR, rather than those of realized PPMR, should be identified to describe size-dependent predation. Future studies are encouraged to explore not only predation but also other interaction types (e.g., competition, mutualism, and herbivory) at the individual level. However, this is not likely to occur while ecological communities are still considered to be interspecific interaction networks. To resolve this situation and more comprehensively understand biodiversity and ecosystem functioning, I suggest that community ecology requires a paradigm shift in the unit of interaction from species to individuals, similar to evolutionary biology, which revolutionized the unit of selection, because interactions occur between individuals.

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Introduction

Ecology, particularly community ecology, has traditionally been species-based. That is, researchers classify organisms according to species-specific representative traits, measure interaction strengths among species, and enumerate coexisting species or quantify their functional diversity (Begon et al. 2006; Verhoef and Morin 2010). An implicit assumption in this approach is that species comprise identical individuals with invariant traits or that trait variations within species are virtually negligible compared with those between species. However, intraspecific trait variations are common in nature and sometimes substantially exceed interspecific variations. This suggests that our current understanding of biodiversity and ecosystem functioning based on species-level community ecology is fundamentally flawed or at least incomplete (Bolnick et al. 2011; Violle et al. 2012; Hart et al. 2016).

To address this issue, some ecologists have recently emphasized body size as the most fundamental functional trait of an organism. The reason for this is twofold. First, many organisms are multicellular and exhibit ontogenetic growth, indicating that intraspecific size variation is ubiquitous. Second, and more importantly, body size is associated with other biological aspects, such as morphology, physiology, and behavior (LaBarbera 1989; Brown et al. 2004). Therefore, body size largely determines demographic performances (e.g., birth, death, and mobility) and ecological niches (e.g., diet and habitat) as well as interactions with other organisms (e.g., predation, competition, and mutualism) (Wilbur 1980; Werner and Gilliam 1984). Currently, there is a growing interest in how the ontogenetic growth of organisms mediates community structure and dynamics (Hildrew et al. 2007; Miller and Rudolf 2011; de Roos and Persson 2013; Nakazawa 2014, 2015a).

Herein, I review recent progress and problems regarding this ontogenetic perspective in community ecology. More specifically, I focus on a key parameter in this research field, the predator–prey mass ratio (PPMR). The PPMR measures the body mass ratio of interacting predators and prey. Body size can be linked with interaction strength, which allows us to describe food webs mediated by size-dependent predation (Brose 2010; Nakazawa et al. 2011). In this review, body size represents individual size, including the concept of age or developmental stage, rather than species-specific representative body size, because this review concerns the community consequences of ontogenetic growth. The main problem with the PPMR is that very few studies have appropriately quantified it. Thus, reliable theoretical predictions accompanied by empirically supported assumptions are not available for any food web patterns. The objective of this review is to address this problem by introducing recent empirical measurements of PPMR and stimulating further research efforts toward its solution.

Ontogenetic niche shift matters in community ecology

First, before beginning the review of PPMR studies, I remark that ontogenetic niche shifts critically affect community dynamics (see Miller and Rudolf 2011; de Roos and Persson 2013; Nakazawa 2014, 2015a for more details). Studies have predicted that an ontogenetic shift of a predator species between the juvenile and adult stages can generate alternative community states, thereby reducing community resilience and causing regime shifts under environmental changes (Schreiber and Rudolf 2008; Guill 2009; Nakazawa 2011a, b). The mechanism involves positive feedback caused by the apparent competition-like interactions between the resources of the juveniles and adults. Suppose that the resource of juveniles increases. This promotes maturation of the juveniles and negatively affects the resource of the adults, which in turn leads to a decrease in reproduction and a further increase in the resource of the juvenile. Thus, a positive feedback loop is created (see Schreiber and Rudolf 2008; Guill 2009; Nakazawa 2011a, b for details). This represents the simplest possible scenario (i.e., trophic module) for a stage-structured community. However, the concept applies to various community contexts, such as aquatic food webs, in which ontogenetic diet shifts of predatory fish from planktivore to benthivore couple energy flows in the surface and bottom waters (Nakazawa et al. 2010, Briones et al. 2012), plant–insect interactions, in which stage structures entangle herbivory and pollination networks (Altermatt and Pearse 2011; Ke and Nakazawa, unpublished data), and interface areas, in which metamorphosis of amphibians or aquatic insects connect aquatic and terrestrial ecosystems (Baxter et al. 2005; Nakazawa 2015b).

However, little is known about the community consequences of ontogenetic niche shifts because previous
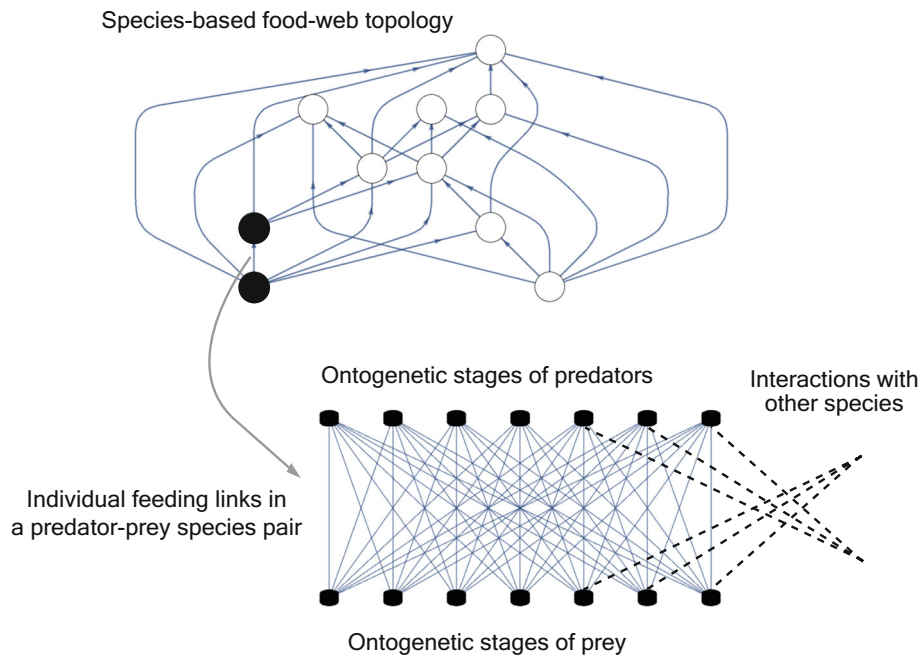

Fig. 1 Schematic example of a food web network based on the ontogenetic perspective. The *upper* network represents the topology of the conventional species-based view of interactions. *Arrows* represent interactions between species. The *lower* bipartite network represents individual feeding links in a predator–prey species pair, in which predator and prey individuals are arranged according to different ontogenetic stages. Some stages of individuals may interact with other species because of ontogenetic niche shifts (*dashed lines*)

community models have used the simple assumption that only a single species undergoes an ontogenetic niche shift only once at the timing of maturation (Schreiber and Rudolf 2008; Guill 2009; Nakazawa 2011a, b). However, the reality is more complex. Nearly all species, including plants (Barton and Koricheva 2010; Boege et al. 2011), exhibit ontogenetic niche shifts. Furthermore, ontogenetic niche shifts may occur more than once or continuously in an organism's lifespan, irrespective of maturation, due to increasing body mass (e.g., Nakazawa et al. 2010, Briones et al. 2012). In such situations, an ecological community can be considered a network of interactions among individuals rather than of species because each interspecific interaction is redefined as a network of individuals at different ontogenetic stages (Fig. 1). This community view is in sharp contrast

the PPMR or tested its fundamental assumptions. To illustrate this point, I present four practical considerations that must be addressed in empirical measurements of the PPMR: (1) definition dependence, (2) gape-unconstrained predation, (3) prey size preference, and (4) variability determinants.

Definition dependence of the predator–prey mass ratio

First, it is important to recognize that the PPMR can be defined at various biological scales depending on the manner in which the predator and prey body masses are measured (Nakazawa et al. 2011). Ideally, the PPMR should be measured using the individual body masses of the predator and prey as follows:

$$\text{Individual} - \text{link PPMR} = \frac{\text{Mass of an individual predator that consumed a prey individual}}{\text{Mass of the prey individual that was consumed by the predator individual}}$$

to the conventional view that species comprise identical individuals. How can we describe such a complex system (i.e., individual interaction-mediated food web) and understand its dynamics or environmental responses?

Predator–prey mass ratio as a tool for describing size-based food webs

A promising approach for describing individual interaction-mediated food webs is to analyze the PPMR in a focal system (Brose 2010; Nakazawa et al. 2011). This idea is reasonable because a predator cannot efficiently utilize excessively large prey because of physical constraints on feeding (e.g., gape limitation) and because a predator should not target excessively small prey because of their limited nutritional values (Brose 2010). In brief, interaction strength will be maximized at a moderate PPMR (Fig. 2). Based on this expectation, numerous studies have examined the predator–prey size relationship (Cohen et al. 1993, 2005; Brose et al. 2005, 2006a; Woodward and Warren 2007; Barnes et al. 2008, 2010; Owen-Smith and Mills 2008; Scharf et al. 2010; de Visser et al. 2011; Naisbit et al. 2011; Nakazawa et al. 2011; Riede et al. 2011; Lurgi et al. 2012; Reum and Hunsicker 2012; Klecka and Boukal 2013; Nakazawa et al. 2013; Tsai et al. 2016) and applied the PPMR to food web models (Andersen and Beyer 2006; Brose et al. 2006b; Otto et al. 2007; Blanchard et al. 2009, 2011; Hartvig et al. 2011; Thierry et al. 2011; Zhang et al. 2013; Guiet et al. 2016).

Nevertheless, according to my review of relevant literature, very few studies have appropriately quantified

This is called the individual-link PPMR and it is typically obtained using gut content analysis that can provide body size information for both predators and prey (Barnes et al. 2008, 2010; Scharf et al. 2010; Nakazawa et al. 2011; Reum and Hunsicker 2012; Tsai et al. 2016).

However, individual-link PPMR data are very limited because most previous studies have evaluated the PPMR at the scale of predator–prey species pairs using species-averaged body masses (Cohen et al. 1993; Brose et al. 2005, 2006a; Owen-Smith and Mills 2008; de Visser et al. 2011; Lurgi et al. 2012). This is called the species-averaged PPMR:
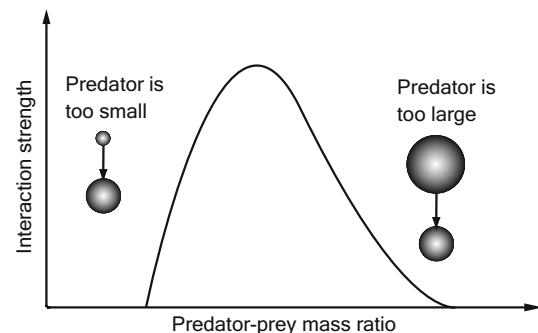

Fig. 2 Expected relationship between the predator–prey mass ratio and interaction strength. Interaction strength is low when the predator–prey mass ratio is excessively small or large and maximized when the ratio is at an intermediate level
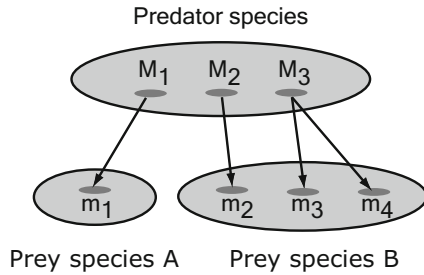
Predator species

Fig. 3 Definition dependence of the predator–prey mass ratio. Suppose a simple scenario in which three individuals of one predator species feed on four individuals of two prey species, as shown here. *Light* and *dark gray circles* indicate species and individual identities, respectively. *Arrows* represent individual feeding links. M_i and m_j denote individual body masses of predators and prey, respectively. For example, suppose that $m_1 = 1$, $m_2 = 2$, $m_3 = 3$, and $m_4 = 3$ for prey and $M_1 = 5$, $M_2 = 10$, and $M_3 = 15$ for predators. The individual-link predator–prey mass ratio (PPMR) is calculated as $M_i/m_j = 5$ for each feeding event. By contrast, the species-averaged PPMR is calculated as $\overline{M_i}/\overline{m_j} = 10$ and 3.75 for two interspecific interactions, respectively, where the *bars* denote the average body sizes. In this example, the mean value of species-averaged PPMRs is greater than that of individual-link PPMRs

Individual-link PPMR

$$\frac{M_1}{m_1}, \quad \frac{M_2}{m_2}, \quad \frac{M_3}{m_3}, \quad \frac{M_3}{m_4}$$

Species-averaged PPMR

$$\frac{(M_1 + M_2 + M_3)/3}{m_1}, \quad \frac{(M_1 + M_2 + M_3)/3}{(m_2 + m_3 + m_4)/3}$$

Species − averaged PPMR

$$= \frac{\text{Mean mass of predator individuals of a species}}{\text{Mean mass of the prey individuals of the predator species}}$$

This PPMR definition only requires descriptive information about species-based food web topology and independent information on species-averaged body masses. In brief, the species-averaged PPMR does not require time-consuming gut content analysis. Mathematically, these different definitions yield different values (Fig. 3). Previous studies have reported that the individual-link PPMR is larger than the species-averaged PPMR by approximately one order of magnitude in freshwater invertebrates (Woodward and Warren 2007) and marine fish predators (Nakazawa et al. 2011). However, this is not always the case (see Fig. 3 for an example of the opposite case). Nakazawa et al. (2013) reported that individual-link and species-averaged PPMRs were comparable for aquatic hemipteran bugs. Theoretically, whether species averaging underestimates or overestimates the PPMR depends on the elements of the data used, such as body masses and sample numbers of predator and prey individuals and species (Nakazawa et al. 2011). Although other definitions are also possible (not shown), the individual-link PPMR is considered to represent the most realistic definition (see Nakazawa et al. 2011 for details).

The definition problem raises another concern: what determines PPMR? In contrast to the original theoretical assumption, PPMRs may not be identical among predators. The individual-link PPMR typically varies with individual predator size (i.e., ontogenetic changes in PPMR) (Barnes et al. 2010; Nakazawa et al. 2011, 2013; Reum and Hunsicker 2012; Tsai et al. 2016). By contrast, species-averaged PPMR tends to be size-invariant (Nakazawa et al. 2011, 2013) but varies according to other factors, such as ecosystem type (e.g., aquatic versus terrestrial), taxonomic identity (e.g., vertebrate versus invertebrate), trophic level, and climatic conditions (Brose et al. 2006a; Naisbit et al. 2011; Riede et al. 2011; Lurgi et al. 2012). These patterns imply that species averaging masks the size-dependent variability of the PPMR, thereby generating a misleading picture of actual feeding relationships (Fig. 3; also see Nakazawa et al. 2011, 2013). Overall, the PPMR should ideally be measured at the individual level (Woodward and Warren 2007; Nakazawa et al. 2011, 2013) and great caution should be exercised when using species-averaged PPMR to parameterize food web models (Andersen and Beyer 2006; Brose et al. 2006b; Otto et al. 2007; Blanchard et al. 2009, 2011; Hartvig et al. 2011; Thierry et al. 2011; Zhang et al. 2013; Guiet et al. 2016).

Predator–prey mass ratio of gape-unconstrained predators

The available data sets on individual-link PPMR are highly biased toward aquatic predators such as fish (Barnes et al. 2008, 2010; Scharf et al. 2010; Nakazawa et al. 2011; Reum and Hunsicker 2012; Tsai et al. 2016). This is because fish predators are typically gape-limited and swallow smaller prey whole; thus, gut content analysis can be used to estimate the individual body masses of prey in predator guts. However, this is not feasible for gape-unconstrained predators (e.g., terrestrial carnivores) because they often attack relatively large prey by using hunting tools (e.g., fangs and claws), and prey body tissues are bitten off or sucked out. To assess the individual prey sizes for such predators, observing each hunting event or converting residual body tissues in predator guts to whole-prey body mass is necessary. According to the current literature, the individual-link PPMR for gape-unconstrained predators is not yet available, except for parasitoid wasps (Cohen et al. 2005) and aquatic hemipteran bugs (Nakazawa et al. 2013). This implies that our understanding of size-dependent predator–prey interactions is limited, particularly regarding terrestrial food webs.

Individual-link PPMR may change ontogenetically, irrespective of whether predators are gape-unconstrained or -limited. By monitoring hunting events and estimating the body masses of interacting predators and prey individuals, Nakazawa et al. (2013) reported that

the individual-link PPMR of gape-unconstrained hemipteran bugs varied according to individual predator size. Notably, this finding (i.e., size-dependent PPMR) is similar to that reported for gape-limited fish predators (Barnes et al. 2010; Nakazawa et al. 2011; Reum and Hunsicker 2012; Tsai et al. 2016). Thus, it is suggested that the original theoretical assumption of size-invariant PPMR is oversimplified. Irrespective of the feeding mode of predators (e.g., gape-limited or -unconstrained) or ecosystem type (e.g., aquatic or terrestrial), size-dependently parameterizing PPMR may be necessary. However, this finding contrasts with the initial objective of simplifying the complex structure of individual-based food webs (Fig. 1).

Realized versus preferred predator–prey mass ratio

Do we actually require such complex models assuming size-dependent PPMR? Although there are limited data to answer this question, available data suggest not (Tsai et al. 2016). This is because the aforementioned inconsistency between theoretical assumption and empirical measurement of PPMR arises because of conceptual confusion. The PPMR was originally invented to represent a preference for relative prey size. Nevertheless, PPMR has been measured using only dietary data (i.e., the realized PPMR) such as gut content analysis or observations of hunting, as previously mentioned. The relative size of prey in the diet is determined not only by the predator's prey size selection (i.e. the preferred PPMR) but also by the prey size composition in the environment (Fig. 4). For example, the realized PPMR increases not only when a predator selectively feeds on small prey but also when small prey are abundant in the environment. Thus, the assessment of the realized
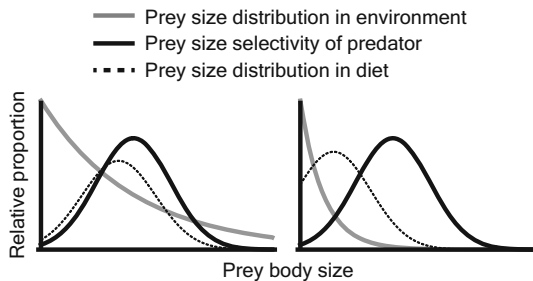
PPMR does not automatically yield the preferred PPMR, and the preferred PPMR may be size-invariant even when the realized PPMR depends on predator body size.

To test this hypothesis, Tsai et al. (2016) reanalyzed long-term dietary data for an omnivorous predatory fish species collected from a lake ecosystem over four decades (Briones et al. 2012) by incorporating environmental abundance data for its major prey, zooplankton and zoobenthos (Ishikawa et al. 2004; Hsieh et al. 2011). Specifically, they compared prey size compositions in predator guts and the environment (i.e., the realized versus the environmental PPMR) to detect deviations between these elements as effects of the preferred PPMR. Notably, their results revealed that preferred PPMR was size-invariant if predators were classified into plankton and benthos feeders, whereas realized PPMR varied depending on the individual predator size irrespective of the feeding mode (Tsai et al. 2016). This is the first evidence of size-invariant prey size preference. Furthermore, in contrast to the previous arguments based on realized PPMR (discussed above), their finding supports the original assumption of a constant PPMR in food web models.

Variability and determinants of the preferred predator–prey mass ratio

Previous studies have argued about what determines the variability of the realized PPMR (refer to "Definition dependence of the predator–prey mass ratio"), but all such arguments are invalid for characterizing prey size preference (refer to "Realized versus preferred predator–prey mass ratio"). We can, however, approach determinants of prey size preference by distinguishing between realized and preferred PPMRs (Fig. 4) using environmental prey abundance information. In this sense, research on the PPMR has just begun and future studies will need to reanalyze its determinants using environmental prey abundance information. In a pioneering study, Tsai et al. (2016) showed that preferred PPMR was not significantly affected by predator body size, but varied according to major prey type, such as zooplankton versus zoobenthos, likely because of different foraging modes. Because their study focused on only a single predator species, it will be crucial to test the robustness of their findings by analyzing other predator species. It may turn out that preferred PPMR tends to be size-invariant according to the original theoretical assumptions, whereas prey size preference may depend on the taxonomic identity of predators if they exploit morphologically or behaviorally distinct prey types or have qualitatively different foraging modes. We expect that gape-unconstrained predators will exhibit different patterns of the preferred PPMR from that of the gape-limited predators (refer to "Predator–prey mass ratio of gape-unconstrained predators"). Testing this hypothesis will be essential for understanding differences between

Fig. 4 Conceptual difference between the relative prey size distributions in the environment and diet. Theoretically, the product of the relative prey size distribution in the environment (*gray lines*) and the prey size selectivity of a predator (*solid lines*) determine the relative prey size distribution in the diet (*dashed lines*). Thus, $f(x) \times p(x) = g(x)$, where $f(x)$ is the environmental prey size distribution, $p(x)$ is the predator's prey size selectivity, and $g(x)$ is the dietary prey size distribution. All these factors depend on prey body size x. When the environmental prey size distribution is skewed and smaller prey become relatively dominant, the dietary prey size distribution shifts toward a smaller size, deviating from the preferred prey size (compare the left and right panels). Here, the absolute scale along the y axis is not relevant, and each curve is rescaled for visual clarity

aquatic and terrestrial food webs (Shurin et al. 2006). Future studies are encouraged to identify determinants of preferred PPMRs for varied organisms and systems.

Conclusions and future perspectives

In this review, I have briefly outlined how the concept of the PPMR has been developed and refined. The ultimate goal of my arguments is to establish effective ways of describing food webs mediated by individual interactions (i.e., ontogenetic niche shifts). Herein, I have highlighted the following points:

1. The PPMR should be measured at the individual level because species-averaged values distort real feeding relationships.
2. Individual-level PPMR data on gape-unconstrained predators (e.g., terrestrial carnivores) are limited because previous studies have targeted gape-limited fish predators.
3. The preferred PPRM is conceptually different from the realized PPMR and should be distinguished by using environmental prey abundance information.
4. Determinants of preferred PPMR, rather than those of realized PPMR, should be identified to describe size-dependent predation.

Overall, the study of PPMR is still at an early stage of development and application. Further research efforts are needed to collect individual interaction data in addition to environmental prey abundance information on various systems.

Below I offer additional future research directions to more firmly establish the ontogenetic perspective in community ecology (Fig. 1). Most importantly, although previous studies and the present review have exclusively focused on prey–predator interactions (i.e., trophic interactions between animals), other types of biological interactions, such as competition (e.g., nutrients and space), mutualism (e.g., pollination and seed dispersal), and herbivory (i.e., trophic interactions between plants and animals) should be considered. For these interaction types, quantifying the body mass ratio of interacting individuals may not always be easy, especially when interaction strengths (preferences) are determined by ages or developmental stages rather than body masses. Nevertheless, it is still possible and would be useful to link age (or stage) relationships to interaction strength, as with the approach using PPMR. Terrestrial plants are commonly involved in the above interactions types. Therefore, I suggest that research on plant–plant or plant–animal interactions could be ontogenetically explicit as model systems. For plant–plant interactions, point pattern analysis has been recently applied to infer mechanisms underlying spatial vegetation structure at the individual level (Wiegand and Moloney 2014). Extending this technique to include

developmental stage information (e.g., diameter at breast height and life-history stage) is useful for determining the extent to which plant–plant interactions are size-dependent (Tsai et al. 2015). Plant–animal interactions also change ontogenetically. For example, defense strategies (e.g., chemical and physical) and herbivore type (e.g., insects and mammals) vary during ontogenetic growth of plants (Barton and Koricheva 2010; Boege et al. 2011). Furthermore, many plants require animals for pollination or seed dispersal at the reproductive stage, suggesting that plant–animal interactions change not only quantitatively but also qualitatively from antagonism to mutualism. Similarly, plants have stage-specific interactions with parasitic and mutualistic soil microbes (Ke et al. 2015). Note also that the herbivorous larvae of some insects (e.g., Lepidoptera) become pollinators at the adult stage (Altermatt and Pearse 2011; Ke and Nakazawa, unpublished data). Such information on ontogenetic changes in interaction patterns remains scattered and should be compiled for various systems to promote the ontogenetic perspective in community ecology.

The present ontogenetic perspective has broad applications not only in community ecology but also in other basic and applied ecologies. For example, incorporating the ontogenetic perspective can provide novel insights into physiological (Nakazawa 2011c) and evolutionary ecology (Chou et al. 2016) by highlighting functional traits (e.g., growth ratio and duration) or processes (e.g., maturation and reproduction) that have otherwise been ignored. Recently, pioneering studies have experimentally or theoretically reported that ontogenetic functional diversity can influence ecosystem functioning more strongly than interspecific functional diversity (Rudolf and Rasmussen 2013a, b; Reichstein et al. 2015), suggesting that the ontogenetic perspective is critical in ecosystem ecology. Furthermore, community ecology plays a crucial role in various applications that concern ecosystem management, such as agriculture (Gliessman 1990), fishery (Mangel and Levins 2005), epidemiology (Nakazawa et al. 2012; Johnson et al. 2015), and biodiversity conservation under global climate change (Nakazawa and Doi 2012; Post 2013). However, these areas have not yet been fully considered from the ontogenetic perspective, except for fisheries management (Hsieh et al. 2010). Future studies should investigate the ecosystem consequences of ontogenetic processes, which will contribute to better ecosystem management.

I conclude this review with more philosophical and challenging questions for future ecologists. A major problem of current interest is the limited availability of individual interaction data. I consider that this lack of data ultimately stems from our stereotype that an ecological community must be considered as a network of interspecific interactions. What is the rationale for the community view when interactions occur between individuals? Such fundamental inconsistency in assumption could result in erroneous conclusions. The species-based

community theory has faced persistent problems, such as the paradoxes of enrichment (Rosenzweig 1971) and the complexity–stability debate (May 1972). There is even debate on whether general patterns exist in community ecology (Lawton 1999; Roughgarden 2009). I do not contend that the ontogenetic perspective can be used to solve all ecological problems. In evolutionary biology, however, the unit of selection has already switched from species to individuals or genes (Williams 1966; Brandon and Burian 1984; Sober and Wilson 1994). Considering that ontogenetic growth and niche shift are ubiquitous and critical in ecological dynamics, I envision that community ecology also requires a similar paradigm shift in the future. Collecting individual-level interaction data requires enomous time and effort. However, such efforts would be warranted from the viewpoint of the long-term development of ecology. I pose the following questions: (1) Why must community ecology be species-based? (2) Do we require a paradigm shift in the unit of biological interaction? (3) If so, how could such a shift be achieved? If this paradigm shift occurred, individual interaction data would be accumulated more widely, which has the intriguing potential to revolutionize our understanding of biodiversity and ecosystem functioning.

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