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REVIEW

Natural mixing of species: novel plant–animal communities on Caribbean Islands

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Abstract

Global anthropogenic activities are responsible for the modification of landscapes, creation of novel environments and movement of species across biogeographic regions. A consequence of this activity is the mixing of native and introduced species and the formation of novel biotic communities. We review the ecological consequences of the mixing of native and introduced species in the Caribbean Islands especially in Puerto Rico and the US Virgin Islands. Here we found documented examples indicating that novel communities of native and naturalized organisms are ubiquitous. The coexistence of species originating from different biogeographical regions raises research questions that demand attention for their ecological and conservation importance. For example: Is animal abundance in novel communities a measure of habitat quality? To what degree are populations in novel communities self-sustaining? What are the consequences of species eradication? How does an introduced animal's trophic position affect its effects on novel and native communities? We suggest that novel communities that emerge in the Caribbean after deforestation and land abandonment could be harbingers of how the biota might respond elsewhere to rapidly changing environmental conditions, including global and climate change.

Introduction

Anthropogenic activities are degrading lands, creating novel environments, extirpating species and accelerating the movement of species across historical biogeographic barriers, which lead to the mixing of organisms from disparate regions. Mixing of organisms occurs as species adopt open niches resulting from environmental changes, now driven by anthropogenic activities but in the past by natural climate and geological change (Williams & Jackson, 2007). Biological invasions and a natural reshuffling of species take place as species fill vacant niches that meet existing or new species-specific requirements. Thus, novel communities of organisms emerge and develop with combinations of species found nowhere else (Hobbs *et al*., 2006). Usually, the new combinations of species include native and introduced species, a situation anticipated by Elton (1958). These novel communities now cover about 35% of the terrestrial surface of the world (Marris, 2009).

In this review, we use Puerto Rico and the US Virgin Islands as an example to describe the species composition of tropical terrestrial communities historically affected by anthropogenic changes. First, we summarize the situation with plants and then review some of the patterns of mixing of introduced and the native animal species in various habitats. Finally, we discuss some of the implications of these patterns of species mixing to conservation and for future research.

Novel plant communities

We start by discussing the extraordinary historical changes in Puerto Rico's vegetation given that plant communities provide the productive and structural base that supports animal communities. The 8959-km^2 island was completely forested when the Europeans arrived, despite earlier occupation by indigenous people (Wadsworth, 1950). By the 1920s, however, Gleason & Cook (1926), in the first systematic assessment of the plant communities, wrote (p 5):

> The dense rural population of Porto Rico, through its constant use of almost all available land for dwellings, agriculture, pasture, lumber and fuel, and through the secondary effect of fire, of drainage, and of irrigation, has destroyed some types of vegetation completely, and with a few exceptions, has modified all the rest to a greater or less degree.

Puerto Rico's forest cover fell from almost 100% in 1493 to 6% by the late 1940s (Birdsey & Weaver, 1987) before recovering to 57% by 2003 because of agricultural abandonment (Brandeis, Helmer & Oswalt, 2007).

The vegetation that emerged from abandoned agricultural lands, which in 1966 covered 68.5% of the island (Picó, 1969), was different from native plant communities present before deforestation (Lugo & Helmer, 2004). These plant communities differed in the diversity of introduced species, which have mixed with the natives to form novel plant communities. For example, of the island's 203 introduced tree species, 118 are regenerating naturally, that is are naturalized (Francis & Liogier, 1991). Despite this new mix of species, after several decades, these novel forests develop a physiognomy and structure similar to that of mature native forests (Aide *et al.*, 1996).

We ask whether or not the island fauna has followed the same path as the flora. Have animal species introductions led to new assemblages of organisms? What is the nature and strength of the interactions among introduced plants and native and introduced animals? How do animal interactions play out in native and novel plant communities and habitats? In addressing these questions we shed light on the consequences of species invasions in terrestrial communities and the natural processes of plant and animal community reorganization following anthropogenic disturbances.

The contemporary big picture on animal species diversity in Puerto Rico and the US Virgin Islands

Puerto Rico has about 26 410 species of organisms (plant, macrofungi and animals) with animals representing 43% of the species total (Joglar, 2005). The number of species in most animal taxa has increased with human introductions making introduced species a substantial component of the biota of Puerto Rico (Table 1) and the Caribbean (Kairo *et al.*, 2003; Wege & Anadón Irizarry, 2008). Anthropogenic activities have also facilitated the natural spread of species across islands. For example, natural colonization from South America by Cattle Egrets (*Bubulcus ibis*) and Shiny Cowbirds (*Molothrus bonariensis*) through the Lesser Antilles into Puerto Rico and other islands was likely facilitated by the human creation of pastures and croplands (Post & Wiley, 1977; Arendt, 1988). In the last 100 years, the creation of scrublands, ecotones and pastures on adjacent islands aided the natural colonization of similar habitats on Puerto Rico by doves (*Zenaida asiatica* and *Z. macroura*) and a flycatcher, *Elaenia martinica* (Raffaele, 1989*a*). Moreover, human introductions have increased Puerto Rico's finches from three native seed-eaters to a remarkable 20 species, mostly introduced from Africa and Asia. Similarly, there are now 10 introduced psittacine species (5 parakeets, 4 parrots, 1 macaw, all introduced from the Neotropical mainland or from nearby islands) where before there were only two native species (extirpated *Aratinga portoricensis* and critically endangered *Amazona vittata*, Raffaele, 1989*a*,*b*).

The introduced finch success is mostly attributed to human disturbances, which produced novel grassland habitats of several types (Raffaele, 1983, 1989*b*). Likewise, essentially all introduced psittacines occur in or near urban habitats and novel forests where they feed on a mixture of native and introduced seeds and fruits (Raffaele, 1989*a*). Introduced finch species differ moderately from each other and from natives in patterns of resource use and behavior (Raffaele, 1989*b*). Some introduced species quickly adapted to the new environments by shifting to habitats different than those used in their native range. The finches *Lonchura cucullata* and *Estrilda melpoda* have accrued significant changes to bill size (including sex differences) since their introduction more than 100 years ago (Raffaele, 1989*b*). These changes contrast with the lack of variability and sex differences in native African populations, and are thought to reflect adaptations to novel food sources in novel Puerto Rican plant communities, as well as intra- and interspecific competition (Raffaele, 1986).

Thus, the big picture of diversity in these islands reveals large numbers of introduced species, many of which are naturalized and even locally adapted to the novel plant communities that now dominate the islands. Still, relatively few of the native and endemic species have become extinct (Table 1), suggesting that integration of native animals into novel plant and animal communities is possible. In the following sections, we describe examples of novel communities and characterize the nature of the interactions that occur between native and introduced animals with native and/or novel plant communities.

Table 1 Approximate number of extant (still living) and extinct and/or extirpated animal species in Puerto Rico by major taxa

Animal group	Number of species	Percent introduced
Insects (Insecta)	5373	?
Oligochaetes[a]	29	39.3
Formicidae[b]	77	23.4
Other invertebrates	4596	?
Fish	983	?
Amphibians	24	25.0
Extinct amphibians	3 (3)	0
Reptiles	55	7.3
Extinct reptiles	0	0
Birds[c]	354	12.7
Extinct birds[d]	9 (3)	0
Marine mammals	27	0
Terrestrial mammals (bats)	16	0
Terrestrial mammals (quadrupeds)	13	100
Extinct terrestrial mammals	6	0
All mammals	62	16.1
Total animal species	11 617	

The 'extinct species' category is only for species that became extinct within the last millennia, numbers in parenthesis are for species extinct since the European colonization. Question mark indicates unknown percentage introduced. The area of Puerto Rico is 8990 km^2. Unless indicated otherwise, the source is Joglar (2005).

[a] Borges 1996.

[b] Torres and Snelling 1997.

[c] Wege and Anadón Irizarry 2008.

[d] Raffaele 1989a.

Native birds in plantations of introduced species

Puerto Rico's native terrestrial avifauna is dominated by forest dwellers, given the prehistoric predominance of forest cover, and thus, few native species specialize in open habitats (Acevedo & Restrepo, 2008). Because of extensive deforestation, seven out of 60 of the native terrestrial bird species were extirpated (Brash, 1987). Surviving species used forest fragments and/or novel habitats such as plantations. Coffee plantations shaded with a mix of native and introduced canopy trees were believed by Brash to be especially important in limiting extinctions during the deforestation period because they accounted for a considerable portion of the remaining tree cover and likely served as refugia for birds. Native birds continue to forage in these plantations, but the berries of the introduced coffee are rarely consumed (Carlo, Collazo & Groom, 2004). Birds also use other types of plantations. For example, Cruz (1987) found 14 native bird species in a 17-year-old mahogany plantation in the Luquillo Mountains. Similarly, 18 native bird species were found in Caribbean pine plantations, where birds that normally foraged in the canopy and edges of native forests shifted to the plantation understory, which had greater resource diversity than the pine canopy (Cruz, 1988). Pine plantations were also attractive to birds (21 native species) relative to nearby native forest (18 native species) in Cayey where the plantations' physiognomy and understory plants were key attractants (Collazo & Bonilla Martínez 1988). These studies indicate that native bird species will use plantations of introduced tree species as long as plantations develop the physiognomy, vertical stratification structure and understory food sources typical of native forests.

Birds in gradients of native to urban forest

Avian density increased in Puerto Rico along a gradient from wet native forest to exurban to suburban and urban centers (Fig. 1). The density of native birds peaked in the suburban environment, but the density of introduced species, although lower than that of native species, increased almost linearly with developed land cover, while the density of synanthropic species was highest in the urban environment. Synanthropic species are those that benefit from human presence and include both native and introduced species. Native endemic species (found only in Puerto Rico) were most abundant and speciose in native forest, in contrast to native and introduced species, which were more abundant and speciose in urban and suburban habitats. Avian species' density was greatest in the suburban habitats, where native species predominated (seven species to two) despite the prevalence of introduced plants in these environments (Lugo & Brandeis, 2005). Granivores, both native and introduced, were common in habitats where grass seeds were available, but absent in forests where grass seeds were unavailable because of the closed canopy. The abundance of avian granivores is high in urban environments because of the abundance of grasses (Chace & Walsh, 2006) following deforestation, but the abundance of nectarivores (native and introduced) was unexpectedly high and attributed to ornamental flower availability. Native and introduced omnivores were also abundant in urban areas, suggesting that omnivory contributed to urban colonization. A common omnivorous native species in urban habitats was the flycatcher *Tyrannus dominicensus*, which benefited from abundant insect prey attracted to lights at night and reduced nest predation from nesting in utility poles (Vázquez Plass, 2008). In addition to increased food supplies and nesting success, Vázquez Plass also hypothesized that demographic traits, such as multiple broods contribute to abundant urban bird populations.

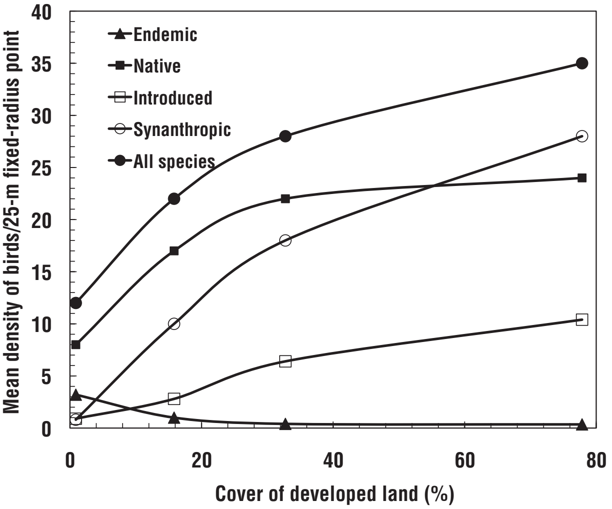

Figure 1 Density of birds in relation to the per cent cover of developed land in northeastern Puerto Rico (Vázquez Plass 2008). Each point on the *x*-axis from left to right corresponds to the following descriptive habitats in terms of per cent cover of developed land: native forest, exurban land, suburban land and urban core. Each line is plotted independently of the others, that is synanthropic species include both native and introduced species, native species include endemic ones, etc. Synanthropic species are those associated with, and which benefit from humans.

The urban environment, including the suburban environment, is not as homogeneous as one might surmise. It contains habitats ranging from pavement to closed canopy forests, pastures, riparian corridors and novel feeding areas such as light poles and gardens where avian guilds can find suitable food sources and breeding sites, which in turn can promote high richness and densities of birds (Germaine *et al.*, 1998). The plant communities of the urban environment include native forests, but are mostly novel communities dominated by introduced plant species. The bird communities are also novel assemblages as they include new combinations of native and introduced avian species as well as new combinations of omnivorous, granivorous and frugivorous species not present in the same proportions in the native forest environments of the Island.

Animals in novel moist forests and grasslands

Communities of reptiles, amphibians and birds in moist novel forests in Puerto Rico are mostly composed of native species (Rios López & Aide, 2007; Acevedo & Aide, 2008; Herrera Montes & Brokaw, 2010). For example, novel forests dominated by the introduced tree *Spathodea campanulata* had a minimum of 37 animal species present (3 snail species, 4 amphibians, 10 reptiles, 17 birds, 3 mammals) of which 81.1% were native (including an endemic anole) and 18.9% introduced (Abelleira Martínez, 2008). Similarly, novel moist forests had more native ant species (11–13 species) than introduced species (one species; Osorio Pérez, Barberena Arias & Aide, 2007). Over a 40-year successional sequence after pasture abandonment, Herrera Montes (2008) found mostly a native herpetofauna, which maintained densities comparable with native successional series, but changed in species composition as the novel grassland developed into a novel forest. As with birds in tree plantations, as described earlier, the structural attributes of novel forests were similar to those of native forests, thus providing suitable habitats to the native herpetofauna. In contrast to patterns observed in native forest succession, the native frog *Lepthodactylus albilabris* colonized abandoned pastures and bred in water-filled hoof prints, but disappeared with canopy closure, whereas artificial substrates such as pipes provided nest sites for other native anurans in 40-year-old novel forests (Herrera Montes, 2008). Notably, the richness and relative abundance of amphibian and reptile species in these novel forests was similar to those of native forests.

Despite the dominance of introduced plant species in novel montane and karst forests and shaded coffee plantations, Carlo (1999) found that only 2.6% of all avian foraging records (insectivory and frugivory) occurred on introduced plants belonging to seven species, six of which were fleshy-fruited species with zoochorous seeds. Overall, 58.2% of all his avian foraging records were consistently from seven native fruiting plant species, which represented less than 10% of the available tree species. On the one hand, these results underscore the degree to which avian feeding relationships in novel plant communities depend on either native or introduced species, but on the other hand, the results show the formation of a new web of interactions among native and introduced species, which we call novel because of the diverse biogeographic origins of the participating organisms.

Carlo, Flores Mangual and Caraballo Ortiz (in press) reports predation by introduced rodents on seeds of 11 of 23 native plant species that were dispersed by birds under trees in a pasture near secondary forest fragments. In general, rodent predation increased significantly with the density and size of seed species arriving at any given location, but not for all species. Because predation is not random across species, introduced rodent seed predation can act as an ecological filter shaping recruitment, and thus the successional trajectory of novel forests. Similarly, naturalized populations of frugivorous monkey species (*Macaca mulatta* and *Erythrocebus patas*) consume and disperse four native and three introduced plant species in Sierra Bermeja, a location with high levels of endemic as well as introduced plant species (Aukema *et al.*, 2006). The long-term outcome of this seed predation pressure on native plants by introduced rodents and primates where none existed before is unknown. However, one should not ignore the fact that seed predation by introduced species can add a new ecological filter to native and introduced plant regeneration, thus contributing to the development of novelty in plant communities.

Introduced animal species in mature native forests

Three introduced earthworm species occur in mature native forest stands along a 1000-m elevation gradient in the Luquillo Mountains (González *et al.*, 2007). One of them, *Pontoscolex corethrurus*, was dominant in density and biomass throughout the gradient with the exception of the elfin forest at the summit and the lowland wetland and dry forests. Another introduced species, *Ocnerodrilus occidentalis*, dominated in lowland dry forest where native earthworms were absent. Introduced species, however, were absent in *Pterocarpus* and mangrove wetlands. Overall, native earthworms were more speciose (12 species, most in elfin forest) than introduced species and they dominated in lowland wetlands and elfin forests. Hendrix *et al*. (2006) concluded that native and introduced earthworms could coexist as the invasions can occur in the absence of disturbances. Nonetheless, the level of competition from native species may determine the success of introduced species and anthropogenic disturbances (particularly land-cover changes) could tilt the competitive balance in favor of introduced species (González *et al.*, 2006; González, Huang & Chuang, 2008). For example, under plantation conditions only the introduced earthworm species occur (González, Zou & Borges, 1996). In contrast, native and introduced earthworms occurred in adjacent secondary forests, where biomass, density and species richness (5 vs. 2 species) were higher than in plantations.

The introduced honeybee *Apis mellifera* has established wild populations in the least disturbed native forests at high elevations in the Luquillo Mountains (Snyder, Wiley & Kepler, 1987). These bees feed on flowers of the native palm *Prestoea montana*, and compete for cavity nesting sites with the endangered and endemic Puerto Rican Parrot and other native cavity nesting species. The swarms of *A. mellifera* coincide with peak flowering of *P. montana*, indicating adaptations to the phenology of native forests. Caraballo Ortiz and Santiago Valentín (2011) also found that *A. mellifera* was as effective as the most abundant native avian pollinator, *Coereba flaveola*, in pollinating *Goetzea elegans*, an endangered and self-incompatible endemic tree.

Goats (*Capra hircus*) and pigs (*Sus scrofa*) were introduced in the 16th century to the dry forest of Mona Island (55 km^2), west of Puerto Rico. Their effects on vegetation include rooting, upturning, and mixing of soil and litter (pigs), and creating a browse line (goats) by decreasing understory vegetation in depression forests (Cintrón, 1979). Goats feed on 20% of the island's 435 plant species including 12 threatened and endangered species (Meléndez Ackerman *et al.*, 2008). Half of the species consumed by goats are canopy or understory tree species, although two leguminous vines and an endemic orchid are most frequently consumed. Goats also eat a variety of plant types and structures (herbs, vines, shrubs, trees, etc) including seeds of an endangered cactus. Clearly, goats are naturalized and now an integral food web component on Mona Island.

For centuries, introduced species of rodents (*Rattus rattus*, *R. norvegicus* and *Mus musculus*) and the mongoose, *Herpestes auropunctatus*, have thrived in mature and even primary forests in the Luquillo Mountains. The density of these animals is low (40 ha^{-1} for *R. rattus*), but increases (up to 281 ha^{-1}) in locations with high human activity (Willig & Gannon, 1996). The mongoose's opportunistic diet of invertebrate and vertebrate prey undoubtedly contributes to its success in mature wet forest (Vilella, 1998), where it has become a component of a complex food web that includes dozens of species (Reagan & Waide, 1996).

The examples mentioned earlier where introduced earthworms, bees, goats, pigs and rodents establish populations in mature tropical forests contrast with the low success that introduced plants have in establishing populations in these forests (Thompson, Lugo & Thomlinson, 2007). However, these introduced animals, with the exceptions of earthworms and goats, become rare components of the overall animal communities of these forests and thus, their overall effects on the food web are minor, although their ecological effects on specific plant or animal populations can be significant.

Are there any patterns?

Introduced species of ants, monkeys, birds, amphibians and reptiles in Puerto Rico have not established naturalized populations in undisturbed native mature forests. However, mammals such as pigs and goats (in dry forests), and mongooses and rodents (in wet forests) do colonize mature forests, as do some insect species. Introduced earthworms also invade mature native forests after low levels of disturbance. Conversely, native species of amphibians, reptiles, birds, ants and earthworms are present in novel plant communities and mix with introduced species. Therefore, it is very difficult to find a plant community in Puerto Rico free of naturalized introduced animal species.

The establishment of introduced species in novel communities may be facilitated by niche conservatism, which is manifested in the tendency of an organism's traits and interactions to remain unchanged over time (Wiens *et al.*, 2010). This is evident in Puerto Rico as native frugivores eat fruit and effectively disperse seeds from introduced plants, and introduced pollinators pollinate native plants. Similarly, the abundance of introduced grasses facilitates introductions of granivorous birds. Thus, niche conservatism and/or niche breath operates when available resources match requirements of species allowing them to flourish, regardless of population status in its native ranges (*sensu* environmental matching, Sol *et al.*, 2005).

Also, niche breadth is equally important in the Caribbean given the disturbance regime that maintains most of its ecosystems in a state of successional flux following hurricanes, droughts, floods or anthropogenic disturbances. Species with broad niches have a better opportunity to find adequate ecological space to fit into emerging biotic communities. Moreover, when native and introduced species mix in novel environments, evolutionary forces come into play (see earlier for examples of bill size of introduced finches) and both behavioral and genetic changes contribute to adaptation to the novel conditions. Regardless of mechanisms, new species combinations have become an integral part of the web of interactions in novel communities and influence native species in multiple direct and indirect ways as discussed next.

Potential complexity of native/introduced species interactions

Tolson (1988) studied the native boa (*Epicrates monensis granti*) in small islands in the US Virgin Islands and offshore Puerto Rico, where different mixes and densities of native animals and introduced rats and cats occur. The boa is nocturnal and arboreal and forages primarily on native lizards (*Anolis* and *Ameiva*). High densities of *Anolis* and *Ameiva* lizards occurred on islands without rats, but only one rat-free island had boas. It was on this rat-free island that boas reached their highest density, presumably because of release from rat predation and competition. Conversely, islands with high rat densities had low *Anolis* and *Ameiva* densities and no boas despite suitable habitat. However, low *Anolis* densities are not always correlated with rat densities, possibly because on some islands, *Anolis* shift their average perch height downwards, presumably to elude predation by the arboreal rats. Furthermore, on islands with rats, *A. cristatellus* rarely sleep exposed on the vegetation, as elsewhere, but instead sleep under rocks. *Anolis*' behavioral shifts may reduce rat-predation risk and the likelihood of predation by the boa, which also forages arboreally. Thus, rats may directly affect boa densities by predation or indirectly by reducing prey accessibility.

Tolson (1988) further concluded that rats and feral cats are major factors affecting animal community composition of islands on Puerto Rico and the Virgin Islands. The presence of cats was associated with a low density of a native snake (*Borikenophis portoricensis*, a diurnal predator), the native bird *Margarops fuscatus* and introduced rats. Without cats there were higher densities of *Anolis* lizards and *Borikenophis*. Although cats are nocturnal and prey on boas, they also take rats and may keep rat densities sufficiently low to benefit the boa. Also, Tolson argued that cats could provide benefits to the boa by preying on *Borikenophis* and *Margarops*, which are boa predators and competitors for *Anolis* prey. Finally, he notes that the diurnal mongoose,

Table 2 Faunal assembly rules in reforesting environments (Rios López & Aide, 2007)

Herpetofaunal species richness increases during secondary succession as woody vegetation cover increases.
The composition of the herpetofaunal organization changes rapidly during early stages of succession while the trophic structure changes slowly.
Reptiles dominate early stages of succession because conditions are drier and warmer, and amphibians dominate later stages of succession when conditions become more humid and cooler.

is likely only a minor threat to nocturnal boas where both occur on Mona Island, but is a threat to the diurnal *Borikenophis* snake (Henderson, 1992).

In summary, this study illustrates several assembly rules associated with the interaction between a native and introduced predators competing for the same prey. The introduced competitors have direct and indirect effects on the native predator, and these are both positive and negative in relation to prey availability for the native predator. Also, the prey may behaviorally adjust to the introduced predator, reducing the likelihood of depredation by both the introduced and native predator. Other examples of assembly rules for animals in novel communities are listed in Table 2.

Some implications for conservation and future research

Without underestimating the ecological and cultural effects of introduced species or the importance of actions aimed to protect native species, one cannot ignore that many introduced and naturalized plant and animal species are now prominent members of many novel communities. What we observe in the Caribbean is that the addition of species coupled to natural (e.g. hurricanes) and anthropogenic (e.g. urbanization) disturbances result in habitat diversification, which promotes the natural assembly of novel communities of plants and animals. Moreover, novel plant communities play a useful conservation role by supporting abundant native flora and fauna as recognized pantropically for secondary forests and agroforestry systems (Perfecto *et al.*, 1996; Carlo *et al.*, 2004; Chazdon *et al.*, 2009). Also, these novel species combinations might be the natural response to rapidly changing environmental conditions, including global and climate change. However, despite their ecological importance, novel communities have not received adequate recognition by ecologists. As more research emphasis is placed on disturbance ecology and climate and land-cover change scenarios, it is critical that novelty of species composition and the effects of species additions be incorporated into mainstream ecological and conservation research programs. Some of the questions waiting in the study of novel plant–animal communities are illustrated later.

Is animal abundance in novel communities a measure of habitat quality?

Measures of animal abundance by themselves can be misleading for interpreting habitat quality (Van Horne, 1983), thus it is important to relate abundance and diversity in novel communities and determine the mechanisms that maintain populations in these novel communities. Also important is to determine if native species in novel communities are doomed or not to pay an 'extinction debt' in the near future that is due to the presence of introduced species (*sensu* Tilman *et al.*, 1994). Key reproductive parameters and age-specific survival have only recently been determined in urban habitats (e.g. Rodewald & Shustack, 2008; Whittaker & Marzluff, 2009). Thus, there is a need to demonstrate if populations in novel communities are self-sustaining (Brawn & Robinson, 1996; McKinney, 2002, DeStafano & DeGraaf 2003), and how populations interact among native and novel communities at the landscape level. Especially needed are studies determining if a focal population in a novel animal community is maintained or not by immigration from a source population in a higher quality habitat (Pulliam, 1988; Pulliam & Danielson, 1993; Runge, Runge & Nichols, 2006).

What are the consequences of species eradication?

Eradication of introduced species that are integrated into novel food webs is fraught with ecological risk (Zipkin *et al.*, 2009) and can reflect the application of an erroneous ecological paradigm, that is that naturalized animal species constitute community additions that can be eradicated without ecosystem-level implications. Moreover, practical and philosophical contradictions arise when trying to apply this paradigm to introduced species that are endangered in their native range, such as the blue and golden macaw (*Ara ararauna*) now naturalized in Puerto Rico. Despite *A. ararauna*'s endangered status in parts of their native range, the island's unprotected population is potentially subjected to eradication because of its 'alien' status. An alternative position is that the cost-free establishment of *A. ararauna* in Puerto Rico provides survival insurance for a species threatened elsewhere. Similarly, Raffaele (1983) argued for the protection of the naturalized red siskin (*Carduelis cucullata*) despite its introduced status in Puerto Rico because it was threatened in its native range.

How does an introduced animal's trophic position affect its effects on novel and native communities?

Both the roles and effects of species introductions on animal community structure and assembly depend on the type of organism being introduced. For example, introducing plants into islands rarely causes extinction of natives (Sax & Gaines, 2008). However, introductions of animals, particularly predators, can change communities more drastically and potentially cause evolutionary changes in natives (Strauss, Lau & Carroll, 2006). Still, ecological outcomes of animal introductions should vary depending on whether species are granivorous finches, herbivorous iguanas or goats, or carnivorous mongooses. In this context, novel plant and animal communities present fertile ground for testing hypotheses and models about the assembly mechanisms, controls, community patterns, and how introduced species at different trophic levels affect community structure. Ultimately, questions about community assembly and stability require more than an understanding of large-scale phenomena such as source–sink dynamics; they demand quantitative studies on the networks of trophic interaction among organisms.

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