Hindawi Publishing Corporation
Psyche
Volume 2016, Article ID 4751280, 15 pages
http://dx.doi.org/10.1155/2016/4751280

Review Article

Reproductive Interference and Niche Partitioning in Aphidophagous Insects

Suzuki Noriyuki[1,2] and Naoya Osawa[3]

[1] *Department of Environmental Science, Policy, and Management, University of California, Berkeley, 201 Wellman Hall, Berkeley, CA 94720, USA*
[2] *Center for Geo-Environmental Science, Rissho University, Tokyo, Japan*
[3] *Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Kyoto, Japan*

Correspondence should be addressed to Suzuki Noriyuki; fvgnoriyuki@gmail.com

Received 6 September 2016; Revised 11 November 2016; Accepted 14 November 2016

Academic Editor: G. Wilson Fernandes

Copyright © 2016 S. Noriyuki and N. Osawa. This is an open access article distributed under the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

The range and quality of prey species differ greatly among closely related species of predators. However, the factors responsible for this diversified niche utilization are unclear. This is because the predation and resource competition do not always prevent species coexistence. In this paper, we present evidence in support of reproductive interference as a driver of niche partitioning, focusing on aphidophagous insect. Firstly, we present closely related generalist and specialist species pairs in aphidophagous lacewings to compare the reproductive interference hypothesis with two other hypotheses that have been proposed to explain niche partitioning in lacewings and sympatric speciation through host race formation and sexual selection. Secondly, we present a case study that shows how reproductive interference can drive niche partitioning in sibling ladybird species. Thirdly, we show that many ladybird genera include species inhabiting the same region but having different food and habitat preferences, raising the possibility that reproductive interference might occur in these groups. Finally, we show that intraguild predation cannot always explain the niche partitioning in aphidophagous insects including hoverflies and parasitoids. On the basis of the evidence presented, we urge that future studies investigating predator communities should take account of the role of reproductive interference.

1. Introduction

In nature, closely related species often occupy niches that diverge with respect to both type and breadth, and such niche divergence is observed not only in herbivores but also in many predators [1–4]. A frequently proposed explanation of niche differentiation is the trade-off hypothesis, according to which adaptations of a species that allow it to exploit one resource decrease its fitness on other resources, and this trade-off leads to different niche utilization by different species [5]. In predators, the main driving force of food specialization may be morphological and behavioral adaptations that enhance a species' prey capture performance against one prey species but simultaneously reduce it against another [6]. However, the trade-off hypothesis is inadequate to explain differences in food choice among some closely related predator species. In particular, some species that possess traits that make them highly efficient foragers specialize in a highly defended prey species, even though they could potentially utilize a wide variety of food items, including less well-defended prey (e.g., [7–9]). For example, large-mouthed marine cottid fish species have been shown in a laboratory setting to have a high feeding performance on both slow-moving prey (e.g., crabs, isopods, and gastropods) and more mobile, and thus more elusive, prey (e.g., fishes and shrimp), but in nature they feed predominantly on elusive prey [10]. Such examples raise the possibility that negative interspecific interaction, rather than a species' own resource-use traits, can restrict its host range in nature.

Examples of negative interspecific interactions that might promote niche partitioning among predators include intraguild predation and parasitism, where species competing for a shared resource also prey on or parasitize one another [11, 12]. Predation by predators on predators has been widely reported under both laboratory and natural conditions [13, 14]. Moreover, multiple species involved in intraguild predation have been observed to persist in the same locality in field studies (see the "Aphidophagous Guilds"). Therefore, the idea that intraguild predation, which combines predation with resource competition, is sufficient to drive niche partitioning in predators is still controversial. Thus, we would propose that it should be fruitful to consider alternative interspecific interactions that might explain the divergent food choices of carnivorous species.

One reported type of interspecific interaction between closely related predator species is heterospecific mating interactions (e.g., [15–17]). For example, in damselflies *(Nehalennia)*, males frequently attempt to form a tandem pair with a heterospecific female, a behavior that may waste the time and energy of both species even if hybridization does not occur [18]. Moreover, in a molecular study, Fitzpatrick et al. [19] detected genetic introgression between specialist and generalist garter snakes, which is indirect evidence that interspecific copulation occurs in nature. In fact, such reproductive interference is a general mechanism that is applicable to various species assemblages with overlapping mating signals, regardless of trophic level, if at least one species engages in sexual reproduction [20, 21]. However, we think that the potential effect of reproductive interference on the spatial distribution and resource use by predator species has been underestimated, possibly because researchers have focused on mechanisms that are specific to predator-prey systems, such as intraguild predation and strong resource competition [22]. Therefore, we assert that reproductive interference should be given greater consideration in the search for a mechanism to explain ecological specialization in predators.

In this paper, we focus on aphidophagous insects. First, we describe aphidophagous lacewing genera that include generalist and specialist predatory species pairs. In lacewings, it has been hypothesized that sympatric speciation has occurred through host race formation or sexual selection. We argue instead that the observed niche partitioning between closely related species may actually be a consequence of niche diversification through reproductive interference after allopatric speciation. Next, we present as a case study of niche partitioning by reproductive interference our own research on two species of ladybirds *(Harmonia)* in Japan. Then, we consider whether reproductive interference-driven niche partitioning can explain niche partitioning in other predatory ladybirds. Finally, we describe some aphidophagous insect communities in which intraguild predation is known to occur and discuss reproductive interference as a possible mechanism that can drive niche partitioning of intraguild predators. We hope that the arguments made in this paper will encourage researchers to pay more attention to interspecific mating behaviors and their ecological consequences in predator communities.

2. Specialist and Generalist Lacewings in North America

In this section we first examine the possible role of reproductive interference in the ecology of two sibling species (i.e., reproductively isolated species that are nearly identical in their appearance [25]) of the lacewings (Neuroptera: Chrysopidae) in North America, one in genus *Chrysopa* and another in *Chrysoperla*. The *Chrysopa* pair includes a strict specialist that uses a strange woolly aphid, and the *Chrysoperla* pair includes a conifer specialist. Then we compare the reproductive interference model with models of sympatric speciation based on host race formation and sexual selection, which have been considered the main drivers of genetic and habitat diversification in sympatric lacewings.

2.1. Chrysopa and Chrysoperla Species Complexes. *Chrysopa quadripunctata* is a generalist predator that preys upon a wide variety of aphids and other soft-bodied arthropods that live on various plant species, including apple, elm, goldenrod, hickory, maple, oak, and rose. In contrast, *Chrysopa slossonae* is a specialist predator that exclusively utilizes the woolly alder aphid, *Prociphilus tessellatus* [31]. Interestingly, the woolly alder aphid covers its body with secreted wax, which it uses to attract the ants that protect the aphid colonies from predators [31]. The wax may also serve as a physical defense against attacking predators [32]. However, *C. slossonae* larvae exhibit a sophisticated behavior in which they scrape the wax from their prey and attach it to their own back, thus preventing their detection by the attending ants [31]. In addition to this camouflage strategy, the specialized morphology (long legs and a large mandible) of *C. slossonae* larvae may enable them to consume the woolly alder aphid efficiently [33].

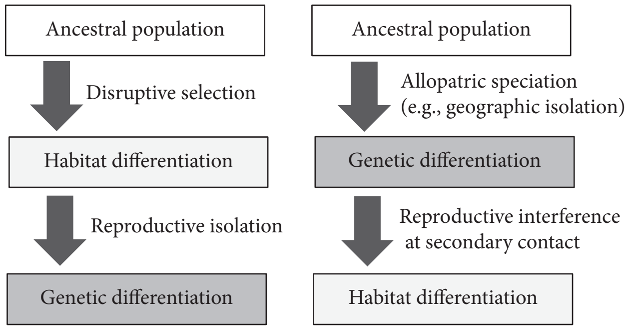
We argue that reproductive interference by *C. quadripunctata* may be responsible for the restricted food range of *C. slossonae*, for the following reasons. First, *C. slossonae* larvae can develop on less elusive prey that they do not utilize in nature, such as *Myzus persicae* and *A. pisum* [7, 34]. These observations are evidence that the fundamental niche of *C. slossonae* is wider than its realized niche. Moreover, interspecific copulation and hybridization occur between *C. slossonae* and *C. quadripunctata*, at least under laboratory conditions [34]. Although interspecific pairs of *C. slossonae* and *C. quadripunctata* can produce viable hybrids, the ecological traits of such hybrids show the intermediate values between their parent species [34]. This indicates that hybridization may hamper the local adaptation to each habitat. Therefore, it is possible that *C. slossonae* is forced to specialize on a highly defended prey to avoid heterospecific mating interactions with *C. quadripunctata*, which utilizes various preferred prey species in nature.

Chrysoperla carnea is a habitat generalist that lives in fields and meadows during the summer and migrates to deciduous trees in autumn. In contrast, its sibling species, *Chrysoperla downesi*, is a habitat specialist, living all year only in coniferous trees, in the region of eastern North America where the two species are sympatric [38]. It can be inferred that *C. downesi* specializes on conifer-associated prey items, but the information about the variety and quality of prey utilized by these species is still scarce. Each species, however, exhibits phenotypic traits that suit it to its preferred habitat. First, both species display cryptic adult body coloration that is specific to their habitats: *C. carnea* is bright green in spring and summer and reddish brown in autumn and winter, whereas *C. downesi* is dark green all year [39]. Second, each species has life-history traits, such as the critical day length for diapause induction (e.g., [40]), that suit it to its voltinism. *Chrysoperla carnea* can utilize a variety of food sources depending on the season and produces several generations each year, whereas *C. downesi* is restricted to a single generation in the spring, probably because the availability of their prey in coniferous trees is more seasonal. As in the *Chrysopa* species complex, hybridization can occur between *C. carnea* and *C. downesi*, at least under laboratory conditions [39], which suggests that reproductive interference might occur in nature.

At present, the available laboratory findings on interspecific mating behavior are insufficient for the role of reproductive interference in these *Chrysopa* and *Chrysoperla* species to be evaluated. The hybrids were experimentally produced to clarify the existence of postmating reproductive isolation [34, 39] and to examine the genetic basis for the phenotypic traits [39, 40]. However, all possible behavioral mechanisms that can reduce adult reproductive success should be considered in investigations of the population dynamics of these two species pairs. For example, interspecific sexual harassment prior to interspecific copulation can reduce a female's oviposition rate, longevity [41], and mating success [42], which might have population dynamics consequences and lead to subsequent niche separation. Thus, future studies of these sibling lacewing species should not only examine hybrid production but also quantify lifetime female reproductive success to evaluate the possibility that reproductive interference has driven the niche separation.

2.2. Sympatric Speciation through Host Race Formation. The difference in niche width between sympatric lacewings has been attributed to sympatric speciation [43, 44]. Sympatric speciation occurs when ecological adaptations to a different host (habitat) also produce nonrandom mating in a conspecific population, which eventually leads to a phenotypically and genetically divergent subpopulation, or species, even without geographical isolation [45]. In lacewings, courtship and copulation generally take place on plants that also serve as the feeding sites for both the adults and their offspring [46], indicating that adaptation and fidelity to a different habitat by each species may contribute to the development of reproductive isolation.

Tauber et al. [44] have argued that the comparative evidence from this *Chrysopa* species pair demonstrates for the first time a sympatric speciation mechanism in predatory insects. They proposed that a generalist ancestor of *C. slossonae* adopted a specialized foraging behavior and morphology as well as cryptic adult coloration that were well suited to a specific habitat. At the same time, a seasonal reproductive cycle, different from that of the ancestor, became established in the specialized subpopulation. This subpopulation then became reproductively isolated, both spatially and temporally, from the original population, which eventually led to its becoming a new specialist species by sympatric speciation.



(a) Sympatric speciation by habitat specialization

(b) Character displacement by reproductive interference

Figure 1: Two models of ecological specialization and niche differentiation in sibling lacewing species. (a) Sympatric speciation model. Disruptive selection within an ancestral population (i.e., ecological adaptation to different habitats) drives reproductive isolation, which leads to genetic differentiation and, subsequently, complete speciation. (b) Reproductive interference model. Reproductive interference drives habitat differentiation between the two species when secondary contact occurs after allopatric speciation.

Here we compare the two evolutionary scenarios, sympatric speciation and ecological specialization via reproductive interference, that have been proposed to explain the current niche partitioning between sibling lacewing species. The assumed order of ecological adaptation and genetic divergence differs between these two models [47] (Figure 1). In the sympatric speciation model, habitat differentiation is the primary impetus of genetic divergence in an originally uniform population. In this model, therefore, reproductive isolation is a by-product of adaptation to a particular habitat [48] (Figure 1(a)). In contrast, in the ecological specialization through reproductive interference model, genetic divergence (speciation) occurs allopatrically and reproductive interference promotes habitat differentiation when the two already distinct species come into secondary contact [49, 50]. In the reproductive interference mechanism of the second model, therefore, genetic incompatibility between the species is the cause of niche diversification (Figure 1(b)). Thus, the two models predict similar ecological consequences, namely, utilization of different habitats by two genetically close species, which prevents interspecific sexual interactions [47]. Accordingly, it is difficult to judge which model is applicable to a particular study system by examining current phenotypic traits and fitness.

The model of sympatric speciation in *Chrysopa* and *Chrysoperla* lacewings has some as yet unresolved problems. Most importantly, the generalist predator has been observed to visit the habitat on which its sibling species specializes, even though that habitat is less suitable for the generalist species. For example, *C. quadripunctata* is sometimes found on alder trees, where *C. slossonae* preys on the woolly alder aphid [34]. In addition, *C. carnea* visits not only meadows and deciduous trees but also coniferous trees, where *C. downesi* is found year-round [39]. This flexible behavior on the part of generalist predators may allow them to add a less suitable prey to their menu when the availability of more suitable prey is limited for some reason (e.g., [51]). Moreover, Henry [38] pointed out that the breeding periods of the sibling lacewing species greatly overlap, even though C. A. Tauber and M. J. Tauber [39] considered the seasonal mismatch to be an important mechanism of temporal reproductive isolation. Therefore, it is possible that observed niche overlap in space and time might be insufficient for sympatric genetic divergence to have occurred in the *Chrysopa* and *Chrysoperla* systems. Nevertheless, because genetic divergence sometimes occurs despite copulation and gene flow between taxa [52–54], the apparent incomplete habitat isolation does not rule out sympatric speciation in these lacewings. At this time, therefore, it is not possible to rule out any particular view of speciation in the lacewing system.

2.3. Speciation through Sexual Selection. Henry [38] proposed that divergence in the courtship song, rather than habitat specialization, might be a primary driver of speciation in *Chrysoperla* lacewing species, whether allopatric or sympatric. In *Chrysoperla*, males produce substrate-transmitted calls on plants by vibrating their abdomen, and females respond to a potential partner by reciprocal signaling according to their own mating preference [55]. Henry [38] proposed that, based on the diversified and complex songs among close relatives, differentiation of courtship signals among populations should create ethological barriers to hybridization, thus accelerating the rate at which complete speciation can be achieved.

However, there is at least one problem with speciation through sexual selection. *Chrysoperla* females sometimes respond to heterospecific mating calls [55], which indicates that negative interspecific mating interactions can occur. In fact, under laboratory conditions copulation and hybridization can occur among populations (species) having different courtship songs [39]. These findings suggest that an ethological barrier alone might not ensure premating reproductive isolation.

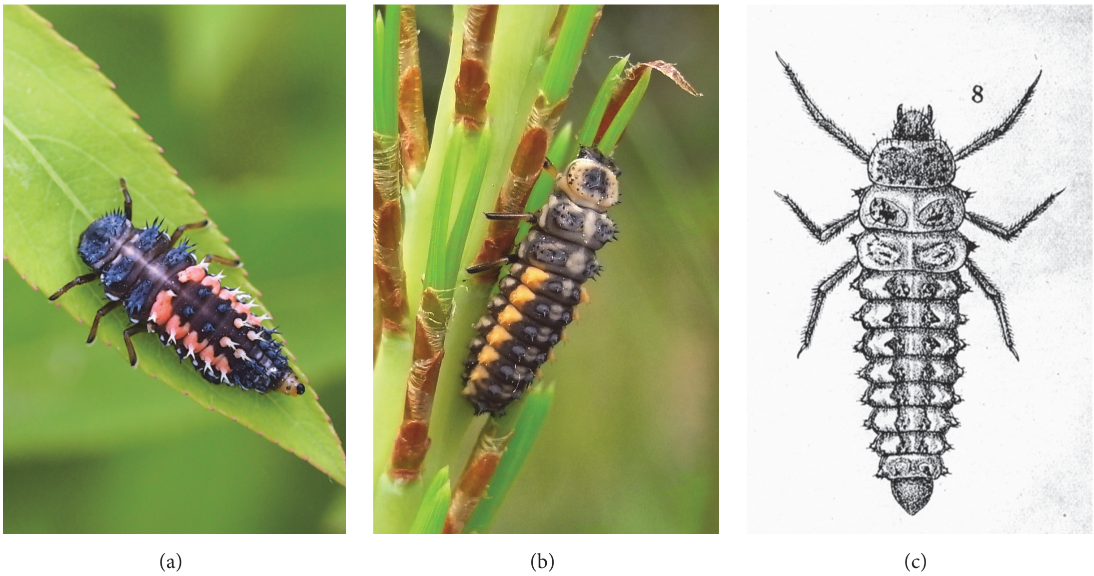
This weak point of the speciation through sexual selection model (i.e., inevitable heterospecific mating interactions), however, supports the reproductive interference model. In general, the maintenance of incomplete species recognition abilities can be interpreted as a consequence of adaptive decision-making in reproductive animals. When the signals of high-quality conspecifics resemble those of heterospecifics, a trade-off is likely to exist between species recognition and mate-quality recognition within a species [56]. In this situation, strict species discrimination skill is unlikely to be maintained because individuals may also lose opportunities for acquiring high-quality conspecific mates. As a result, promiscuous mating occurs between the species. By this logic, reproductive interference is likely to be common in sibling species (because their mating signals are likely to be similar), and the reproductive interference might drive niche partitioning.

3. A Case Study in *Harmonia*

3.1. A Brief History of Studies of Harmonia Sibling Species. The multicolored Asian ladybird *Harmonia axyridis* is a common aphidophagous predator originally distributed in Russia, China, the Korean Peninsula, and Japan [24]. Because of its extreme polymorphism with regard to elytral color, *H. axyridis* has been extensively used for genetic studies. Theodosius Dobzhansky famously discovered geographic variation in the frequency of elytral color morphs across Siberia and East Asia [57]. Subsequently, extensive surveys established that elytral color morph frequencies change along a geographic (latitudinal) cline in Japan, where red (nonmelanistic) morphs at higher latitudes are gradually displaced by black (melanistic) morphs as latitude decreases [58]. Then, Hosino, who worked at an agricultural high school in Sanage, central Japan, discovered that elytral color morph frequencies were slightly different between *Harmonia* ladybirds collected from Japanese red pine *(Pinus densiflora)* and those collected from agricultural crops such as wheat, pear, and peach [59]. In addition, he reported that a ridge at the tip of the elytron, which is a genetic character exhibited by approximately 40% of *H. axyridis* individuals in the Sanage population, was seldom observed in individuals collected from pine trees [59]. For a few decades, Japanese entomologists were unable to account for these strange patterns.

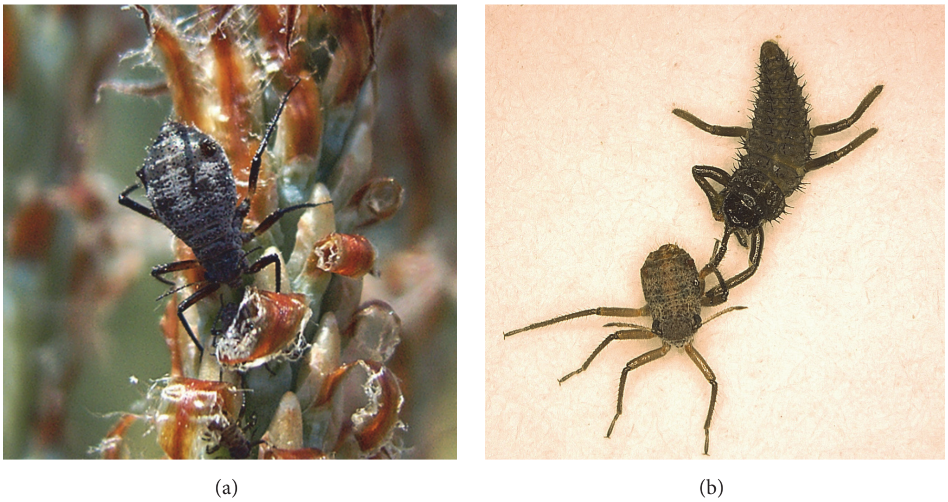
Eventually, Hiroyuki Sasaji demonstrated the existence of a cryptic *Harmonia* species. He did so by experimentally demonstrating that a clear postmating reproductive barrier existed between *H. axyridis* individuals and those found on pine trees, even though they were observed to copulate together and produce eggs [60]. He also showed that larval coloration was distinct between these groups of individuals [61] (Figure 2), even though the adults were difficult to distinguish by their external and genital morphology [60], and, furthermore, he showed that the characteristic ridge at the tip of the elytra of *H. axyridis* adults never emerged in the pine-associated individuals [60]. On the basis of these findings, he concluded that the pine-associated individuals belonged to a cryptic species that could be clearly distinguished from *H. axyridis* by its postreproductive isolation and some phenotypic traits.

However, when Sasaji proposed denominating the new, pine-associated cryptic species, he discovered that Takizawa [62], at the dawn of insect taxonomy in Japan, had already described a species of ladybird collected from a pine tree and had named it *Ptychanatis yedoensis* (*Ptychanatis* is a currently unused synonym for genus *Harmonia*). Takizawa's illustration of a larva of his new species (Figure 2(c)) clearly shows the larval characteristics of the cryptic species "discovered" by Sasaji. Sasaji [63], therefore, identified the cryptic species as *Harmonia yedoensis* Takizawa. In addition, deeply moved by Takizawa's insight, Sasaji proposed *Kurisaki-tento* as the Japanese name of this species, because Takizawa had adopted



(a) (b) (c)

Figure 2: (a) A final instar larva of *H. axyridis* on a *Spiraea thunbergii* leaf. (b) A final instar larva of *H. yedoensis* on Japanese red pine, *Pinus densiflora*. (c) Illustration of a final instar larva of *H. yedoensis* by Kurisaki [23].



(a) (b)

Figure 3: (a) A giant pine aphid, *Cinara pini*, on Japanese red pine, *Pinus densiflora*. (b) *Harmonia yedoensis* hatchling capturing a *C. pini* individual, observed in a laboratory experiment. Because *C. pini* has long legs and is highly mobile, *H. yedoensis* larvae are often unsuccessful in their attempts to capture this aphid.

the name "Kurisaki" when he became a Buddhist priest, and *tento* is the Japanese word for ladybird.

3.2. Host Specialization in H. yedoensis. The existence of these two species, *H. yedoensis* and *H. axyridis*, living in close proximity raises some questions; namely, what determines their habitat ranges? And how did two such phylogenetically close species with such a close morphological resemblance, at least in adults, come to occupy dramatically different niches? *Harmonia axyridis* is a truly generalist predator found in many different habitats, including scrub, orchards, grasslands, and coniferous and deciduous woodlands (e.g., [51]). In contrast, *H. yedoensis* is a specialist in central Japan that breeds exclusively on pine trees, where its larvae are regarded to prey mainly on the giant pine aphid *(Cinara pini)* [24] (Figure 3(a)). Because aphid colonies are spatially heterogeneous and temporally variable in terms of both quality and quantity, a generalist strategy that allows the ladybird to utilize multiple food patches has obvious advantages for maximizing lifetime fitness [51], as it does for other generalist insect species (e.g., [64–66]). Therefore, how to explain host specialization, a strategy that appears to forego potentially available resources, has been an interesting problem in ecology and evolutionary biology.

It is clear from field surveys that *H. yedoensis* is much less abundant than *H. axyridis*. One result of this situation is that much more effort is required to collect enough *H. yedoensis* individuals to carry out research projects, compared with that required for *H. axyridis*. The rarity of *H. yedoensis* might be at least partly due to the low abundance of its prey item on pine trees. Although the yellow egg batches of *H. yedoensis* are easy to locate on dead or live pine tree needles, it is hard to locate nearby colonies of the giant pine aphid, which are usually very small (S. Noriyuki personal observation), unlike those of other aphid species, which tend to congregate on young shoots of their host plants. Syunsuke Shimamoto, a junior high school student studying the ecology of *H. yedoensis*, once remarked to one of the authors (S. Noriyuki), "I wonder why *H. yedoensis* larvae stay where there is so little food to eat, while *H. axyridis* larvae are on plants with lots of aphids." We, too, ask this simple question.

Not only are giant pine aphids rare, they are also so mobile that ladybirds seem to have difficulty capturing them. In contrast to most arboreal aphids, which walk very slowly at best, the giant pine aphid has long legs and can walk fast (Figure 3(b)). We therefore experimentally evaluated the prey capture performance of *H. yedoensis* and *H. axyridis* hatchlings against the giant pine aphid and other aphid species [9]. As predicted, it was hard for *H. axyridis* hatchlings to capture the giant pine aphids. Interestingly, however, although *H. yedoensis* apparently specializes on the giant pine aphid, this species is not the easiest prey for *H. yedoensis* hatchlings to catch. Rather, we found that *H. yedoensis* hatchlings could capture other aphid species more easily, even though they never encounter them or prey upon them in nature. These results led us to hypothesize that *H. yedoensis* mothers deliberately choose a host that is less suitable for the prey capture activities of their offspring even though other suitable hosts are available in the region.

Harmonia yedoensis mothers help their offspring cope with their elusive aphid prey by investing more maternal resources in each hatchling. In aphidophagous ladybirds, the hatch rate of an egg batch is often less than 100% and the newly hatched larvae consume the unhatched sibling eggs. These unhatched eggs are not just an unavoidable developmental side effect; they are an adaptive maternal strategy known as trophic egg provisioning, because ladybird mothers are able to control the proportion of unhatched eggs in a clutch according to food availability [67]. In fact, trophic egg provisioning is more intense in *H. yedoensis* than in *H. axyridis* [26, 28]. Moreover, artificial manipulation of the trophic egg number provided to each hatchling has revealed that trophic egg consumption enhances the prey capture performance of *H. yedoensis* hatchlings against the giant pine aphid [9]. In addition, *H. yedoensis* eggs are significantly larger than *H. axyridis* eggs [26, 28]. Consequently, the amount of maternal resource invested per offspring is much higher in *H. yedoensis* than in *H. axyridis*. Importantly, however, the number of offspring that a mother can produce in her lifetime is lower in *H. yedoensis* than in *H. axyridis*, because of the trade-off between offspring size and number in the similar-sized species [26]. Therefore, *H. yedoensis* mothers apparently sacrifice reproductive success in order to supply more resources to each of her larvae, which are obligated to prey on the elusive aphid.

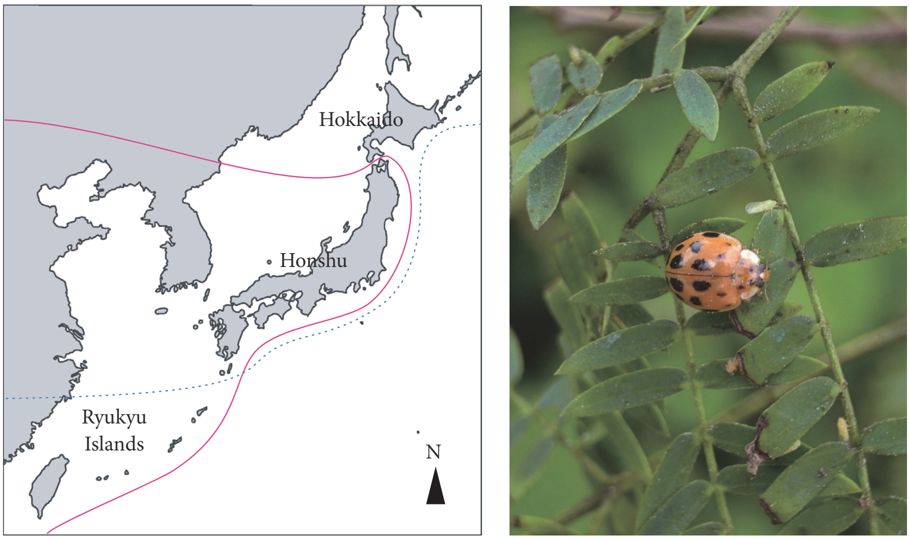
Furthermore, we found by experiment that the giant pine aphid is nutritionally less suitable for the larval development of ladybirds. We froze some aphids, to exclude the effects of prey mobility on larval performance, and then fed them to larvae of *H. yedoensis* and of *H. axyridis* to evaluate their intrinsic suitability as food [27]. The result showed that in both ladybird species larval developmental performance was lower in larvae fed the giant pine aphid than in those fed the other prey species. Although we have not yet examined the proximate mechanism for the lower developmental performance, secondary compounds derived from the pine trees and stored in the aphid's body (see [68, 69]), or simply an insufficient nutrient content, might be responsible.

Taken together, these findings show that the giant pine aphid is poor prey for both *H. yedoensis* and *H. axyridis* larvae with respect to abundance, capture difficulty, and its intrinsic suitability as food. Therefore, we conclude that food quality per se does not determine the food range of *H. yedoensis*. In contrast to the rarity and niche specialization of *H. yedoensis*, *H. axyridis* is abundant and utilizes various preferred prey species. These differences suggest that negative interactions between *H. yedoensis* and *H. axyridis* might greatly influence the food utilization of *H. yedoensis* in nature.

3.3. Reproductive Interference between the Two Harmonia Species.

The results summarized in Section 3.2 led us to hypothesize that reproductive interference by *H. axyridis* against *H. yedoensis* is responsible for the specialization on less suitable prey by *H. yedoensis*. When *H. yedoensis* was first identified as a cryptic *Harmonia* species, it was already known that although interspecific copulation occurred, a postmating reproductive barrier existed between *H. yedoensis* and *H. axyridis* [60, 70]. Sasaji [60] also showed that the male genitalia were very similar between the two species with respect to both size and morphology, so there was no structural barrier to interspecific copulation. To examine the possible influence of reproductive interference on niche partitioning, it was necessary to quantify the effects of interspecific mating behaviors on reproductive success, which might affect the population dynamics of the two species.

Therefore, we performed some laboratory experiments to examine interspecific mating behaviors and their subsequent effect on reproductive success [29]. Both *H. yedoensis* and *H. axyridis* males attempted to mate with both conspecific and heterospecific females, and these attempts often resulted in interspecific copulation lasting a few hours or more. Females of both species can lay eggs even after interspecific copulation, but no viable offspring hatched. However, *H. axyridis* males tended to choose conspecific over heterospecific females, whereas *H. yedoensis* males promiscuously copulated with both conspecific and heterospecific females. We are unable to account for this difference in discrimination skill between *H. yedoensis* and *H. axyridis*, although chemical signals based on cuticular hydrocarbons or visual cues related to body size and color might be important for the interspecific communications. But, probably owing to this difference in discrimination skill, most *H. yedoensis* individuals failed to copulate with conspecifics, especially when the density of *H.*



(a)

(b)

Figure 4: (a) Natural distribution of *H. yedoensis* (red solid line) and *H. axyridis* (blue dotted line) around the Japanese archipelago (modified from Sasaji [24]). The two species are sympatric in central Japan (Honshu), whereas only *H. yedoensis* is found in the Ryukyu Islands and only *H. axyridis* in Hokkaido. (b) *Harmonia yedoensis* on a lead tree, *Leucaena leucocephala*, on Miyako Island, southern Ryukyus. In areas where *H. axyridis* does not occur, *H. yedoensis* adopts a generalist strategy.

axyridis was high in the experimental arena. By contrast, most *H. axyridis* individuals successfully copulated with conspecifics regardless of whether *H. yedoensis* was present [29]. Here, it is important to note that the fitness reduction at the mating stage is asymmetric between these two species; that is, *H. yedoensis* is inferior to *H. axyridis* in terms of reproductive interference.

These results support the hypothesis that reproductive interference from *H. axyridis* has led to host specialization in *H. yedoensis*. In nature, *H. yedoensis* might suffer from a considerable fitness reduction if they utilize less elusive aphids in a patch occupied by *H. axyridis*. By specializing to the habitat of the giant pine aphid, which is especially elusive prey for *H. axyridis*, *H. yedoensis* can mitigate the cost of reproductive interference. Therefore, we argue that *H. yedoensis* mothers are obligated to choose lower quality prey for offspring performance where the ranges of these sibling species overlap.

Biogeographical distribution patterns also suggest that reproductive interference plays a nonnegligible role in determining the food range of *H. yedoensis*. In the Ryukyu Islands, southern Japan, where *H. axyridis* is not found (Figure 4), *H. yedoensis* often visits various deciduous tree species [71, 72] (S. Noriyuki, personal observation). In contrast, on Hokkaido Island, northern Japan, where *H. yedoensis* does not occur, *H. axyridis* is a generalist predator, just as it is in regions of central Japan where the two species are sympatric. These patterns suggest that *H. axyridis* utilizes various preferred prey species without regard to the presence of *H. yedoensis*, whereas the negative impact of reproductive interference of *H. axyridis* on *H. yedoensis* forces the latter to become a specialist predator on less preferred prey where the two species coexist.

Comparison of *Harmonia* (ladybirds) and *Chrysopa* (lacewings) (Table 1) reveals many similarities in the relationships between these sympatric sibling species pairs. Both specialist species can potentially develop on a variety of food sources that are in nature utilized exclusively by their generalist counterpart. Moreover, the specialist species have morphological, behavioral, and physiological adaptations that enable them to handle their less suitable prey. Furthermore, interspecific copulation can occur between members of each pair, at least under laboratory conditions. Given these observations, it would be interesting to explore whether the mechanism of ecological specialization/niche differentiation is the same in these two aphidophagous taxa.

Of course, alternative interspecific interactions, not necessarily mutually exclusive with reproductive interference, must also be considered as possible mechanisms of the ecological specialization of *H. yedoensis*. In particular, intraguild predation may drive host specialization in *H. yedoensis*, because *H. axyridis* is known to be a strong intraguild predator against other ladybird species. However, the results of a laboratory experiment suggest that at the larval stage *H. axyridis* might not be dominant over *H. yedoensis* as an intraguild predator [73]. It is probable that the body size of the individual larvae, rather than their species identity, mainly determines the winner in interactions between these two predatory larvae, because the final instar larvae of both species feed on earlier instar larvae of the other species when they are put together in a Petri dish [73]. We think it is likely that intraguild predation and reproductive interference jointly contribute to niche partitioning between these two ladybird species, because both mechanisms can destabilize species coexistence locally. However, the direction of the food specialization, with *H. yedoensis* feeding on

Table 1: Comparison of the niche, life-history traits, and interspecific mating interactions in sibling species between *Harmonia* ladybirds and *Chrysopa* lacewings.

	Harmonia ladybirds		*Chrysopa* lacewings	
	H. axyridis (generalist)	*H. yedoensis* (specialist)	*C. quadripunctata* (generalist)	*C. slossonae* (specialist)
Niche				
Habitat	Various deciduous trees including pine trees	Pine trees	Various deciduous trees including alder trees	Alder trees
Prey	Various aphid species	The giant pine aphid	Various aphid species	The woolly alder aphid (with attended ants)
Alternative prey	Various aphid species and artificial diet	Various aphid species and artificial diet	Various aphid species	Various aphid species
Life-history traits				
Adult body size	Similar		Small	Large
Egg size	Small	Large	Small	Large
Rate of oviposition	High	Low	High	Low
Sibling cannibalism within clutch	Low	High	NA	
Hatchling head size	Small	Large	Small	Large
Larval leg length	Short	Long	Short	Long
Larval behavior	Low walking ability	High walking ability	Camouflage	Camouflage with wax
Seasonality	Bivoltine (central Japan)	Univoltine	Bivoltine and a partial third generation per year	Univoltine
Critical photoperiod for diapause induction	NA		Short	Long
Interspecific reproduction				
Interspecific mating attempt	Yes		Yes	
Interspecific copulation	Yes		Yes	
Viable hybrid offspring	No		Yes	
Reproductive interference	Superior	Inferior	NA	

Information on *Harmonia* is from Sasaji [24], Osawa and Ohashi [26], Noriyuki and Osawa [27], and Noriyuki et al. [9, 28–30]; information on *Chrysopa* is from Albuquerque et al. [7], Eisner et al. [31], Milbrath et al. [32], Tauber et al. [33], and C. A. Tauber and M. J. Tauber [34].

more elusive and *H. axyridis* feeding on less elusive prey, might be determined by the asymmetry of the reproductive interference. Nevertheless, the combined effect of predation and competition on individual fitness and species coexistence is predicted by mathematical models to produce complex outcomes [74, 75]. We therefore think that it would be very interesting to see how the incorporation of reproductive interference in a trophic module along with intraguild predation would alter population dynamics and community structure.

Now, about 100 years after Takizawa first described a new *Harmonia* ladybird species and several decades since its rediscovery by Sasaji, it is becoming clear that the mechanism of ecological specialization and generalization in *H. yedoensis* and *H. axyridis* involves negative interspecific interactions. This case study illustrates how the integration of taxonomy, ecology, and evolution can deepen our understanding of natural history and the great principles that underpin biological communities.

4. Other Specialist Ladybirds

Reproductive interference may have led to niche partitioning not only in *Harmonia* species but also in predatory ladybirds belonging to other genera. Therefore, we picked congeneric species pairs known to show different food (habitat) ranges or types in the same geographical region and examined the incidence of interspecific mating interactions in these congeneric pairs. Then we investigated conifer- (pine) associated specialist ladybirds in Britain and Japan to assess the generality of our hypothesis that reproductive interference can lead to niche partitioning in closely related species.

4.1. Niche Partitioning between Congeneric Ladybird Species Pairs

4.1. Niche Partitioning between Congeneric Ladybird Species Pairs. To examine niche partitioning in other ladybirds, we selected genera that contain at least two species with different food (habitat) types in the same region of Britain or Japan (Table 2). In both these countries, the natural history of ladybirds has been well studied by professional

Table 2: Comparison of niche utilization among sympatrically distributed congeneric ladybird species of the United Kingdom (UK) and Japan.

Genus	Species	Food, host plants, and habitats
UK		
Adalia	*A. bipunctata*	Various herbaceous and arboreal habitats
	A. decempunctata	Various arboreal habitats, but more specialized than *A. bipunctata*
Chilocorus	*C. renipustulatus*	Coccids; broad-leaved deciduous trees
	C. bipustulatus	Coccids; *Calluna*, Leyland cypress, and other trees; heathland
Coccidula	*C. rufa*	Reeds, reed-mace, rushes, and wetland grasses
	C. scutellata	Reeds, reed-mace, and rushes
Coccinella	*C. undecimpunctata*	Aphids; herbaceous habitats, especially in coastal areas
	C. quinquepunctata	Aphids; low-growing herbaceous plants such as nettle, thistles, bitter-cress, and angelica; unstable river shingle
	C. septempunctata	A variety of aphid species on an extensive range of low-growing herbaceous host plants; habitats including agroecosystem, grassland, heathland, and coniferous and deciduous woodland
	C. magnifica	Ant-attended aphids; Scots pine and other plants close to ant nests of genus *Formica*
	C. hieroglyphica	Larvae of the heather leaf beetle *Lochmaea suturalis* and the heather aphid *Aphis callunae*
Nephus	*N. bisignatus*	Low-growing vegetation in coastal regions
	N. quadrimaculatus	Coniferous and deciduous woodlands
	N. redtenbacheri	Various low-growing vegetation in both inland and coastal regions
Scymnus	*S. nigrinus*	Needleleaf conifers
	S. frontalis	Low-growing vegetation in dry habitats and on coastal dunes
	S. femoralis	Low-growing vegetation on well-drained soils
	S. schmidti	Various types of low-growing vegetation
	S. haemorrhoidalis	Low-growing vegetation and small shrubs, particularly in damp areas
	S. auritus	Oak trees
	S. limbatus	Willow, sallow, and poplar trees
	S. suturalis	Needleleaf conifers, occasionally deciduous trees
	S. interruptus	Pseudococcids and diaspidids in diverse habitats
Rhyzobius	*R. chrysomeloides*	Pine trees, deciduous trees, and ivy
	R. litura	Low-growing vegetation, especially grasses and thistles
	R. lophanthae	Coccids and diaspidids on trees
Japan		
Calvia	*C. quindecimguttata*	Reeds
	C. muiri	Various habitats, especially bamboo grasses
Chilocorus	*C. kuwanae*	Coccids such as *Pseudaulacaspis pentagona*
	C. rubidus	*Kermococcus* coccids on plum, cherry, chestnut, and oak
	C. mikado	*Quercus gilva*
Harmonia	*H. axyridis*	Various habitats, mainly arboreal
	H. yedoensis	Pine trees
Oenopia	*O. scalaris*	Pine trees
	O. hirayamai	Various arboreal habitats
Pseudoscymnus	*P. sylvaticus*	Inside galls of *Tuberocephalus sasakii* on cherry and of *Ceratovacuna nekoashi* on storax
	P. pilicrepus	Eusocial aphid *Colophina arma* on the subshrub *Clematis stans*
Scymnus	*S. posticalis*	Various herbaceous and arboreal habitats
	S. yamato	Wetland, mainly on reeds
	S. babai	Wetland
	S. ohtai	Wetland
	S. hoffmanni	Wetland
	S. nakaikemensis	Wetland
	S. otohime	Chestnut; prey is *Moritziella castaneivora,* which infects chestnut cases

Information on UK ladybirds is from Roy et al. [35] and Majerus [36]. Information on Japanese ladybirds is from Sasaji [24] and Shiyake [37].

and amateur entomologists. Because, in this paper, our focus is on aphidophagous insects, we exclude phytophagous and mycophagous ladybirds from the list in the table, but this exclusion does not mean that reproductive interference might not be important in these functional groups [47]. We identified numerous closely related species in various ladybird genera that exhibited niche partitioning (Table 2). For example, *Pseudoscymnus sylvaticus* mothers lay their eggs on galls of certain aphid species (*Tuberocephalus sasakii*, which forms galls on cherry tree leaves, or *Ceratovacuna nekoashi*, which forms galls on fruits of Japanese snowbell, *Styrax japonica*), and the hatched larvae forage exclusively on the aphids in the gall. In contrast, a sympatric congener, *Pseudoscymnus pilicrepus*, utilizes the eusocial aphid *Colophina arma* on the subshrub *Clematis stans* [24]. At present, the drivers of this niche partitioning in regionally coexisting predatory ladybirds are not well understood. Here, we focus on *Adalia* and *Coccinella* species pairs, because each of these genera contains generalist and specialist species pairs distributed sympatrically in Britain and other parts of Europe and considerable information is available about their ecology.

Adalia bipunctata is one of the most common ladybird species in Europe and it occupies a great variety of habitats, including woodlands, scrub, and grassland. By contrast, its sibling species, *Adalia decempunctata*, is more habitat-specific; it is found mainly on deciduous trees and in hedgerows [76–78]. Because in *A. decempunctata* larvae can develop and forage on various aphid species [79] and mothers produce more eggs when fed on an aphid that is not regularly used in the field [80], this habitat restriction cannot be explained solely by food suitability. Moreover, Sloggett and Majerus [78] have shown that the prevalence of parasitoids is similar between *A. bipunctata* and *A. decempunctata*, suggesting that the habitat specialization of the latter is not driven by a need for a habitat with low predation risk (i.e., an enemy-free space [81]).

Under laboratory conditions, interspecific copulation occurs between *A. bipunctata* and *A. decempunctata*, and the resulting sterile hybrids occasionally develop into adults [82]. Thus, interspecific mating interactions should reduce their reproductive success when the two species occupy the same local patch. During fieldwork in the Netherlands, Brakefield [76] importantly observed that the principal spring mating habitats of *A. bipunctata* were shrubs, whereas he found almost all mating *A. decempunctata* on trees. This use of different mating habitats suggests that past negative mating interactions might have caused small-spatial-scale divergence of reproductive sites in these species. It would be interesting to explore this possibility empirically in the future.

Coccinella septempunctata is also very common in gardens and agroecosystems, but it is also found in heathland, scrub, and coniferous and deciduous woodlands. In contrast, each of the four other *Coccinella* species in Britain specializes in a different niche (Table 2). In particular, *Coccinella magnifica* is a myrmecophile that lives only near ant nests and it preys on aphids that are attended by the ants [83]. Obviously, foraging on ant-attended aphids is costly for *C. magnifica* adults and larvae, because the ants often attack the foraging ladybirds [84, 85], suggesting that the ant attendance itself cannot explain the niche differentiation between *C. septempunctata* and *C. magnifica*. Importantly, *C. magnifica* can be successfully reared in the laboratory from adult to adult by feeding nonattended aphid species such as *Acyrthosiphon pisum* and *Aphis fabae* (i.e., alternative foods). Thus, its potential dietary breadth appears to be similar to that of its generalist congener *C. septempunctata* [83]. Even though interspecific mating behaviors have not been thoroughly studied in these two ladybird species, the adult body size and color pattern are very similar between them. It might be illuminating, therefore, to consider interspecific mating interactions in future investigations of niche partitioning among *Coccinella* species. For example, to test the hypothesis that reproductive interference prevents a species from occupying its fundamental niche and restricts it to a narrower realized niche, experiments should be performed to examine whether reproductive interference occurs in these species and whether the cost of the interaction is incurred more by *C. magnifica* than by *C. septempunctata*.

4.2. Conifer Specialists. It is well known that some species of predatory ladybirds utilize specialized habitats on pine trees and other conifers (Table 3) and that this specific specialization has independently evolved several times in the ladybird lineage [86]. Not all conifer-specialist species coexist in the same region with a congeneric relative (Table 3), which suggests that, assuming that reproductive interference is mainly likely to occur among phylogenetically close species, these specializations might have occurred through mechanisms other than reproductive interference. Some conifer specialists, however, do have sympatrically distributed generalist congeners (Table 3). In Britain, the habitats of *Scymnus nigrinus* and *Scymnus suturalis* are restricted to conifer trees, whereas a congener, *Scymnus schmidti*, utilizes a wide range of habitat types [35]. A similar pattern has been observed in Japan in specialist and generalist species belonging to genus *Oenopia* [24]. Therefore, we can hypothesize that, as in *Harmonia* species in Japan, this specialization to conifers might have been driven by reproductive interference from sympatric congeners. To test this hypothesis, it will be necessary to quantify the cost of interspecific mating interactions as well as the quality of the conifer habitat with respect to larval and adult development. It would be interesting to know if reproductive interference has caused some species to specialize to conifers more than once in the ladybird phylogeny.

5. Aphidophagous Guilds

In this section we consider intraguild predation as an alternative mechanism of the niche partitioning of aphidophagous insects. Multiple species of aphidophagous insect predators, as well as parasitoids that attack aphids, often coexist despite the occurrence of intraguild predation. Osawa [87], for example, studied aphidophagous ladybirds and hoverflies preying on eight species of aphids infecting seven species of deciduous trees in the Botanical Garden of Kyoto University, central Japan. He collected five aphidophagous ladybird species and

Table 3: Conifer-associated specialist ladybird species in the UK and Japan.

Species	Detail	Sympatric congeners
UK		
Exochomus quadripustulatus	Coccids on needleleaf conifers, sallows, and willows	NA[1]
Myrrha octodecimguttata	Aphids on Scots pine	NA
Sospita (Myzia) oblongoguttata	Aphids on Scots pine	NA
Harmonia quadripunctata	Aphids on needleleaf conifers	*H. axyridis*[2]
Anatis ocellata	Aphids on needleleaf conifers, particularly pines	NA
Scymnus nigrinus	Scots pine	*S. schmidti* and other species[3]
Scymnus suturalis	Needleleaf conifers, particularly Scots pine, but occasionally deciduous trees	*S. schmidti* and other species
Japan		
Harmonia yedoensis	Aphids on Japanese red pine and Japanese black pine	*H. axyridis*
Sospita (Myzia) oblongoguttata	Pine trees	NA
Oenopia scalaris	Pine trees	*O. hirayamai*

Information on UK ladybirds was adapted from Roy et al. [35] and Majerus [36]; information on Japanese ladybirds was adapted from Sasaji [24] and Shiyake [37]. [1]NA indicates that no congeneric species is distributed in the same region; [2]*H. axyridis* is an exotic species in the UK; [3]refer to Table 2 for other *Scymnus* species.

eight hoverfly species (see also [88]). Notably, both field [89] and laboratory studies [90, 91] have shown that four of the collected ladybird species (except *Scymnus posticalis*) engage in intraguild predation. *Harmonia axyridis*, in particular, is an intraguild predator that preys predominantly on other ladybird species [89, 92, 93]. Nevertheless, the abundance of *H. axyridis* is not negatively correlated with the abundance of the other four ladybird species in this area [88]. Thus, some mechanism must exist that allows these ladybird species to coexist in the same patch.

Similarly, in hoverfly communities generalist predators often use many of the same prey species [94, 95]. Moreover, aphidophagous ladybirds and hoverflies often coexist where their distributions overlap [88, 89, 96], even though predatory ladybirds often attack hoverflies with which they compete for the shared aphid resource (reviewed by [97]). Thus, in aphidophagous communities, predation and resource depletion do not necessarily result in strict niche partitioning.

If parasitoids that attack aphids are assumed to belong to the same guild as aphidophagous insects [13], then aphidophagous communities become even more species-rich and complex. In this case, intraguild predation includes predators such as ladybirds that feed on parasitized aphids (e.g., aphids that have been mummified), as well as different parasitoid species that, when parasitizing the same aphid, attack each other. Despite this complex food web structure, multiple parasitoid species are known to utilize the same aphid colonies simultaneously. For example, Müller et al. [98] reported that, in Silwood Park, southern England, some species of aphids were infected with multiple parasitoid species. Moreover, Osawa [87] identified various primary and secondary parasitoids on aphids on which both predatory ladybirds and hoverflies intensively foraged. These observations suggest that some factor must exist that permits the coexistence of multiple species in aphidophagous communities with multiple and complex prey-predator links.

The conditions that allow the stable coexistence of a predator and its prey, together with a shared prey species, have been extensively analyzed by mathematical models, as well as by some empirical studies. One classic model [12] predicts that stable coexistence should be possible if a trade-off exists between resource consumption and predation ability, but only under a limited range of environmental conditions. In addition, mechanisms such as a temporary refuges for prey [99], optimal predator foraging behavior [100, 101], and intense intraspecific interactions [102] have been proposed to allow species coexistence despite the occurrence of intraguild predation. These mechanisms likely explain the seemingly paradoxical robust persistence of many natural intraguild predation systems.

The local coexistence of phylogenetically closely related species, however, may still be inhibited. In Japan, two sibling aphidophagous ladybirds, *Propylea japonica* and *Propylea quatuordecimpunctata*, are distributed parapatrically; the former lives at low elevation and the latter at high elevation, but within a narrow zone they coexist [24]. In Britain, *Coccinella septempunctata* utilizes a wide range of prey types and habitats, whereas *Coccinella hieroglyphica* is mainly found on heather, where it forages on the heather aphid, *Aphis callunae*, and on larvae of the heather leaf beetle, *Lochmaea suturalis* [35]. It has often been demonstrated that in both animal and plant communities local assemblages tend to be composed of phylogenetically distant species (e.g., [103–105]), probably owing to exclusive interactions among closely related species. Therefore, to understand the observed spatial distributions of aphidophagous insects, in addition to intraguild predation, some factor that is tightly connected to phylogenetic closeness should be considered.

Interspecific mating behavior is more likely to occur among phylogenetically close species because they often share similar mating signals [56, 106]. The resulting, often costly mating interactions can lead to local species extinction, which in turn can cause diversification of niche use and resource-use traits [49]. In contrast, phylogenetically distant species, which generally have distinctive, easily discriminated mating signals, focus their mating efforts on high-quality conspecifics even when their ecological niches largely overlap. As a result, distantly related species can stably coexist within a patch [49]. These observations suggest that reproductive interference might be a mechanism of niche diversification in closely related species.

6. Conclusion

We have shown that the effect of reproductive interference on local population dynamics has probably been underestimated, in contrast to the intraguild predation mechanism, which is specific to the predator community. Therefore, to evaluate the validity and generality of the reproductive interference mechanism, more empirical studies, and extensions of published studies, of various predator species are needed. We have suggested some possible approaches earlier in this paper. Moreover, the relative importance and synergistic effects of predation, exploitative competition, and reproductive interference are largely unknown. Because these mechanisms of species exclusion are not mutually exclusive, the impact of each individually, and of their interactions, on niche partitioning needs to be quantified. A theoretical research priority is the incorporation of reproductive interference into the intraguild predation model to examine how it changes the population dynamics. Together, such empirical and theoretical efforts will enable us to evaluate whether niche partitioning in predators is explicable mainly by reproductive interference, a mechanism that occurs in several functional groups, including herbivores [42, 50] and plants [107], or by a specific mechanism that is unique to carnivores such as intraguild predation.

At present, it cannot be conclusively decided whether the observed niche partitioning between phylogenetically close species has been caused by sympatric speciation or reproductive interference after allopatric speciation, because it is difficult to distinguish between these two evolutionary scenarios by examining current phenotypic traits and fitness. Thus, a fruitful approach might be to identify the locality of the origin of the species by appropriate techniques such as phylogeography and genomics. Sympatric speciation has been frequently assumed to explain niche partitioning among phylogenetically similar relatives such as cryptic species complexes [108], but compelling evidence that two sympatrically distributed species (races) have diverged is still lacking [109]. A theoretical basis now exists for ecological character displacement via reproductive interference [49]. Incorporation of reproductive interference into existing models should make it possible to design more rigorous tests and to further refine the models and thus improve their skills in reconstructing the natural world.

Competing Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

Acknowledgments

The authors thank Yasuko Kawakami for information on Japanese ladybirds and Jun-Ya Ide for useful comments on the manuscript. This study was funded by support from the Japan Society for the Promotion of Science to Suzuki Noriyuki (no. 24-3112, no. 26840137, and no. 26650154) and to Naoya Osawa (no. 20405047 and no. 24255013).

References

[1] E. R. Pianka, “The structure of lizard communities,” *Annual Review of Ecology and Systematics*, vol. 4, no. 1, pp. 53–74, 1973.

[2] C. J. F. Huckins, “Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish,” *Ecology*, vol. 78, no. 8, pp. 2401–2414, 1997.

[3] P. Schausberger and B. A. Croft, “Nutritional benefits of intraguild predation and cannibalism among generalist and specialist phytoseiid mites,” *Ecological Entomology*, vol. 25, no. 4, pp. 473–480, 2000.

[4] J. Terraube, B. Arroyo, M. Madders, and F. Mougeot, “Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators,” *Oikos*, vol. 120, no. 2, pp. 234–244, 2011.

[5] R. Levins, *Evolution in Changing Environments*, Princeton University Press, Princeton, NJ, USA, 1968.

[6] D. Schluter, “Ecological causes of adaptive radiation,” *American Naturalist*, vol. 148, pp. S40–S64, 1996.

[7] G. S. Albuquerque, M. J. Tauber, and C. A. Tauber, “Life-history adaptations and reproductive costs associated with specialization in predacious insects,” *Journal of Animal Ecology*, vol. 66, no. 3, pp. 307–317, 1997.

[8] S. B. Yamada and G. E. Boulding, “Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs,” *Journal of Experimental Marine Biology and Ecology*, vol. 220, no. 2, pp. 191–211, 1998.

[9] S. Noriyuki, N. Osawa, and T. Nishida, “Prey capture performance in hatchlings of two sibling Harmonia ladybird species in relation to maternal investment through sibling cannibalism,” *Ecological Entomology*, vol. 36, no. 3, pp. 282–289, 2011.

[10] S. F. Norton, “Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics,” *Ecology*, vol. 72, no. 5, pp. 1807–1819, 1991.

[11] G. A. Polis, C. A. Myers, and R. D. Holt, “The ecology and evolution of intraguild predation: potential competitors that eat each other,” *Annual Review of Ecology and Systematics*, vol. 20, pp. 297–330, 1989.

[12] R. D. Holt and G. A. Polis, “A theoretical framework for intraguild predation,” *The American Naturalist*, vol. 149, no. 4, pp. 745–764, 1997.

[13] J. A. Rosenheim, H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee, “Intraguild predation among biological-control agents: theory and evidence,” *Biological Control*, vol. 5, no. 3, pp. 303–335, 1995.

[14] M. Arim and P. A. Marquet, “Intraguild predation: a widespread interaction related to species biology,” *Ecology Letters*, vol. 7, no. 7, pp. 557–564, 2004.

[15] C. Vilà and R. K. Wayne, “Hybridization between wolves and dogs,” *Conservation Biology*, vol. 13, no. 1, pp. 195–198, 1999.

[16] E. A. Dame and K. Petren, “Behavioural mechanisms of invasion and displacement in Pacific island geckos (Hemidactylus),” *Animal Behaviour*, vol. 71, no. 5, pp. 1165–1173, 2006.

[17] Y. Okuzaki, Y. Takami, and T. Sota, “Resource partitioning or reproductive isolation: the ecological role of body size differences among closely related species in sympatry,” *Journal of Animal Ecology*, vol. 79, no. 2, pp. 383–392, 2010.

[18] H. Van Gossum, K. Beirinckx, M. R. Forbes, and T. N. Sherratt, “Reproductive interference between *Nehalennia* damselfly species,” *Ecoscience*, vol. 14, no. 1, pp. 1–7, 2007.

[19] B. M. Fitzpatrick, J. S. Placyk Jr., M. L. Niemiller, G. S. Casper, and G. M. Burghardt, “Distinctiveness in the face of gene flow: hybridization between specialist and generalist gartersnakes,” *Molecular Ecology*, vol. 17, no. 18, pp. 4107–4117, 2008.

[20] J. Gröning and A. Hochkirch, “Reproductive interference between animal species,” *The Quarterly Review of Biology*, vol. 83, no. 3, pp. 257–282, 2008.

[21] D. Kyogoku, “Reproductive interference: ecological and evolutionary consequences of interspecific promiscuity,” *Population Ecology*, vol. 57, no. 2, pp. 253–260, 2015.

[22] W. E. Snyder and E. W. Evans, “Ecological effects of invasive arthropod generalist predators,” *Annual Review of Ecology, Evolution, and Systematics*, vol. 37, pp. 95–122, 2006.

[23] M. Kurisaki, “Studies on the genus *Ptychanatis* crotch,” *Kontyu Sekai*, vol. 24, pp. 369–372, 1920 (Japanese).

[24] H. Sasaji, *Natural History of the Ladybirds*, University of Tokyo Press, Tokyo, Japan, 1998 (Japanese).

[25] P. H. Adler, “Sibling species,” in *Encyclopedia of Entomology*, J. L. Capinera, Ed., pp. 3371–3372, Springer, Dordrecht, The Netherlands, 2008.

[26] N. Osawa and K. Ohashi, “Sympatric coexistence of sibling species *Harmonia yedoensis* and *H. axyridis* (Coleoptera: Coccinellidae) and the roles of maternal investment through egg and sibling cannibalism,” *European Journal of Entomology*, vol. 105, no. 3, pp. 445–454, 2008.

[27] S. Noriyuki and N. Osawa, “Intrinsic prey suitability in specialist and generalist *Harmonia* ladybirds: a test of the trade-off hypothesis for food specialization,” *Entomologia Experimentalis et Applicata*, vol. 144, no. 3, pp. 279–285, 2012.

[28] S. Noriyuki, Y. Kameda, and N. Osawa, “Prevalence of male-killer in a sympatric population of two sibling ladybird species, *Harmonia yedoensis* and *Harmonia axyridis* (Coleoptera: Coccinellidae),” *European Journal of Entomology*, vol. 111, no. 2, pp. 307–311, 2014.

[29] S. Noriyuki, N. Osawa, and T. Nishida, “Asymmetric reproductive interference between specialist and generalist predatory ladybirds,” *Journal of Animal Ecology*, vol. 81, no. 5, pp. 1077–1085, 2012.

[30] S. Noriyuki, K. Kawatsu, and N. Osawa, “Factors promoting maternal trophic egg provisioning in non-eusocial animals,” *Population Ecology*, vol. 54, no. 3, pp. 455–465, 2012.

[31] T. Eisner, K. Hicks, M. Eisner, and D. S. Robson, “‘Wolf-in-sheep's-clothing’ strategy of a predaceous insect larva,” *Science*, vol. 199, no. 4330, pp. 790–794, 1978.

[32] L. R. Milbrath, M. J. Tauber, and C. A. Tauber, “Prey specificity in *Chrysopa*: an interspecific comparison of larval feeding and defensive behavior,” *Ecology*, vol. 74, no. 5, pp. 1384–1393, 1993.

[33] C. A. Tauber, J. R. Ruberson, and M. J. Tauber, “Size and morphological differences among the larvae of two predacious species and their hybrids (Neuroptera: Chrysopidae),” *Annals of the Entomological Society of America*, vol. 88, no. 4, pp. 502–511, 1995.

[34] C. A. Tauber and M. J. Tauber, “Food specificity in predacious insects: a comparative ecophysiological and genetic study,” *Evolutionary Ecology*, vol. 1, no. 2, pp. 175–186, 1987.

[35] H. Roy, P. Brown, R. Frost, and R. Poland, *Ladybirds (Coccinellidae) of Britain and Ireland*, Centre for Ecology and Hydrology, Oxfordshire, UK, 2011.

[36] M. E. N. Majerus, *Ladybirds*, Harper Collins, London, UK, 1994.

[37] S. Shiyake, *A Guide to Ladybirds of Osaka*, Osaka Museum of Natural History, Osaka, Japan, 2005 (Japanese).

[38] C. S. Henry, “Sibling species, call differences, and speciation in green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*),” *Evolution*, vol. 39, no. 5, pp. 965–984, 1985.

[39] C. A. Tauber and M. J. Tauber, “A genetic model for sympatric speciation through habitat diversification and seasonal isolation,” *Nature*, vol. 268, no. 5622, pp. 702–705, 1977.

[40] C. A. Tauber and M. J. Tauber, “Inheritance of seasonal cycles in *Chrysoperla* (Insecta: Neuroptera),” *Genetical Research*, vol. 49, no. 3, pp. 215–223, 1987.

[41] S. Kishi, T. Nishida, and Y. Tsubaki, “Reproductive interference determines persistence and exclusion in species interactions,” *Journal of Animal Ecology*, vol. 78, no. 5, pp. 1043–1049, 2009.

[42] M. Friberg, O. Leimar, and C. Wiklund, “Heterospecific courtship, minority effects and niche separation between cryptic butterfly species,” *Journal of Evolutionary Biology*, vol. 26, no. 5, pp. 971–979, 2013.

[43] C. A. Tauber and M. J. Tauber, “Sympatric speciation based on allelic changes at three loci: evidence from natural populations in two habitats,” *Science*, vol. 197, no. 4310, pp. 1298–1299, 1977.

[44] M. J. Tauber, C. A. Tauber, J. R. Ruberson, L. R. Milbrath, and G. S. Albuquerque, “Evolution of prey specificity via three steps,” *Experientia*, vol. 49, no. 12, pp. 1113–1117, 1993.

[45] P. Nosil, *Ecological Speciation*, Oxford University Press, Oxford, UK, 2012.

[46] C. S. Henry and M. L. M. Wells, “Adaptation or random change? The evolutionary response of songs to substrate properties in lacewings (Neuroptera: Chrysopidae: *Chrysoperla*),” *Animal Behaviour*, vol. 68, no. 4, pp. 879–895, 2004.

[47] S. Noriyuki, “Host selection in insects: reproductive interference shapes behavior of ovipositing females,” *Population Ecology*, vol. 57, no. 2, pp. 293–305, 2015.

[48] C. A. Tauber and M. J. Tauber, “Sympatric speciation in insects: perception and perspective,” in *Speciation and Its Consequences*, D. Otte and J. A. Endler, Eds., pp. 307–344, Sinauer Associates, Sunderland, UK, 1989.

[49] J. Konuma and S. Chiba, “Ecological character displacement caused by reproductive interference,” *Journal of Theoretical Biology*, vol. 247, no. 2, pp. 354–364, 2007.

[50] D. W. Crowder, A. R. Horowitz, H. Breslauer et al., “Niche partitioning and stochastic processes shape community structure following whitefly invasions,” *Basic and Applied Ecology*, vol. 12, no. 8, pp. 685–694, 2011.

[51] N. Osawa, “Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics,” *Population Ecology*, vol. 42, no. 2, pp. 115–127, 2000.

[52] M. L. Niemiller, B. M. Fitzpatrick, and B. T. Miller, “Recent divergence with gene flow in Tennessee cave salamanders (Plethodontidae: *Gyrinophilus*) inferred from gene genealogies,” *Molecular Ecology*, vol. 17, no. 9, pp. 2258–2275, 2008.

[53] J. L. Feder, S. P. Egan, and P. Nosil, “The genomics of speciation-with-gene-flow,” *Trends in Genetics*, vol. 28, no. 7, pp. 342–350, 2012.

[54] I. Ohshima, "Genetic mechanisms preventing the fusion of ecotypes even in the face of gene flow," *Scientific Reports*, vol. 2, article no. 506, 2012.

[55] M. M. Wells and C. S. Henry, "The role of courtship songs in reproductive isolation among populations of green lacewings of the genus *Chrysoperla* (Neuroptera: Chrysopidae)," *Evolution*, vol. 46, no. 1, pp. 31–42, 1992.

[56] K. S. Pfennig, "The evolution of mate choice and the potential for conflict between species and mate-quality recognition," *Proceedings of the Royal Society B: Biological Sciences*, vol. 265, no. 1407, pp. 1743–1748, 1998.

[57] T. Dobzhansky, "Geographical variation in lady-beetles," *The American Naturalist*, vol. 67, no. 709, pp. 97–126, 1933.

[58] T. Komai, M. Chino, and Y. Hosino, "Contributions to the evolutionary genetics of the lady-beetle, *Harmonia*. I. Geographic and temporal variations in the relative frequencies of the elytral pattern types and in the frequency of elytral ridge," *Genetics*, vol. 35, no. 5, pp. 589–601, 1950.

[59] T. Komai, M. Chino, and Y. Hosino, "Population genetics on the lady-beetle *Harmonia axyridis*," in *Population Genetics*, T. Komai and K. Sakai, Eds., pp. 45–60, Baifukan, Tokyo, Japan, 1956 (Japanese).

[60] H. Sasaji, "Biosystematics on *Harmonia axyridis*-complex (Coleoptera: Coccinellidae)," *Memoirs of the Faculty of Education, Fukui University, Series II Natural Science*, vol. 30, pp. 59–79, 1980.

[61] H. Sasaji, "Larval characters of Asian species of genus *Harmonia* Mulsant (Coleoptera: Coccinellidae)," *Memoirs of the Faculty of Education, Fukui University, Series II Natural Science*, vol. 27, pp. 1–17, 1977.

[62] M. Takizawa, "Some new species of *Coccinellidae* in Japan. I," *Transactions of the Sapporo Natural History Society*, vol. 4, pp. 220–224, 1917 (Japanese).

[63] H. Sasaji, "On the sibling species of *Harmonia*," *Kontyu to Shizen*, vol. 12, no. 11, pp. 4–13, 1977 (Japanese).

[64] J. Jaenike, "Resource predictability and niche breadth in the *Drosophila quinaria* species group," *Evolution*, vol. 32, no. 3, pp. 676–678, 1978.

[65] S. P. Courtney and J. Forsberg, "Host use by two pierid butterflies varies with host density," *Functional Ecology*, vol. 2, no. 1, pp. 67–75, 1988.

[66] C. Wiklund and M. Friberg, "The evolutionary ecology of generalization: among-year variation in host plant use and offspring survival in a butterfly," *Ecology*, vol. 90, no. 12, pp. 3406–3417, 2009.

[67] J. C. Perry and B. D. Roitberg, "Ladybird mothers mitigate offspring starvation risk by laying trophic eggs," *Behavioral Ecology and Sociobiology*, vol. 58, no. 6, pp. 578–586, 2005.

[68] T. Ikeda, F. Matsumura, and D. M. Benjamin, "Chemical basis for feeding adaptation of pine sawflies *neodiprion rugifrons* and *neodiprion swainei*," *Science*, vol. 197, no. 4302, pp. 497–499, 1977.

[69] S. G. Codella Jr. and K. F. Raffa, "Host plant influence on chemical defense in conifer sawflies (Hymenoptera: Diprionidae)," *Oecologia*, vol. 104, no. 1, pp. 1–11, 1995.

[70] I. Okada, K. Nijima, and Y. Toriumi, "Comparative studies on sibling species of lady beetles, *Harmonia yedoensis* and *H. axyridis* (Coleoptera: Coccinellidae)," *Bulletin of the Faculty of Agriculture Tamagawa University*, vol. 18, pp. 60–68, 1978 (Japanese).

[71] S. Azuma, M. Kinjo, M. Murayama, S. Hori, K. Minato, and K. Uesugi, *A Field Guide to Insects in Okinawa*, Okinawa Press, Okinawa, Japan, 1996 (Japanese).

[72] M. Moriguchi, *Ladybirds in Islands*, Chijin Shokan, Tokyo, Japan, 2015 (Japanese).

[73] Y. Yamada, *Larval survival in Harmonia axyridis and Harmonia yedoensis [M.S. dissertation]*, Yamagata University, Yamagata, Japan, 2010 (Japanese).

[74] J. M. Chase, P. A. Abrams, J. P. Grover et al., "The interaction between predation and competition: a review and synthesis," *Ecology Letters*, vol. 5, no. 2, pp. 302–315, 2002.

[75] P. Chesson and J. J. Kuang, "The interaction between predation and competition," *Nature*, vol. 456, no. 7219, pp. 235–238, 2008.

[76] P. M. Brakefield, "Polymorphic Müllerian mimicry and interactions with thermal melanism in ladybirds and a soldier beetle: a hypothesis," *Biological Journal of the Linnean Society*, vol. 26, no. 3, pp. 243–267, 1985.

[77] A. Honěk and I. Hodek, "Distribution in habitats," in *Ecology of Coccinellidae*, A. Honěk and I. Hodek, Eds., pp. 95–141, Kluwer Academic, Dordrecht, The Netherlands, 1996.

[78] J. J. Sloggett and M. E. N. Majerus, "Habitat preferences and diet in the predatory coccinellidae (Coleoptera): an evolutionary perspective," *Biological Journal of the Linnean Society*, vol. 70, no. 1, pp. 63–88, 2000.

[79] N. J. Mills, "Essential and alternative foods for some British Coccinellidae (Coleoptera)," *Entomologica Germanica*, vol. 32, pp. 197–202, 1981.

[80] A. Ferrer, A. F. G. Dixon, and J.-L. Hemptinne, "Habitat or prey specialization in predatory ladybird beetles: a case study of two closely related species," *Journal of Applied Entomology*, vol. 140, no. 3, pp. 199–208, 2016.

[81] M. J. Jeffries and J. H. Lawton, "Enemy free space and the structure of ecological communities," *Biological Journal of the Linnean Society*, vol. 23, no. 4, pp. 269–286, 1984.

[82] H. Ireland, P. W. E. Kearns, and M. E. N. Majerus, "Interspecific hybridisation in the Coccinellidae: some observations on an old controversy," *The Entomologist's Record and Journal of Variation*, vol. 98, pp. 181–185, 1986.

[83] J. J. Sloggett, W. Völkl, W. Schulze, J. H. G. V. D. Schulenburg, and E. N. Majerus, "The ant-associations and diet of the ladybird *Coccinella magnifica* (Coleoptera: Coccinellidae)," *European Journal of Entomology*, vol. 99, no. 4, pp. 565–569, 2002.

[84] J. J. Sloggett, R. A. Wood, and M. E. N. Majerus, "Adaptations of *Coccinella magnifica* redtenbacher, a myrmecophilous coccinellid, to aggression by wood ants (*Formica rufa* Group). I. Adult behavioral adaptation, its ecological context and evolution," *Journal of Insect Behavior*, vol. 11, no. 6, pp. 889–904, 1998.

[85] J. J. Sloggett and M. E. N. Majerus, "Adaptations of Coccinella magnifica, a myrmecophilous coccinellid to aggression by wood ants (Formica rufa group). II. Larval behaviour, and ladybird oviposition location," *European Journal of Entomology*, vol. 100, no. 3, pp. 337–344, 2003.

[86] A. Magro, E. Lecompte, F. Magné, J.-L. Hemptinne, and B. Crouau-Roy, "Phylogeny of ladybirds (Coleoptera: Coccinellidae): are the subfamilies monophyletic?" *Molecular Phylogenetics and Evolution*, vol. 54, no. 3, pp. 833–848, 2010.

[87] N. Osawa, *Ecology of Harmonia axyridis in the field population [Ph.D. dissertation]*, Kyoto University, Kyoto, Japan, 1991 (Japanese).

[88] N. Osawa, "Ecology of *Harmonia axyridis* in natural habitats within its native range," *BioControl*, vol. 56, no. 4, pp. 613–621, 2011.

[89] Y. Hironori and S. Katsuhiro, "Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field," *Entomophaga*, vol. 42, no. 1, pp. 153–163, 1997.

[90] B. K. Agarwala and H. Yasuda, "Overlapping oviposition and chemical defense of eggs in two co-occurring species of ladybird predators of aphids," *Journal of Ethology*, vol. 19, no. 1, pp. 47–53, 2001.

[91] S. Sato, A. F. G. Dixon, and H. Yasuda, "Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds," *Ecological Entomology*, vol. 28, no. 5, pp. 628–633, 2003.

[92] H. Yasuda, E. W. Evans, Y. Kajita, K. Urakawa, and T. Takizawa, "Asymmetric larval interactions between introduced and indigenous ladybirds in North America," *Oecologia*, vol. 141, no. 4, pp. 722–731, 2004.

[93] R. L. Ware and M. E. N. Majerus, "Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird *Harmonia axyridis*," *BioControl*, vol. 53, no. 1, pp. 169–188, 2008.

[94] F. Gilbert and J. Owen, "Size, shape, competition, and community structure in hoverflies (Diptera: Syrphidae)," *Journal of Animal Ecology*, vol. 59, no. 1, pp. 21–39, 1990.

[95] M. Mizuno, T. Itioka, Y. Tatematsu, and Y. Itô, "Food utilization of aphidophagous hoverfly larvae (Diptera: Syrphidae, Chamaemyiidae) on herbaceous plants in an urban habitat," *Ecological Research*, vol. 12, no. 3, pp. 239–248, 1997.

[96] Y. Hironori and S. Katsuhiro, "Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field," *Entomophaga*, vol. 42, no. 1-2, pp. 153–163, 1997.

[97] É. Lucas, "Intraguild predation among aphidophagous predators," *European Journal of Entomology*, vol. 102, no. 3, pp. 351–364, 2005.

[98] C. B. Müller, I. C. T. Adriaanse, R. Belshaw, and H. C. J. Godfray, "The structure of an aphid-parasitoid community," *Journal of Animal Ecology*, vol. 68, no. 2, pp. 346–370, 1999.

[99] P. Amarasekare, "Trade-offs, temporal variation, and species coexistence in communities with intraguild predation," *Ecology*, vol. 88, no. 11, pp. 2720–2728, 2007.

[100] V. Krivan, "Optimal intraguild foraging and population stability," *Theoretical Population Biology*, vol. 58, no. 2, pp. 79–94, 2000.

[101] R. D. Holt and G. R. Huxel, "Alternative prey and the dynamics of intraguild predation: theoretical perspectives," *Ecology*, vol. 88, no. 11, pp. 2706–2712, 2007.

[102] P. Amarasekare, "Coexistence of intraguild predators and prey in resource-rich environments," *Ecology*, vol. 89, no. 10, pp. 2786–2797, 2008.

[103] N. Cooper, J. Rodríguez, and A. Purvis, "A common tendency for phylogenetic overdispersion in mammalian assemblages," *Proceedings of the Royal Society B: Biological Sciences*, vol. 275, no. 1646, pp. 2031–2037, 2008.

[104] N. J. B. Kraft, R. Valencia, and D. D. Ackerly, "Functional traits and niche-based tree community assembly in an Amazonian forest," *Science*, vol. 322, no. 5901, pp. 580–582, 2008.

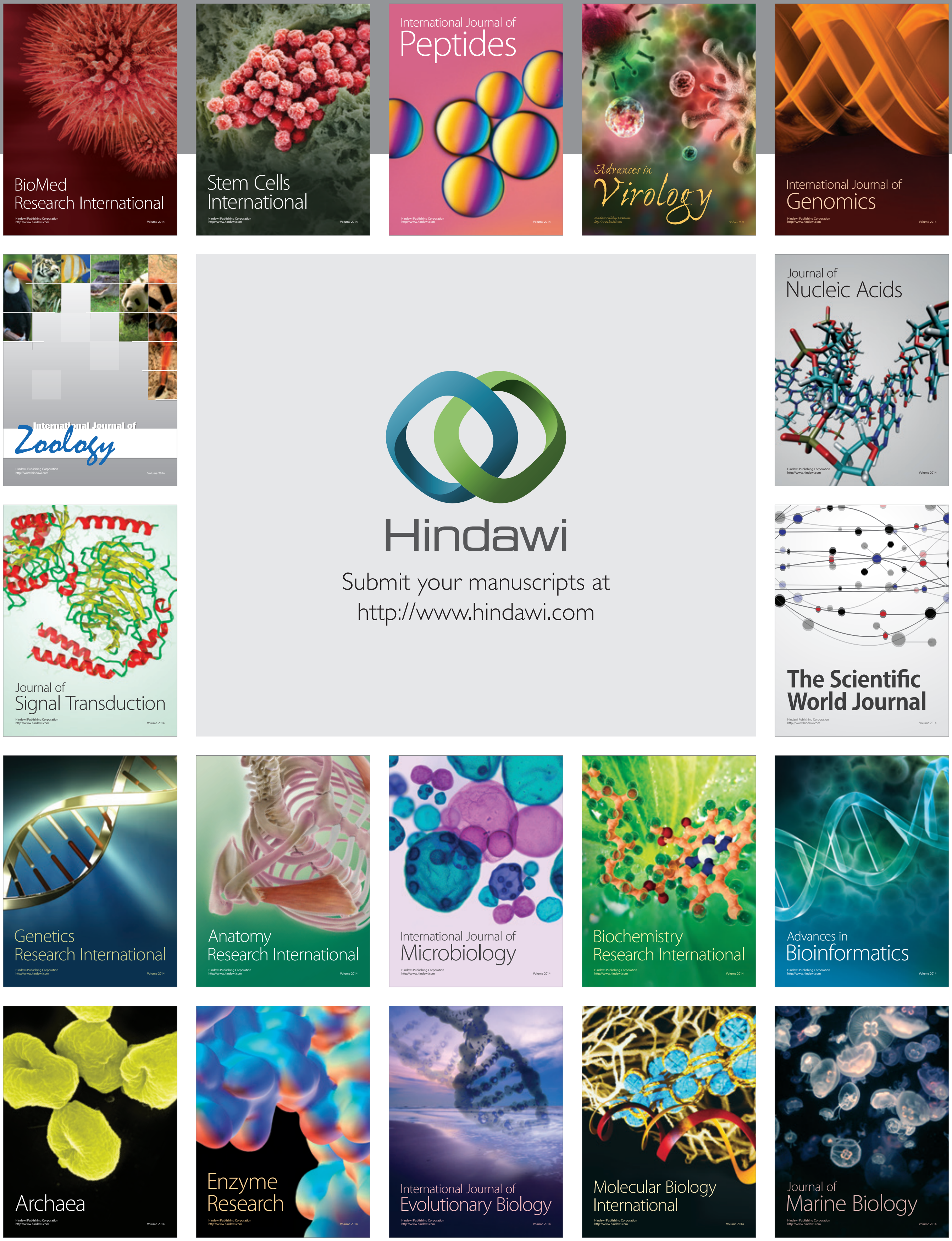
[105] C. H. Graham, J. L. Parra, C. Rahbek, and J. A. McGuire, "Phylogenetic structure in tropical hummingbird communities," *Proceedings of the National Academy of Sciences of the United States of America*, vol. 106, S2, pp. 19673–19678, 2009.

[106] T. J. Ord, L. King, and A. R. Young, "Contrasting theory with the empirical data of species recognition," *Evolution*, vol. 65, no. 9, pp. 2572–2591, 2011.

[107] K.-I. Takakura and S. Fujii, "Reproductive interference and salinity tolerance differentiate habitat use between two alien cockleburs: *Xanthium occidentale* and *X. italicum* (Compositae)," *Plant Ecology*, vol. 206, no. 2, pp. 309–319, 2010.

[108] K. W. Matsubayashi, I. Ohshima, and P. Nosil, "Ecological speciation in phytophagous insects," *Entomologia Experimentalis et Applicata*, vol. 134, no. 1, pp. 1–27, 2010.

[109] J. A. Coyne and H. A. Orr, *Speciation*, Sinauer Associates, Sunderland, Mass, USA, 2004.



Hindawi

Submit your manuscripts at
http://www.hindawi.com