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(Citation)
Ecological Research,31(2):155-164

(Issue Date)
2016-03

(Resource Type)
journal article

(Version)
Version of Record

(URL)
https://hdl.handle.net/20.500.14094/90003466

Ecol Res (2016) 31: 155–164
DOI 10.1007/s11284-016-1336-0

MIYADI AWARD

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Impacts of introduced species on the biota of an oceanic archipelago: the relative importance of competitive and trophic interactions

Received: 30 June 2015 / Accepted: 13 January 2016 / Published online: 8 February 2016

Abstract Introduced species negatively impact native species through competitive and trophic interactions, particularly on oceanic islands that have never been connected to any continental landmass. However, there are few studies on the relative importance of competitive interactions (resource competition with introduced species) and trophic interactions (predation or herbivory by introduced species) with respect to the negative impacts on native organisms on oceanic islands. A literature review on introduced and native species of the oceanic Ogasawara (Bonin) Islands in the western Pacific Ocean indicated that many native species (e.g., bees, beetles, damselflies, butterflies, land snails, birds, and plants) have been negatively impacted by introduced predators and herbivores (e.g., lizards, rats, flatworms, and goats). Several native plants and bees have been negatively affected by introduced competitors. However, the native species that have competed with introduced species have also suffered from either intense herbivory or predation by other introduced species. Thus, introduced predators and herbivores have had greater impacts on native species than introduced competitors in the Ogasawara Islands.

Keywords Invasive species · Ogasawara (Bonin) Islands · Resource competition · Predation · Top-down effects

Introduction

Biological invasion is a common phenomenon worldwide (Elton 1958; Mack et al. 2000). Introduced species have negatively impacted native species, particularly on oceanic islands that have never been connected to a continental landmass (Elton 1958; Reaser et al. 2007; Corlett 2010). Native species are considered to have less highly evolved defensive, competitive, and reproductive abilities on oceanic islands that originally lacked strong predators, herbivores, and competitors (Carlquist 1974; Vermeij 1991; Paulay 1994).

When both native and introduced species use the same resource, introduced species can competitively exclude native species. In Hawaii, an introduced passerine bird, *Zosterops japonicus*, has reportedly caused a decrease in juvenile survival and the size of several coexisting native birds through exploitative competition for food resources (Freed and Cann 2009). However, the extinction of native species caused by such resource competition with introduced species has rarely been reported (Davis 2003; Gurevitch and Padilla 2004; Sax and Gaines 2008). Rather, intense predation by introduced species has caused the extinction of many native species (Davis 2003; Sax and Gaines 2008). For example, the introduction of mammalian predators has caused the extinction of many island-endemic birds (Blackburn et al. 2004). Other examples include the accidental introduction of the brown tree snake, *Boiga irregularis*, to Guam, which led to a dramatic population decrease or the extinction in some native birds, bats, and reptiles (Fritts and Rodda 1998). Furthermore, intentional introductions of the snail-eating land snail, *Euglandina rosea*, on several Pacific islands to control the giant African snail, *Achatina fulica*, has resulted in the extinction of various native land snail species (Civeyrel and Simberloff 1996; Cowie 2001; Lydeard et al. 2004). Additionally, intense herbivory by introduced mammals such as goats has caused the extinction of or decline in native plant species on islands (e.g., Campbell and Donlan 2005). Therefore, top-down impacts by introduced predators and herbivores may be a more important factor driving the extinction and decline of native species than resource competition with introduced species in island ecosystems (Sax and Gaines 2008). However, few studies have investigated the relative

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importance of intertrophic (predation or herbivory) and intratrophic interactions (resource competition) between introduced and native organisms on oceanic islands.

Clarifying the relative importance of trophic and competitive interactions with introduced species on oceanic islands would not only contribute to a better understanding of how island communities can be structured by species interactions, but would also facilitate the development of eradication strategies to mitigate the impacts of introduced species on island-endemic organisms. For example, introduced predators and/or herbivores should be eradicated before introduced competitors to conserve island-endemic species, if introduced predators exert a greater impact on endemic species than do introduced competitors. In this article, I surveyed the literature on introduced and native species of the oceanic Ogasawara Archipelago to clarify which intertrophic or intratrophic interactions with introduced species have significantly negatively affected the oceanic island's biota.

The Oceanic Ogasawara Archipelago

The Ogasawara (Bonin) Islands are subtropical islands located in the western Pacific Ocean approximately 1000 km south of the largest island (Honshu) of Japan (20°25′–27°40′ N, 136°13′–153°59′ E; Ogasawara Village, Tokyo Metropolitan, Japan; Shimizu 2003). The archipelago comprises four island groups: the Mukojima, Chichijima, Hahajima, and Kazan Retto (Volcano) Islands. Three islands, Chichijima, Hahajima, and Iwoto, are inhabited, while the others are uninhabited. The mean annual temperature is 23.0 °C, and the mean annual precipitation is 1269 mm based on measurements taken from 1969 to 2014 (Chichijima Meteorological Station, 27°55′ N, 142°11′ E). The total land area of the islands is approximately 106 km^2, which is much smaller than that of many continental islands (Toyoda 2003). Like other oceanic islands, the Ogasawara Islands support many endemic organisms, including vascular plants (137 species; Toyoda 2003), land birds (four species and nine subspecies; Kawakami 2008), insects (379 species; Kishimoto 2010), and land snails (98 species; Chiba 2009). However, many exotic species have been introduced and established on the islands (Kawakami 2008). Thus, the Ogasawara Islands provide a useful site for investigating the negative impacts of introduced species on oceanic island biota.

Literature survey

To study the effects of introduced species on native biota, I surveyed papers and book chapters of terrestrial organisms that either are or were found in the Ogasawara Islands using the online search engines Google Scholar and Web of Science®. The keywords 'Ogasawara Islands' and 'Bonin Islands' were used for the online search. Papers and reports published in the local journals *Ogasawara Research* and *Ogasawara Kenkyu Nenpo* (*Annual Report of Ogasawara Research*) were also surveyed (up to March 2015). Aquatic organisms were not included in this survey. In each paper, I looked for the negative effects of introduced species on native species in terms of intertrophic and intratrophic interactions (Table 1, Appendix Table 2). Introduced species can reduce the potential resources available to native species and/or become mortality factors. I considered such cases negative impacts of introduced species on natives. Introduced and native species can interact either across different trophic levels (intertrophic interactions) or within a single trophic level (intratrophic interactions); intertrophic interactions include predator–prey and herbivore–plant relationships, while intratrophic interactions include exploitative competition for resources (c.f., Gonzales and Arcese 2005). For extinct and declining native species at local sites and/or islands, I considered studies that reported direct observations of feeding on native species by introduced species as evidence of predation and herbivory impacts. Gut content analysis that documented feeding on native species by introduced species was also considered evidence of predation. Native species that are in decline can share resources (e.g., foods) with introduced species. I considered such resource sharing between native and introduced species a competition impact.

Disturbance by introduced species (e.g., disturbance of seabird colonies by goats) is an important factor leading to the local extinction of native species (Chiba et al. 2007). Other factors can also affect local extinction of and/or declines in native organisms; e.g., habitat destruction by human activities affects native biota (Shimizu 2003; Toyoda 2003; Chiba et al. 2009). These impacts were not included in this survey. Additionally, positive impacts of introduced species on native organisms and negative impacts of native species on introduced species were excluded from this study.

Intertrophic interactions

Predation

Many diurnal insect populations have been declining as a result of predation by introduced lizards (Fig. 1a, d) (Karube and Suda 2004; Makihara et al. 2004; Abe et al. 2008a). The green anole lizard, *Anolis carolinensis*, which was originally distributed in the southeastern United States and the Caribbean islands, was introduced to the Ogasawara Islands in the 1960s (Hasegawa et al. 1988; Toda et al. 2010; Sugawara et al. 2015). This arboreal lizard is a diurnal ambush hunter (Toda et al. 2010). Gut content analysis and feeding experiments have indicated that green anoles prey on various arthropods (ants, bees, wasps, flies, beetles, bugs, butterflies, moths, and spi-

Table 1 Summary of negative impacts of introduced species on native organisms in the Ogasawara Islands

Native organisms[a]	Impacts by introduced species[b]	
	Intertrophic interactions (predation/herbivory)	Intratrophic interactions (resource competition)
Arthropod		
Ants	Green anole, cane toad	Ant
Bees	Green anole	Honeybee
Wasps	Green anole	
Butterflies	Green anole	
Cicada	Green anole, cat	
Damselflies	Green anole, mosquitofish	
Crickets	Cane toad	
Ground beetles	Cane toad	
Diving beetles	Cane toad	
Longicorn beetles	Green anole	
Weevils	Green anole	
Isopods	Cane toad	
Mollusk		
Land snails	Flatworms, predatory snail, cane toad, green anole, black rat, pig	Land snails
Reptile		
Skinks	Green anole, cat	Green anole
Bird		
Land birds	Cat	Black rat
Sea birds	Cat, black rat	
Plant		
Herbs	Goat, black rat, land snails	
Palms/pandanus	Goat, black rat, weevil	
Trees/shrubs	Goat, black rat, land snails	Trees/shrubs

References: see Appendix Table 2

[a] Native organisms; ants, e.g., *Camponotus ogasawarensis*; bees, e.g., *Heriades fulvohispidus*, *Hylaeus* spp.; wasps, e.g., *Stenodynerus ogasawarensis*; butterflies, *Celastrina ogasawaraensis*; cicada, *Meimuna boninensis*; damselflies, e.g., *Ischnura ezoin*; crickets, e.g., *Velarifictorus politus*; ground beetles, e.g., *Chlaenius ikedai*; diving beetles, *Copelatus ogasawarensis*; longicorn beetles, e.g., *Chlorophorus* spp.; weevils, *Ogasawarazo* spp.; isopods, e.g., *Ligia boninensis*; land snails, e.g., *Mandarina* spp., *Boninosuccinea* spp.; land birds, e.g., *Columba janthina nitens*; sea birds, e.g., *Bulweria bulwerii*; skinks, *Cryptoblepharus boutonii nigropunctatus*; herbs, e.g., *Crepidiastrum grandicollum*; palms/pandanus; *Clinostigma savoryana*, *Pandanus boninensis*; trees/shrubs, e.g., *Morus boninensis*, *Lobelia boninensis*

[b] Introduced species; ant, *Pristomyrmex punctatus*; black rat, *Rattus rattus*; cane toad, *Bufo marinus*; cat, *Felis catus*; flatworms, e.g., *Platydemus manokwari*, *Platydemus* spp., *Bipalium* sp.; goat, *Capra aegagrus*; green anole, *Anolis carolinensis*; honeybee, *Apis mellifera*; land snails, e.g., *Achatina fulica*; mosquitofish, *Gambusia affinis*; pig, *Sus scrofa domesticus*; predatory snail, *Euglandina rosea*; trees/shrubs; e.g., *Bischofia javanica*, *Casuarina equisetifolia*, *Leucaena leucocephala*, *Pinus luchuensis*; weevil, *Rhabdoscelus obscurus*. Underlined species are considered to have substantially impacted native species

ders), skinks, and arboreal snails (Table 1) (Karube and Suda 2004; Makihara et al. 2004; Abe et al. 2008a; Takahashi et al. 2014). Comparisons of native species densities between anole-invaded and uninvaded sites (islands) have revealed that anole predation has caused the local extinction of and/or rapid declines in native damselflies, butterflies, bees, weevils, and longicorn beetles (Table 1) (Makihara et al. 2004; Karube and Suda 2004; Karube 2004a, b; Takakuwa and Suda 2004; Abe et al. 2008a; Sugiura et al. 2009; Abe et al. 2011b).

The cane toad, *Bufo marinus*, which derives from Central and South America, was intentionally introduced to the islands in 1949 (Matsumoto et al. 1984). Gut content analysis has indicated that cane toad adults prey on various soil animals, such as ground beetles, crickets, isopods, and land snails, suggesting that cane toads may have impacted nocturnal ground-dwelling arthropods (Table 1) (Matsumoto et al. 1984; Karube 2004a; Kishimoto 2009). In fact, an endangered carabid species, *Chlaenius ikedai*, was found in the gut of a cane toad (Kishimoto 2009). However, whether cane toads have caused the rapid declines in native arthropods remains unclear because few studies have compared the densities of native arthropods between toad-invaded and uninvaded sites (Hasegawa et al. 2009).

Native land snails, most of which are endemic species in the islands (Chiba 2009), have either become extinct or have been declining as a result of predation by introduced flatworms (Fig. 1b, e) (Ohbayashi et al. 2007; Sugiura and Yamaura 2009; Sugiura 2009; Chiba and Roy 2011). The flatworm, *Platydemus manokwari*, which was first discovered in New Guinea, was introduced to the inhabited island Chichijima in the early 1990s (Kawakatsu et al. 1999). Field and laboratory observations have indicated that *P. manokwari* prey on various soil animals, such as land snails, earthworms, and isopods (Ohbayashi et al. 2005; Sugiura 2010c). Although *P. manokwari* has rarely been observed feeding on endemic snails in the field, investigations of surviving snails between flatworm-invaded and uninvaded sites have indicated that *P. manokwari* predation may have caused the local extinction of native snails on Chichijima (Su-

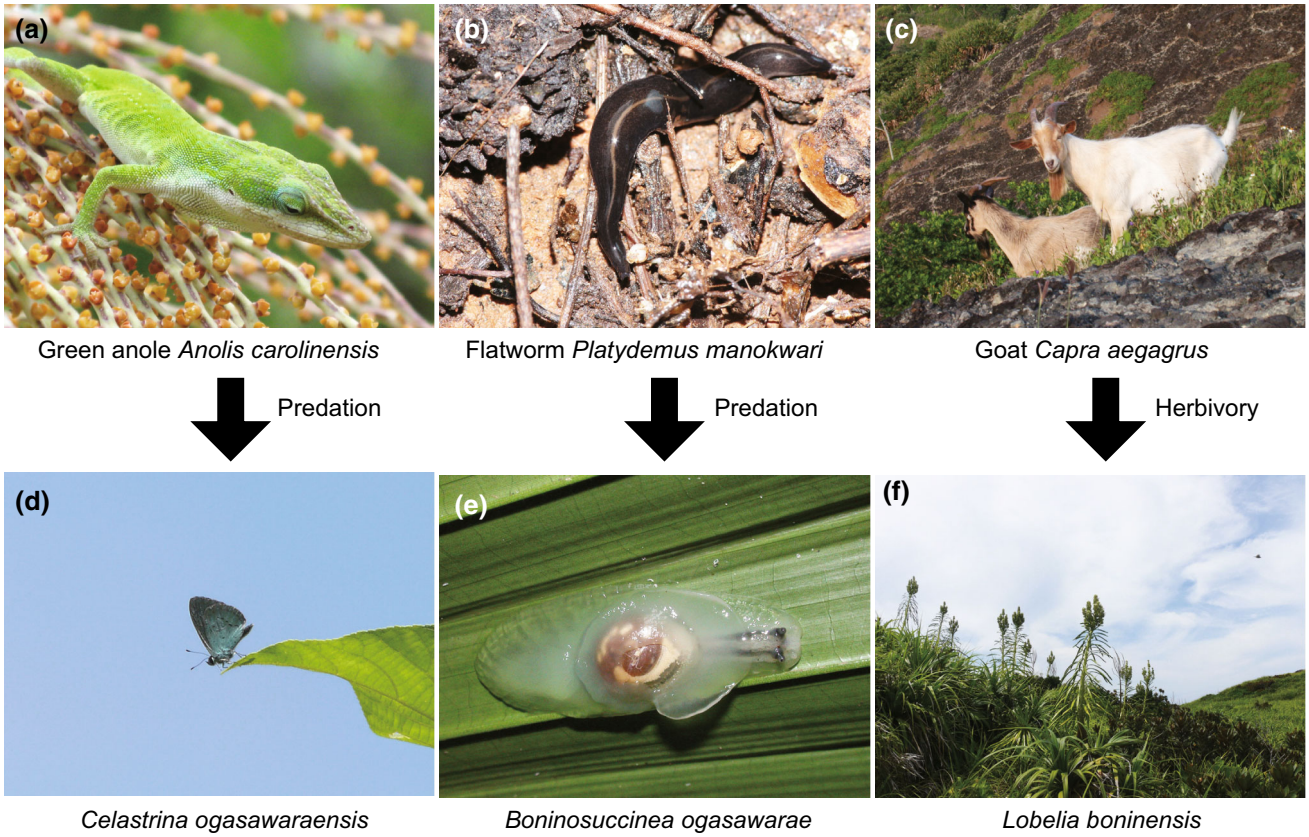

Fig. 1 Representative examples of top-down impacts by introduced species on native species in the Ogasawara Islands. **a** introduced green anole lizard, *Anolis carolinensis*; **b** introduced flatworm, *Platydemus manokwari*; **c** introduced goat, *Capra aegagrus*; **d** endemic butterfly, *Celastrina ogasawaraensis*; **e** endemic snail, *Boninosuccinea ogasawarae*; **f** endemic plant, *Lobelia boninensis*

giura et al. 2006; Ohbayashi et al. 2007). *Platydemus manokwari* also climbs trees and attacks arboreal snails, in addition to ground-dwelling snails (Sugiura and Yamaura 2009). Although *P. manokwari* has not invaded most of the Ogasawara Islands (Kawakatsu et al. 1999), other snail-eating flatworm species (e.g., unidentified species of the genus *Bipalium*) have invaded many parts of the islands (Okochi et al. 2004). Field experiment and distribution studies have indicated that these snail-eating flatworms have also reduced native land snail numbers (Okochi et al. 2004; Chiba et al. 2009). Furthermore, the introduced black rat, *Rattus rattus*, reportedly preys on land snails (Chiba 2007, 2010a, b). Several species of snails have been declining in a shelter-poor habitat because of rat predation on one of the uninhabited islands (Chiba 2007).

Native skinks have been declining as a result of predation by introduced lizards and cats (Suzuki and Nagoshi 1999; Kawakami and Mashiko 2008; Takahashi et al. 2014). Gut content analysis has indicated that the introduced green anole lizard, *A. carolinensis*, frequently attacks the native skink *Cryptoblepharus boutonii nigropunctatus* (Suzuki and Nagoshi 1999; Takahashi et al. 2014). Skink density has been declining on the inhabited island Chichijima, while anole density has remained high (Toda et al. 2010), suggesting that anole predation is responsible for the decrease in the native skink population. Analysis of fecal samples has also indicated that the introduced cat, *Felis catus*, preys on the native skink (Kawakami and Mashiko 2008), although no studies have provided sufficient evidence of declines in native skink populations because of cat predation.

Seabird colonies have been disappearing on the islands and are now rarely found on inhabited islands (Chiba et al. 2007). The introduced cat has been observed attacking an adult brown booby, *Sula leucogaster*, on the inhabited island Hahajima (Horikoshi et al. 2009). Hence, introduced cats are thought to have caused the destruction of seabird colonies on inhabited islands (Horikoshi et al. 2009; Kawakami et al. 2010). Although seabird nests are more abundant on uninhabited than inhabited islands, the introduced rat reportedly preys on adults and eggs of the Bulwer's petrel, *Bulweria bulwerii*, on one of the uninhabited islands (Horikoshi et al. 2009; Yabe et al. 2009; Kawakami et al. 2010). High densities of seabird nests are found on the uninhabited island Minami-iwo-to, where no mammals have been introduced (Kawakami et al. 2008), indicating that introduced cats and rats have strongly impacted seabirds on the islands that they have invaded.

Land birds may have also been impacted by introduced cats and rats (Kawakami and Higuchi 2002; Kawakami and Mashiko 2008; Yabe et al. 2009). Analysis of cat prey items and fecal samples collected from an inhabited island has suggested that cats prey upon the endangered greenfinch, *Carduelis sinica kittlitzi*, and other native birds (Kawakami and Higuchi 2002; Kawakami and Mashiko 2008). However, whether introduced cats have caused the rapid declines in the native bird populations remains unclear because few studies have compared the densities of native land birds between cat-invaded and uninvaded areas.

Herbivory

Native herbs, shrubs, trees, and palms have been impacted by introduced goats and rats (Fig. 1c, f) (Yasui 2002; Shimizu 2003; Abe 2007). The goat, *Capra aegagrus*, which was introduced to the islands in the early days of human settlement, feeds on the seedlings and saplings of most trees, resulting in the destruction of island forest ecosystems (Yasui 2002; Shimizu 2003). On the uninhabited Mukojima Islands, vegetation has completely changed from dense forests to grassland because of the extremely high density of goats (Shimizu 1993,2003; Yasui 2002). Goats have also caused local extinctions and population declines in endangered plants, such as *Lobelia boninensis* and *Crepidiastrum grandicollum*, in the archipelago (Ono 1998). Furthermore, the introduced rat reportedly eats and/or damages the seeds, fruits, and twigs of many native plant species (Toyoda 2003; Watanabe et al. 2003; Yamashita et al. 2003; Abe 2007; Hashimoto 2010; Yabe et al. 2010; Abe and Umeno 2011). Although reports on the negative impacts of introduced phytophagous insects on native plants are rare (Sugiura 2010a), the introduced weevil, *Rhabdoscelus obscurus*, reportedly damages the basal parts of leaves in the endemic palm *Clinostigma savoryana* (Karube et al. 2008, 2009).

Intratrophic interactions

Interspecific competition

Native herbs, shrubs, trees, and palms have been impacted by introduced plant species, e.g., *Bischofia javanica* and *Casuarina equisetifolia* (Shimizu 2003; Toyoda 2003; Hata et al. 2010a, b). The tall tree species *B. javanica*, which was introduced and planted in the Ogasawara Islands before 1905 as a forestry tree, has invaded native forests via bird-dispersed seeds (Shimizu 2003). *Bischofia javanica* has advantageous features in terms of competition for resources with other plants, which include rapid seedling and sapling growth, vigorous sprouting ability, shade-tolerant juveniles, and high fecundity (Yamashita et al. 2000, 2003; Shimizu 2003). Hence, *B. javanica* has gradually replaced native forests (Tanaka et al. 2010). The endangered tree *Morus boninensis*, which was a representative tree in mesic forests, may have been affected by competition with *B. javanica* (Kawahara and Yoshimaru 2002). Another introduced tree species, *C. equisetifolia*, which was introduced to the islands for forestry in 1905, has invaded grasslands and dry forests (Toyoda 2003; Abe et al. 2011a; Sugiura et al. 2013). Large quantities of *C. equisetifolia* litter prevent native plant seedlings from establishing (Hata et al. 2010a, b). Hence, *C. equisetifolia* is considered to have competitively excluded native trees. Other introduced plants, such as *Leucaena leucocephala*, outcompete native plant species in disturbed environments and become dominant (Shimizu 2003; Toyoda 2003; Hata et al. 2007). Thus, resource competition with introduced plant species has negatively impacted native plant species.

Native bees may have been impacted by introduced honeybees (Kato 1992; Kato et al. 1999). The Ogasawara Islands support nine native bee species, all of which are solitary; i.e., the islands originally lacked eusocial bees such as honeybees and bumblebees (Kato 1992; Kato et al. 1999). The European honeybee, *Apis mellifera*, which was introduced to the islands for apiculture in the 1880s, competes for flower resources (pollen and nectar) with native bees (Kato 1992; Kato and Nagamasu 1995; Kato et al. 1999). Because the honeybees' competitive ability in foraging is superior to that of solitary bees, they have impacted native bee fauna through exploitative competition for flower resources in various parts of the world (Traveset and Richardson 2006; but Paini 2004). Comparison of native bee densities between honeybee-invaded islands and uninvaded islands has suggested that the presence of honeybees has been decreasing native bee numbers on the Ogasawara Islands (Kato 1992; Kato et al. 1999).

The endemic ant, *Camponotus ogasawarensis*, has been observed escaping from the introduced ant, *Pristomyrmex punctatus*, on native plants (Sugiura 2010b). When introduced *P. punctatus* worker ants were experimentally excluded from native plants, *C. ogasawarensis* visited the extrafloral nectaries immediately after the exclusion (Sugiura 2010b). Therefore, native ants may suffer from interference or exploitative competition with introduced ants. However, no studies have provided sufficient evidence of either declines in or extinction of native ants as a result of such competition.

Native land snails are rarely found on inhabited islands where introduced land snails are abundant (Tomiyama 1991), suggesting that introduced land snails may have reduced native snail numbers (Tomiyama 1991, 2002). However, there have been no experimental studies to clarify the importance of resource competition between native and introduced land snails.

The native skink, *C. boutonii nigropunctatus*, may have suffered from resource competition with the introduced anole lizard, *A. carolinensis* (Suzuki and Nagoshi 1999). The prey items of these two species

partially overlap (Suzuki and Nagoshi 1999). Such competition is supported by the declining density of native skinks and the increasing density of introduced lizards on Chichijima (Toda et al. 2010).

Native land birds may also have suffered from resource competition with introduced species (Takano 2002; Toyoda 2003). The introduced rat *R. rattus* feeds on the seeds of many native trees such as *Elaeocarpus photiniaefolius* (Yamashita et al. 2003), resulting in less food (native tree seeds) for the endangered wood pigeon, *Columba janthina nitens* (Takano 2002; Toyoda 2003). However, few studies have elucidated the negative impacts of resource competition on *C. janthina nitens*. Additionally, the introduced white-eye *Z. japonicus*, which has led to decreased juvenile survival in native birds through resource competition in the Hawaiian Islands (Freed and Cann 2009), has had no impact on the native white-eye, *Apalopteron familiare*, in the Ogasawara Islands (Kawakami and Higuchi 2003).

Relative importance of intertrophic and intratrophic interactions

The present literature survey has revealed that the impacts of introduced predators and herbivores have been more frequently documented than those by introduced competitors. Nineteen groups have suffered from either predation or herbivory by introduced species, while only six (31.6 %) of these groups could have been negatively impacted by introduced competitors (Table 1). Does this suggest that introduced predators and herbivores have affected native species more than introduced competitors? Predation and herbivory can be more important factors in native species mortality than resource competition. However, predation and herbivory may be more easily observed in the field and/or gut content analysis than interspecific competition. In this section, I focus on the native species that have been affected by both predation (or herbivory) and interspecific competition to discuss the relative importance of each.

Predation and interspecific competition in bees

Introduced honeybees have reportedly reduced native bee populations through resource competition (Kato 1992; Kato et al. 1999). However, the native bee, *Lithurgus ogasawarensis*, which is in decline, does not appear to share flower resources (*Hibiscus* spp.) with introduced honeybees (Goubara 2002). Furthermore, not all native bees have declined, e.g., the largest bee, *Xylocopa ogasawarensis*, which frequently shares flower resources with honeybees, is a common flower visitor on inhabited islands where introduced honeybees are abundant (Abe et al. 2008a; Sugiura 2008). This cannot be explained by resource competition with honeybees. Recent studies have reported the importance of predation by the introduced lizard *A. carolinensis* in the decline of native bees (Karube and Suda 2004; Abe et al. 2008a). Small bees, which can be easily preyed upon by the introduced lizard, have been declining on the inhabited islands that *A. carolinensis* has invaded, while the large bee, *X. ogasawarensis*, which is too large for *A. carolinensis* to feed on, has not declined on any of the islands (Karube and Suda 2004; Makihara et al. 2004; Abe et al. 2008a, 2011b). Therefore, predation by introduced lizards has more likely reduced native bees than resource competition with introduced honeybees (Karube and Suda 2004; Abe et al. 2008a).

Predation and interspecific competition in land snails

Introduced land snails, such as *A. fulica*, may have reduced native snail numbers (Tomiyama 1991, 2002), although few studies have provided clear evidence of interspecific resource competition between the two. Even when native and introduced land snails apparently use the same habitat, introduced species can indirectly reduce native populations via shared introduced predators (apparent competition; Holt and Lawton 1994); i.e., a prey species (introduced land snail) with a high population growth rate can greatly impact another prey species (native land snail) with lower population growth by enabling the density of a shared predator (introduced flatworm or rat) to increase. In fact, introduced flatworms, such as *P. manokwari*, have been reported to eat introduced snails and earthworms and maintain high population densities in areas where native snails are extinct (Ohbayashi et al. 2005; Sugiura et al. 2006; Sugiura 2010c). Thus, predation by introduced species is a more important factor in the extinction of and decline in native land snails than resource competition with their introduced counterparts.

Predation and interspecific competition in native skinks

Introduced anole lizards have reportedly reduced native skink populations through predation and resource competition (Suzuki and Nagoshi 1999; Takahashi et al. 2014). However, anole predation has likely been the stronger factor in reducing *C. boutonii nigropunctatus* density. Predation by *A. carolinensis* has become a more direct mortality factor in native skink populations than has interspecific competition with *A. carolinensis* (Suzuki and Nagoshi 1999).

Herbivory and interspecific competition in plants

Several studies have provided clear evidence of interspecific competition among native and introduced plant species (Table 1, Appendix 2). However, seed predation

and/or herbivory as well as interspecific competition may have impacted native plant species (Shimizu 2003; Toyoda 2003; Hashimoto 2010); for example, seed predation on the native tree *E. photiniaefolius* by introduced rats was much higher than that on the introduced tree *B. javanica*, and seedling survival (higher shade tolerance) in the first 2 years was significantly higher in *B. javanica* than in *E. photiniaefolius* (Yamashita et al. 2003). Additionally, goats eat the seedlings of many native trees (Shimizu 1993, 2003; Toyoda 2003). Thus, native plant species that have competed with introduced plant species have also been impacted by introduced herbivores, although which introduced competitors and herbivores have significantly harmed native plants remains unclear.

Conclusions

In this study, I investigated intratrophic and intertrophic interactions by introduced species that have had significant negative impacts on native species in the Ogasawara Islands. Many native species have been negatively impacted by introduced predators and herbivores (Table 1). Several native plant and bee species have suffered from resource competition with introduced species (Table 1). However, native species that have competed with introduced species have also been impacted by introduced predators and herbivores (e.g., apparent competition) (Table 1). Furthermore, predation and herbivory are likely to be more direct factors in mortality than resource competition. Introduced predators and herbivores combined have negatively affected native organisms more than introduced competitors in the Ogasawara Islands. This suggests that in the conservation of the island biota, it is important to prevent further introductions of predacious and herbivorous animals and to eradicate previously introduced predators and herbivores.

Can this scenario be applied to other oceanic islands? Because predation and herbivory may have been more frequently detected than interspecific competition in my literature survey, more quantitative data (e.g., numbers of introduced predator and competitor species) will be needed to apply this scenario to other islands.

Acknowledgments I thank the Ecological Society of Japan for the honor of receiving the 18th Denzaburo Miyadi Award and the editors of *Ecological Research* for their invitation to submit this article. The editors and reviewers also provided helpful suggestions on the manuscript. This study was based on discussions with many researchers, and their advice, considerations, and encouragement are greatly appreciated.

Appendix

See Table 2.

Table 2 Literature cited for negative impacts of introduced species on native organisms in the Ogasawara Islands

Invasion impacts	Native organisms	Introduced organisms	References
Predation	Ants	Green anole	Makihara et al. (2004); Karube and Suda (2004); Toda et al. (2010); Takahashi et al. (2014)
		Cane toad	Matsumoto et al. (1984); Kishimoto (2009)
	Bees	Green anole	Karube and Suda (2004); Abe et al. (2008a); Takahashi et al. (2014)
	Wasps	Green anole	Takahashi et al. (2014)
	Butterflies	Green anole	Takakuwa and Suda (2004); Makihara et al. (2004); Yago (2014)
	Cicada	Green anole	Makihara et al. (2004); Karube and Suda (2004)
		Cat	Kawakami and Mashiko (2008)
	Damselflies	Green anole	Karube (2004b); Makihara et al. (2004); Yoshimura and Okochi (2005)
		Mosquitofish	Yoshimura and Okochi (2005)
	Crickets	Cane toad	Kishimoto (2009)
	Ground beetles	Cane toad	Karube and Suda (2004); Kishimoto (2009)
	Diving beetles	Cane toad	Kishimoto (2009)
	Longicorn beetles	Green anole	Makihara et al. (2004); Karube and Suda (2004; Takahashi et al. (2014)
	Weevils	Green anole	Makihara et al. (2004); Karube and Suda (2004); Takahashi et al. (2014)
	Isopods	Cane toad	Kishimoto (2009)
	Land snails	Flatworms	Okochi et al. (2004); Ohbayashi et al. (2005, 2007); Sugiura et al. (2006); Sugiura and Yamaura (2009); Sugiura (2010c); Chiba and Roy (2011)
		Predatory snail	Tomiyama (2002)
		Cane toad	Matsumoto et al. (1984); Kishimoto (2009)
		Black rat	Chiba (2007, 2010a, b)
		Green anole	Takahashi et al. (2014)
		Pig	Tomiyama (1991, 2002)
	Skinks	Green anole	Suzuki and Nagoshi (1999); Toda et al. (2010); Takahashi et al. (2014)
		Cat	Kawakami and Mashiko (2008)
	Land birds	Cat	Kawakami and Higuchi (2002); Kawakami and Mashiko (2008)

Table 2 continued

Invasion impacts	Native organisms	Introduced organisms	References
	Sea birds	Cat	Kawakami and Fujita (2004); Kawakami and Mashiko (2008)
		Black rat	Chiba et al. (2007); Yabe et al. (2009); Horikoshi et al. (2009); Kawakami et al. (2010)
Herbivory	Herbs	Goat	Shimizu (1993); Yasui (2002); Toyoda (2003)
		Black rat	Shimada and Goto (2014)
		Land snail	Toyoda (2003)
	Palms/pandanus	Goat	Shimizu (1993); Yasui (2002);
		Black rat	Watanabe et al. (2003); Abe (2007)
		Weevil	Karube et al. (2008, 2009)
	Trees/shrubs	Goat	Shimizu (1993); Yasui (2002); Toyoda (2003); Abe et al. (2008b)
		Black rat	Toyoda (2003); Watanabe et al. (2003); Yamashita et al. (2003); Abe (2007); Yabe et al. (2010); Abe and Umeno (2011)
		Land snail	Toyoda (2003)
Resource competition	Ants	Ant	Sugiura (2010b)
	Bees	European honeybee	Kato (1992); Kato and Nagamasu (1995); Kato et al. (1999)
	Land snails	Land snail	Tomiyama (1991, 2002)
	Skinks	Green anole	Suzuki and Nagoshi (1999); Toda et al. (2010)
	Land birds	Black rat	Takano (2002); Toyoda (2003)
	Trees/shrubs	*Bischofia javanica*	Yamashita et al. (2000, 2003); Kawahara and Yoshimaru (2002); Toyoda (2003); Shimizu (2003)
		Pinus lutchuensis	Shimizu and Tabata (1985)
		Casuarina equisetifolia	Hata et al. (2010a, b)
		Leucaena leucocephala	Hata et al. (2007)
	Herbs	*Leucaena leucocephala*	Hata et al. (2010c)

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