Adaptive foraging in the Anthropocene: can individual diet specialization compensate for biotic homogenization?

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Biotic homogenization is a ubiquitous consequence of human disturbance. Through a mix of local extinctions and invasions, diverse communities of specialists are often replaced by or inundated with generalist species, resulting in uncertain consequences for ecological functions. While concern about biotic homogenization is growing, intraspecific variation and individual diet specialization (IS) have also emerged as key drivers of ecological functions. The niche variation hypothesis predicts that when a population is released from interspecific competition (ie "ecological release"), intraspecific competition will promote resource niche expansion and IS. It then follows that if biotic homogenization reduces taxonomic diversity and *interspecific* competition, *intraspecific* competition within the remaining taxa should expand population resource niches and increase the prevalence of IS. Here, we integrate the rapidly growing fields of biotic homogenization and intraspecific variation and assess the potential for generalist species to compensate for multiple forms of biotic homogenization via adaptive foraging, resource niche expansion, and IS.

More than 20 years ago, McKinney and Lockwood (1999) formally introduced the concept of biotic homogenization. They documented simplified communities dominated by non-native biota, and reasoned that contemporary human disturbances were diminishing biodiversity and fundamentally restructuring selective pressures to favor generalist species. Two decades of ensuing research have shown that biotic homogenization is indeed a ubiquitous consequence of human disturbance (Clavel *et al*. 2011) and that multiple processes drive the observed changes in diversity (Baiser *et al*. 2012). Species invasions frequently flood local communities with non-native species and diverse communities of specialists are replaced by generalist species, potentially reducing ecosystem

In a nutshell:

- Biotic homogenization has led to the rise of generalists and the loss of specialists, potentially impacting ecological functions like predation, pollination, and seed dispersal
- The primary way animals influence most ecological functions is through foraging; adaptive foraging, and individual diet specialization in particular, may therefore compensate for local extinctions by filling lost functional roles
- Ecologists often equate extinctions to the removal of bricks in a wall, warning that the wall will eventually collapse; we argue that organisms, especially generalist species, are more plastic than bricks, and empty niches and their functional roles do not necessarily remain unfilled

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functions (Clavel *et al*. 2011). The consequences of this homogenization for ecosystem function, however, remain conspicuously absent (Olden *et al*. 2016).

Interest in the ecology of individuals and the impact of intraspecific variation on ecological processes has also grown over the past 20 years (Bolnick *et al*. 2003, 2011). Evidence now suggests that variation within species can have equivalent or even greater effects on ecosystems than taxonomic diversity itself (Des Roches *et al*. 2018). Individual diet specialization (IS) in particular has received considerable empirical and theoretical consideration because it influences populations, communities, and evolutionary trajectories (Van Valen 1965; Roughgarden 1972; Bolnick *et al*. 2003, 2011), but as with biotic homogenization, how IS impacts ecosystem-level processes remains largely unknown. We briefly review the mechanisms underlying biotic homogenization and IS, apply the theory of ecological release to biotic homogenization, and identify testable predictions for when IS could compensate for functional losses.

◼ Biotic homogenization: few winners, many losers

Biotic homogenization generally occurs via species invasions and extinctions, leading to increased genetic, taxonomic, or functional similarity of communities over space and time (Clavel *et al*. 2011; Olden *et al*. 2016). While the proximate drivers of biotic homogenization range from altered climate and land-use patterns to species invasions, studies have revealed two distinct but ubiquitous processes by which communities homogenize: species turnover and changes in species richness (Dornelas *et al*. 2014). Turnover occurs when species are replaced within a local community but richness (α-diversity) remains constant, as when specialists are replaced by
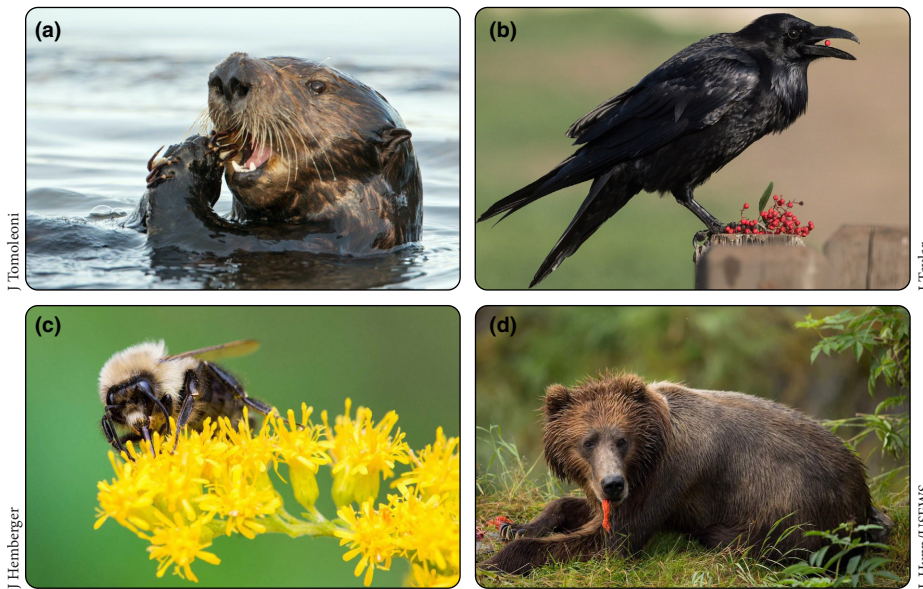
Figure 1. Critical ecological functions like (a) top-down predation, (b) seed dispersal, (c) pollination, and (d) nutrient transport (eg aquatic to terrestrial) are all driven by individual foraging decisions. Increased diet specialization on any given resource could therefore fundamentally alter the functional roles performed by species or individual consumers.

specialize on a narrow set of resources relative to the total niche width of the population, leading to greater intraspecific niche partitioning and resource niche expansion at the population level (NVH); (2) individuals generalize and consume a broad set of resources, thereby increasing both individual niche width and the total niche width of the population ("parallel release"); or (3) individuals generalize and consume a broader set of resources but total niche width remains constant ("individual release") (Bolnick *et al*. 2010). While these mechanisms are not mutually exclusive, empirical research has largely supported the first mechanism, with generalist populations composed of individual specialists (Bolnick *et al*. 2007; Araújo *et al*. 2011; but see Costa-Pereira *et al*. 2019). IS therefore appears to be the result of complex trade-offs in inter- and intraspecific competition as organisms minimize niche overlap both within populations and between species (Araújo *et al*. 2011).

generalists. Conversely, net increases or decreases in richness reduce differences between communities (β-diversity) through space or time. These changes in species diversity have received widespread attention, but functional homogenization and the convergence of ecological niches is arguably more concerning due to feedbacks that can impact both biodiversity and ecosystem processes (Clavel *et al*. 2011). For example, the functional homogenization of urban pollinators reduces the diversity of plant visitors, limiting plant recruitment and ultimately floral diversity (Deguines *et al*. 2016). Such functional homogenization generally occurs when disturbances like urbanization filter regional species pools to favor widespread generalists, resulting in the loss of biodiversity and potentially ecosystem function (Clavel *et al*. 2011).

Individual specialization: adaptive foraging and competition trade-offs

Ecologists have long recognized that phenotypic differences between individuals of the same species can lead to divergent resource niches and unique functional roles (ie Eltonian niches; Van Valen 1965; Roughgarden 1972). For instance, dietary or resource niches can vary with body size or age class, but resource niches also vary among individuals independent of age, sex, or discrete morphology (Bolnick *et al*. 2003). Van Valen's (1965) niche variation hypothesis (NVH) first articulated how this individual variability would respond to competitive interactions and predicted that populations released from interspecific competition would expand their resource niches through adaptive foraging. Subsequent research has shown that this "ecological release" can occur in three ways: (1) individuals

How can IS compensate for homogenization?

Understanding how changes in community structure like biotic homogenization impact compensatory dynamics and ecosystem function is an unresolved issue in ecology (Kremen 2005). Foraging ecology provides a direct link between biodiversity and ecosystem function (Figure 1; Thompson *et al*. 2012), and we suggest that adaptive foraging and IS can therefore compensate for functional diversity lost to biotic homogenization. For example, if homogenization occurs via local extinctions (ie reduced richness), NVH predicts that population-level niche expansion among the remaining species could fill the vacant resource niche(s) via competitive release and greater IS (Figure 2; Roughgarden 1972). Numerous studies have shown that communities of specialists are key to maintaining ecosystem processes, arguing that specialists perform ecological functions most efficiently whereas generalists are largely redundant (Clavel *et al*. 2011). But such studies generally assign functional roles at the taxonomic level assuming that functional variation between species exceeds variation within species, despite a growing body of evidence that intraspecific differences like individual diet variation are widespread and play critical roles in ecological processes (Bolnick *et al*. 2011; Des Roches *et al*. 2018; Zwolak 2018). For example, Harmon *et al*. (2009) demonstrated that diet variation in three-spined stickleback (*Gasterosteus aculeatus*) had significant effects on multiple ecosystem properties, including prey biomass and diversity, primary production, and ecosystem respiration, while diet variation in pumpkinseed sunfish (*Lepomis gibbosus*) significantly influenced primary production and respiration via differential excretion rates (Evangelista *et al*. 2017). Individual

differences in seed consumption and gut retention among common carp (*Cyprinus carpio*) similarly led to dramatic differences in seed dispersal (Pollux 2017), while individual diet variation in Lilford's wall lizard (*Podarcis lilfordi*) simultaneously mediated both pollination and seed dispersal (Fuster and Traveset 2020).

We extend the concept of individual diet variation to propose that the loss of specialized taxa will promote adaptive foraging, resource niche expansion, and IS among generalist taxa, and that specialized *individuals* could in turn fill the ecological roles of extirpated taxa (Figure 2). Such functional compensation, however, depends on a combination of phenotypic variation, competitive release, and intraspecific competition, each of which is impacted by biotic homogenization and ongoing global change (Figure 3). Here, we review these conditions and identify ways in which biotic homogenization will either promote or restrict the ability of generalist taxa to compensate for species losses via niche expansion and IS.

Phenotypic variation

Phenotypic variation in behavior, morphology, and physiology is critical to niche evolution and the emergence of IS (Roughgarden 1972; Maldonado *et al*. 2019). For example, maternally transmitted foraging behaviors maintain IS within sea otter (*Enhydra lutris*; Figure 1a; Tinker *et al*. 2008) populations, while variation in bill size enables resource niche expansion among species of passerine birds (Hsu *et al*. 2014). Flexible physiological traits, like digestive enzymes, can also facilitate resource niche expansion and IS, though an excess of such plasticity can also promote individual generalization (Maldonado *et al*. 2019).

Biotic homogenization is simultaneously increasing *and* decreasing phenotypic variation (Figure 3). For instance, introduced species have almost tripled functional trait diversity in freshwater fish communities worldwide (Toussaint *et al*. 2018), leading to increased community niche width (Sagouis *et al*. 2015) and trophic diversity (Pool *et al*. 2016). This expanded trait diversity and foraging plasticity increases the potential for both IS and functional compensation (Gagic *et al*. 2015). Similarly, climate and land-use change select for physiologically plastic individuals (Latimer *et al*. 2018), a process that should promote resource niche expansion (Maldonado *et al*. 2019). Numerous studies have also shown that climate and land-use change reduce functional trait and
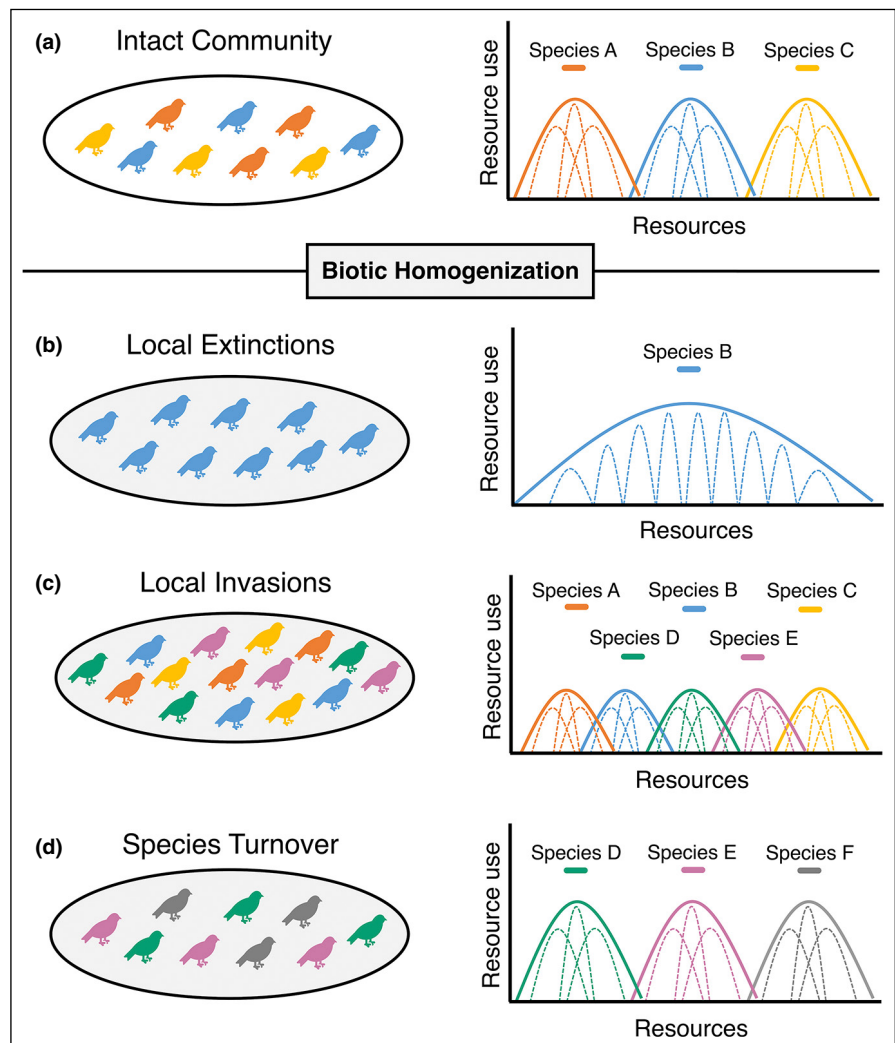

Figure 2. Biotic homogenization (left panel) and the hypothesized impact (right panel) on population resource niches (solid lines) and individual resource niches (dashed lines). (a) Intact communities partition resources to minimize population niche overlap and interspecific competition. Because intraspecific competition must exceed interspecific competition to enable coexistence, the overlap between individual resource niches is greater than the overlap between population resource niches. (b) Homogenization via local extinctions (ie decreased alpha diversity [α-diversity]) reduces interspecific competition, enabling ecological release and population resource niche expansion. This occurs via multiple mechanisms, most often increased individual diet specialization (IS) in order to reduce intraspecific niche overlap. (c) Homogenization through invasions (ie increased α-diversity) heightens interspecific competition, limiting the potential for ecological release and IS. (d) Homogenization via species turnover (ie constant α-diversity) maintains inter- and intraspecific resource niche dynamics, limiting the potential for ecological release and IS.

population genetic diversity among animals, thereby limiting the potential for resource niche expansion and functional compensation (Flynn *et al*. 2009; Deguines *et al*. 2016; Miraldo *et al*. 2016). However, functional diversity is often correlated with taxonomic diversity, a property more likely to influence foraging and IS through competitive interactions. Moreover, many functional traits measure physical characters (eg bill size) and assume tightly coupled consumer–resource dynamics mediated by morphology, but these traits often do not promote foraging
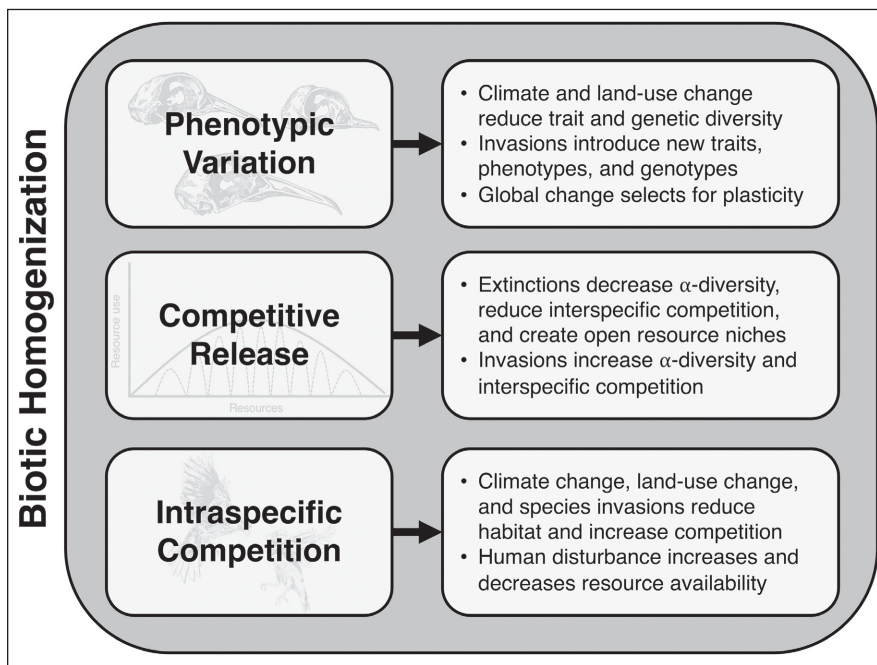
Figure 3. Primary impacts of biotic homogenization on individual diet specialization (IS). Diet specialization has three general conditions (phenotypic variation within a population, release from interspecific competition, and increased intraspecific competition), each of which is directly impacted by biotic homogenization.

plasticity and respond to other confounding variables (eg sexual selection, temperature; Hsu *et al*. 2014). Despite the focus on these traits, morphological variation appears to be only loosely related to resource niches and IS, most likely because they are unresponsive to rapid ecological change (Bolnick *et al*. 2007; Maldonado *et al*. 2019). Future research should therefore shift attention to the impact of global change on plastic traits directly related to foraging dynamics (eg behavior, physiology; Maldonado *et al*. 2019). It is also important to consider the impact of biotic homogenization on "response" and "effect" traits to determine which phenotypes are most likely to persist (response) and impact (effect) ecosystem function (Raffard *et al*. 2017). In particular, a suite of correlated response and effect traits likely regulate foraging plasticity and functional roles, and identifying this "functional syndrome" will be key to predicting which species have the greatest potential to impact ecosystems via adaptive foraging (Raffard *et al*. 2017).

Competitive release

Interspecific competition is a principal driver of resource use and niche dynamics (Bolnick *et al*. 2010). Assuming resources are limiting, the NVH predicts that the absence of interspecific competitors will increase resource availability, thereby promoting resource niche expansion and IS (Van Valen 1965; Roughgarden 1972, 1974). This ecological release following the reduction of interspecific competition has been documented across a range of taxa, from insect pollinators (Inouye 1978) to predatory fishes (Bolnick *et al*. 2010) to *Anolis* lizards (Roughgarden 1974).

Biotic homogenization directly affects interspecific competition and the potential for competitive release via turnover and changes in species richness (Figures 2 and 3). We predict that ecological release will most likely occur when biotic homogenization is driven by local extinctions (ie decreased α-diversity) that allow for population-level resource niche expansion by the remaining species (Figure 2b; sensu Roughgarden 1974). Conversely, when invasions drive homogenization (ie increased α-diversity), we expect competition for limited resources to increase, thereby reducing opportunity for resource niche expansion and ecological release at the population level (Figure 2c). This prediction is again supported by evidence from *Anolis* lizards, where experimental invasions induced resource niche contraction among endemic consumers (Pringle *et al*. 2019). The impact of species turnover (ie constant α-diversity) on ecological release has received less attention, but we predict that interspecific competition should remain relatively constant, thereby inhibiting resource niche expansion by extant species (Figure 2d). Indeed, species turnover has had seemingly little impact on trophic structure in freshwater fish communities (Pool *et al*. 2016) or coastal marine ecosystems (Villéger *et al*. 2008), while Andean birds and coral reef fishes maintain functional and trophic diversity despite high species turnover (Gajdzik *et al*. 2018; Dehling *et al*. 2020). These studies suggest that colonizing species maintain resource niches and functional roles similar to those of the species they replace, although this is likely a function of phylogenetic turnover and trophic niche conservatism as well (Olalla-Tárraga *et al*. 2016). It is also possible that changes in community composition could induce individual or parallel release, resulting in individual generalism. For example, if biotic homogenization reduces interspecific competition but also prey availability, individuals could generalize on the remaining prey with varying degrees of resource niche expansion at the population level. To date, studies of biotic homogenization among consumers have focused almost exclusively on correlative analyses and macroecological patterns, but future research must also consider experimental manipulations of species richness and turnover to directly assess our predictions and the impact of different homogenization processes (eg richness versus turnover) on ecological release and resource niche dynamics.

Intraspecific competition

Empirical research has regularly identified intraspecific competition as a primary driver of resource niche expansion and IS (Svanbäck and Bolnick 2007; Tinker *et al*. 2008; Araújo *et al*. 2011). These observations are consistent with both niche theory and optimal foraging theory, which

postulate that intraspecific competition limits access to shared resources, thereby promoting niche expansion and IS through the use of alternative resources – a process also contingent on the presence of phenotypic variation (Svanbäck and Bolnick 2005, 2007). Thus, the impact of intraspecific competition on IS is driven by complex interactions between population density, resources, and phenotypic variation (Svanbäck and Bolnick 2005), all of which are subject to biotic homogenization (Figures 3 and 4).

Biotic homogenization impacts population density in several ways, most simply through increased abundances. For example, increased abundance of non-native species is common, particularly in urban landscapes (Clavel *et al.* 2011; Galbraith *et al.* 2015). Alternatively, biotic homogenization can increase population density and intraspecific competition when invasive plants, competitors, or predators induce spatio-temporal shifts in habitat use through either avoidance (Pringle *et al.* 2019) or aggregation (Figure 4c; Pearson 2009). Similar dynamics can occur through changes in climate and land use that limit habitat availability and increase abundance in the remaining fragments (Figure 4c; Bender *et al.* 1998). Finally, reductions in α-diversity can induce density compensation, whereby the remaining species become more abundant in the absence of competitors (MacArthur *et al.* 1972). In all cases, increases in abundance and density can promote intraspecific competition, resource niche expansion, and IS (Figure 4, a–c; Svanbäck and Bolnick 2007).

Resources also interact with population dynamics to mediate the prevalence of IS (Figure 4, d and e). For instance, Tinker *et al.* (2008) found that low resource availability and high population density drove resource niche expansion and IS in sea otters, while Svanbäck *et al.* (2011) tested interactions between resource availability and consumer density to show that specialization was mediated entirely by resources, with low resource availability again inducing niche expansion and individual specialization. As with population density, biotic homogenization and human expansion are also rapidly altering resource availability, with unknown consequences for IS. For instance, phytoplankton production – the principal source of organic energy in marine systems – is declining as sea-surface temperatures rise in response to anthropogenic climate change (Boyce *et al.* 2010), yet urban ecosystems provide abundant resource subsidies like human refuse and supplementary food (eg bird seed) that sustain dense populations of generalist and non-native species (Galbraith *et al.* 2015; Manlick and Pauli 2020). Niche theory predicts that if human disturbances decrease resource availability (eg resource quantity), then intraspecific competition, resource niche expansion, and IS can all increase (Figure 4d), while phenomena like nutrient loading and resource subsidies likely have the opposite effect. However, resource *diversity*, like that provided by human subsidies, also creates ecological opportunity for resource niche expansion and IS (Figure 4e; Araújo *et al.* 2011).
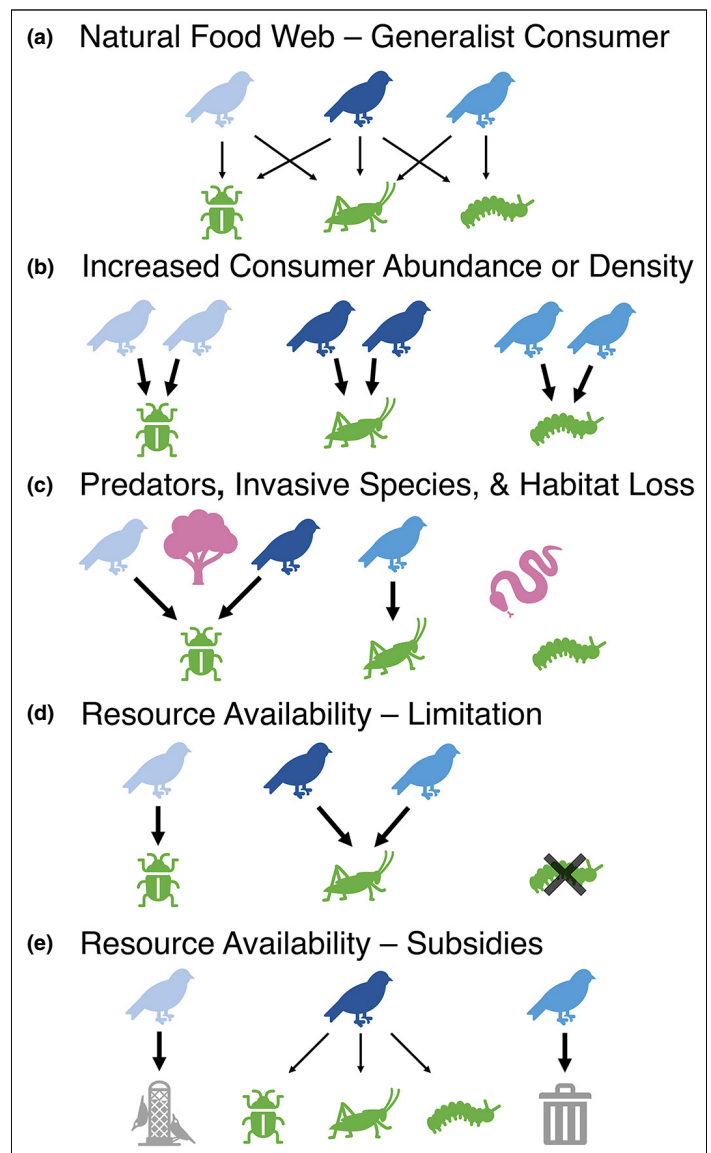

Figure 4. Hypothesized impacts of biotic homogenization on population density, resource availability, and individual diet specialization (IS). Arrows from consumers (blue) to resources (green, gray) represent consumption, and arrow thickness indicates proportional contribution of resources to individual consumers. Shades of blue represent phenotypic differences within a population. (a) Natural food web with a generalist consumer. (b) Higher consumer abundance increases intraspecific competition, and individuals specialize on resources based on phenotypic differences. (c) Habitat loss and invasive species (eg predators: purple snake) can alter access to resources, while invasive plants (purple tree) can provide novel cover. Both processes can promote IS through increased population density or intraspecific competition, but also reduce individual specialization by limiting access to resources. Both scenarios are contingent on phenotypic differences. (d) Human disturbances limit resource diversity or availability, increase intraspecific competition, and individuals specialize based on phenotypic differences. (e) Human disturbances increase resource diversity or availability (eg food subsidy: gray), creating ecological opportunity for individuals to specialize based on phenotypic differences.

Panel 1. Functional compensation by generalist and non-native taxa

Non-native and invasive taxa can have devastating impacts on biodiversity, often precipitating local extinctions and biotic homogenization (McKinney and Lockwood 1999; Clavel *et al*. 2011). Oceanic islands like New Zealand have experienced considerable defaunation and the widespread loss of native pollinators due to non-native predators like black rats (*Rattus rattus*), yet these generalist invaders also have considerable potential to compensate for the species they extirpate. Pattemore and Wilcove (2012) found that in the absence of native vertebrate pollinators, black rats and silvereyes (*Zosterops lateralis*), an introduced passerine, expanded their resource niches to include nectar, thereby maintaining pollination among several common endemic plants on New Zealand's North Island (Figure 5). If individuals were to specialize on nectar resources or exhibit floral fidelity, it would increase pollination efficiency (Brosi 2016) and further the compensatory value of these non-native taxa. While non-native and invasive species undoubtedly impact biodiversity, increasing evidence also suggests that these taxa can play important ecological roles in depauperate communities through adaptive foraging.

Figure 5. An invasive black rat (*Rattus rattus*) visiting an inflorescence of the endemic rewarewa (*Knightia excelsa*) in New Zealand.

For example, urban coyotes (*Canis latrans*) in metropolitan Chicago, Illinois, maintain high population densities that are heavily subsidized by various human foods, but individuals exhibit extensive inter-individual diet variation and individual specialization (Newsome *et al*. 2015). Elsewhere, many plant communities have seen increased species richness (Dornelas *et al*. 2014), and this augmented resource diversity could similarly increase resource niches and IS among herbivores or pollinators. Lastly, predation risk – both natural and human-induced – can alter access to resources, either increasing or decreasing diet specialization (Araújo *et al*. 2011). However, apex consumers are particularly vulnerable to biotic homogenization, and the ongoing loss of predators is likely to impact resource use, population density, and IS among residual taxa. Collectively, the evidence for intraspecific competition promoting IS is resounding, but the interacting effects of population density, resource availability, and resource diversity on IS need to be better resolved, particularly in human-dominated landscapes where population and resource dynamics are changing rapidly.

■ Linking theory with empirical support

To date, no single study has documented the process linking biotic homogenization to resource niche expansion, IS, and functional compensation. This remains a tall order with many moving pieces to consider, but recent studies lend empirical support for this hypothesized process. Plant–pollinator mutualisms provide a classic example. Often viewed as specialized interaction networks, increasing evidence suggests that many pollinator communities are actually composed of generalist species with individuals specializing on different plants (Tur *et al*. 2014; Brosi 2016). Numerous

studies have also shown that trade-offs between inter- and intraspecific competition, as well as population density, drive resource niche expansion (Inouye 1978; Fontaine *et al*. 2008) and IS among pollinators (Tur *et al*. 2014; Brosi 2016). In addition, urban pollinator populations have expanded their resource niches (Baldock *et al*. 2015) and exhibit substantial foraging specialization (MacIvor *et al*. 2014), while generalist pollinators have likewise expanded their resource niches to fill the roles of extirpated specialists, with no apparent loss of ecological function (sensu Figure 2b; Hiraiwa and Ushimaru 2017). Even the invasive black rat (*Rattus rattus*) has been shown to compensate for the loss of endemic pollinators (Pattemore and Wilcove 2012), further illustrating the potential for functional compensation by generalist or non-native species (Panel 1; Figure 5). A novel colonizer similarly compensated for the experimental removal of a keystone desert rodent via consumptive effects (Ernest and Brown 2001), while density-mediated resource niche expansion and functional compensation appear to be common among island pollinators and seed dispersers (Traveset *et al*. 2015). Such compensation is likely possible because specialized consumers interact with only a nested subset of the resources used by generalists, thereby supplying a level of functional redundancy that allows generalist species to expand their niches and compensate for the extirpation of specialists (Memmott *et al*. 2004). This nestedness ultimately extends well beyond plant–pollinator mutualisms and is also prevalent in seed dispersal networks and food webs (Bascompte *et al*. 2003), indicating that generalist consumers and adaptive foraging play a critical role in stabilizing ecosystem processes through functional compensation (Kaiser-Bunbury *et al*. 2010).

Future directions

We have focused on IS compensating for changes in α-diversity through trade-offs in competition because there is strong theoretical and empirical support for these processes. Indeed, we do not seek to minimize the impacts of biodiversity loss; rather, we wish to point out that biotic homogenization and IS provide two well-established lines of ecological theory that can help ecologists and conservationists untangle the complex relationship between biodiversity change and ecosystem function. Empirical data linking these fields, however, are currently lacking. For example, we have illustrated that local extinctions provide ecological opportunity for adaptive foraging and resource niche expansion by generalists, but biotic homogenization can also occur via species invasions and community turnover. The impact of these processes on the relationship between interspecific competition and IS remains nascent. Interactions between population density and resource availability provide a similar challenge for understanding intraspecific competition and IS, particularly in human-dominated landscapes where populations, communities, and resources are all shifting rapidly. We have outlined the conditions necessary for adaptive foraging and functional compensation, as well as the impact of biotic homogenization on each (Figure 3), but numerous permutations of phenotypic variation, ecological release, and intraspecific competition remain untested. When does phenotypic variation promote niche expansion and IS, and when does it promote individual generalism? How do changes in α-diversity interact with shifting resource baselines to regulate competitive interactions at both the inter- and intraspecific level? How does the loss of predators influence the potential for IS among remaining taxa? Important caveats also must be noted. For instance, generalists can only replace specialists when intraspecific variation overlaps with that of lost taxa, and, while they remain a minority, highly specialized foragers with coevolved mutualisms are unlikely to be compensated for if extirpated. Moreover, even if individual diet specialists expand into vacant resource niches left by extirpated species there is no guarantee that they will forage at the same rate or with the same efficiency necessary to compensate for the lost specialists, although examples of partial compensation do exist (Panel 1; Pattemore and Wilcove 2012). It is also possible that adaptive foraging will lead to novel consumer–resource dynamics (eg Panel 1) that could influence the ecological function of both consumers and prey, potentially limiting compensation over evolutionary timescales. Quantifying functional compensation via IS therefore requires improved measurement of individual foraging dynamics – across both space *and* time – to assess whether intraspecific diet variation and foraging rates overlap with those of lost taxa, and whether compensatory dynamics are stable across spatiotemporal scales. Niche theory and the hypotheses presented here provide theoretical considerations for these questions, but careful combinations of case studies, experimental manipulations, and ecological gradients will be needed to tease apart the proximate mechanisms regulating adaptive foraging, resource niche expansion, and functional compensation.

Ecologists and natural resource managers currently collect part of the data needed to address these questions and quantify functional compensation. Common measurements like population abundance and species richness are critical for estimating inter- and intraspecific competition and should continue to be monitored. The primary way most animals impact ecosystem functioning, however, is via foraging (Figure 1), yet these impacts are often inferred by placing animals in coarse functional groups or by measuring morphological traits with little relationship to actual foraging dynamics (Maldonado *et al*. 2019). Although these macroecological approaches have enhanced our understanding of biodiversity and ecosystems substantially, they cannot mechanistically link biotic homogenization to ecological functions. For example, we have stressed that consumer populations are often composed of individual dietary specialists; thus, weekly or even seasonal changes in individual foraging dynamics have the potential to fundamentally alter the functional role of an individual or population (Brosi 2016). Understanding this spatiotemporal variation in foraging and functional roles will be critical to developing management and conservation policies that optimize ecosystem functioning. Broad categorizations of functional roles at the species level (or higher) therefore lack the resolution to truly assess functional compensation. Instead, we recommend researchers and managers measure diets at the individual level so that adaptive foraging and functional roles can be assessed directly. While this may seem a daunting task, emerging techniques like stable isotope analysis of consumer tissues and their food (eg Manlick and Pauli 2020), as well as DNA metabarcoding of feces, stomach contents, and pollen loads (eg Pringle *et al*. 2019), are increasingly accessible and enable efficient and accurate assessment of diet variation at the individual level. Moreover, these approaches can be implemented non-invasively and used in tandem to assess individual foraging dynamics at unprecedented spatiotemporal scales (Pringle *et al*. 2019). Individual measurements of diet can also be tied to phenotypic variation – a critical component of functional compensation (Figure 3) – and we encourage future research to focus on plastic behavioral or physiological traits that enable adaptive foraging and functional compensation (Maldonado *et al*. 2019). In addition to the dearth of individual diet data, there is also an enduring lack of data on resource availability and diversity, which play critical roles in determining dietary niche expansion and IS (Figure 4, d and e). Though it remains a challenge to assess, researchers and managers should prioritize measurements of resource availability and diversity in order to test the predictions outlined herein.

We provide a blueprint for testing the impacts of global change on adaptive foraging and functional compensation, but to fully assess this interaction we must also shift our focus from species to individual-level processes that directly impact

ecosystem functions. Many researchers have suggested that the loss of ecosystem function is a likely outcome of biotic homogenization, but studies of intraspecific variation indicate that phenomena like IS may have greater impacts on function than taxonomic diversity itself (Des Roches *et al.* 2018). To integrate these emerging areas of study, scientists should embrace foraging ecology as a means to track ecological processes from individuals to ecosystems.

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