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Opinion

The Evolution of 'Ecological Release' into the 21st Century

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Ecological release, originally conceived as niche expansion following a reduction in interspecific competition, may prompt invasion success, morphological evolution, speciation, and other ecological and evolutionary outcomes. However, the concept has not been recently reviewed. Here, we trace the study of 'ecological release' from its inception through the present day and find that current definitions are broad and highly varied. Viewing this development as a potential impediment to clear communication and hypothesis testing, we suggest a consensus definition for ecological release: niche expansions and shifts when a constraining interspecific interaction is reduced or removed. In rationalizing this definition, we highlight the various ways ecological release can unfold and address its potential evolutionary consequences.

Highlights

Ecological release, as both a concept and a term, has not been recently reviewed.

Ecological release was originally conceived as niche expansion following a reduction in interspecific competition.

Modern definitions are broad and varied – they encompass underlying mechanisms other than competition and accept signals other than niche expansion as potential evidence that ecological release has occurred.

Niche changes during ecological release may prompt consequent morphological evolution and/or adaptive speciation, but these evolutionary outcomes themselves do not constitute ecological release.

Hypotheses about evolutionary outcomes may be improved by explicitly considering how population- and individual-level niche dynamics can vary during ecological release.

A Critical Examination of Ecological Release Is Overdue

Over a half-century ago, Wilson and colleagues coined several terms to describe how **interspecific competition** (see Glossary) can affect species' ecology and morphology. Initially, **ecological character displacement** was introduced to describe the pattern of competition-driven **niche** divergence and associated morphological shifts of species when in **sympatry**, relative to when in **allopatry** [1]. Subsequently, **ecological release (original definition)** and **character release** were used to describe a complementary scenario; an expansion in ecological niche and morphological variation when in allopatry [2,3]. As such, these concepts are closely related, jointly encompassing a suite of population-level ecological and evolutionary responses to changes in the intensity of interspecific competition [3].

In the years since these terms were introduced, ecological character displacement has received major conceptual overviews [4–8], amassed numerous detailed empirical case studies [4,9,10], and been explicitly incorporated into modern ecoevolutionary frameworks [11,12]. In contrast, ecological release has attracted relatively little attention. Despite claims that it can prompt major ecological and evolutionary phenomena, such as range expansions [13], morphological evolution [14], and speciation [15], we argue that ideas concerning what ecological release represents are in need of critical examination and development.

Historical Conception of Ecological Release: Niche Expansion Following Reduced Interspecific Competition

The foundational ideas of ecological release stem largely from the biologist David Lack [16–18], who hypothesized that population density and habitat use of island birds were regulated by interspecific competition. The term ecological release was formally introduced two decades later by Wilson [2], who in his studies of Melanesian ant communities noted that on islands with lower species richness, species that are forced into marginal, coastal habitats on species-rich islands instead 'penetrate the inner forest, mount dense populations there, and fill the available nesting sites.' He attributed this pattern to 'the role of interspecific competition' limiting resource use in sympatry.

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Wilson's original description encompasses two population-level responses to reduced interspecific competition: **niche expansion** – an increase in the breadth of habitats or resources used – and **density compensation** – an increase in population density. However, Wilson himself later explicated the relationship between these two responses, treating niche expansion as related to, but distinct from, density compensation [3]. A trend toward marrying ecological release with niche expansion and distinguishing it from density compensation took hold in the 1970s [19–21], continued into the 1980s [22–24], and is supported by more recent empirical and theoretical works (Box 1).

Although the issue of niche expansion versus density compensation has received explicit attention, there are other, implicit aspects of how ecological release was historically defined and studied that we believe are underappreciated. For example, comparative studies in the 1960s and 70s often tested for ecological release in focal species by measuring whether their population-level variances in habitat use or diet were higher in the absence of competitors [25–29]. Thus, an early defining feature of ecological release was its focus on niche *expansions* as opposed to **niche shifts**. This variance-centric approach has become well entrenched even though shifts in mean resource are also a common feature of ecological release (see following text).

An additional aspect of ecological release often overlooked, perhaps because researchers have long been interested in the evolutionary consequences of ecological release, is that ecological release itself was commonly interpreted as a purely ecological phenomenon; niche expansion following a reduction in interspecific competition need not be the result of evolution [30]. Concurrent with early comparative tests for ecological release, manipulative field experiments in the 1960s and 70s that reduced or removed competitors often demonstrated that the consequent niche expansion can occur within a single generation [31].

Box 1. Density Compensation May Cause Niche Expansion, but it Does not Have to

Density compensation can be the proximate cause of niche expansion during ecological release. If **intraspecific competition** increases with population density, then population-level niche expansion may occur as preferred resources become limited, favoring individuals using habitats and resources that were previously suboptimal [44,58,59]. However, it is also possible for increasing intraspecific resource competition to initially reduce, rather than expand, the range of resources used by a population [60]. Empirical and theoretical evidence suggest that the outcome depends on both resource availability and consumption rates; when favored resources are depleted quickly and suboptimal resources are either inaccessible or extremely inefficient to consume, a population may exhaust subsets of its original niche without incorporating new types of resources [55,61,62]. Under these conditions, density compensation leads to narrowing of the niche, at least temporarily. For example, alewife (*Alosa pseudoharengus*), which are efficient consumers in eastern North American lakes, exhibit a negative relationship between population density and diet variation in both natural and experimental settings [63].

Alternatively, niche expansion during ecological release can also occur without density compensation; prior to any density response, extant individuals may choose to use resources from which they were previously excluded, either because these resources are inherently more valuable than previously used resources or because they have become relatively more valuable in the absence of costs no longer imposed by the presence of antagonists [44].

It is possible, therefore, for density compensation to either promote niche expansion or niche contraction, and for niche expansion to occur in the absence of density compensation. For this reason, we consider density compensation to not be part of the definition of ecological release; rather, the nuances of how density compensation is related to ecological release warrant continued study. Specifically, identifying the conditions under which niche expansion and density compensation fuel each other via positive feedback loops may be a key to determining whether the consequences of ecological release are transient or long-lasting.

Glossary

Allopatry: the state of being separated in space in such a way as to prevent organisms from interacting during normal activity.
Character release: morphological changes associated with ecological release.
Density compensation: an increase in abundance per unit area in response to the absence of a competitor, such that the increased abundance compensates for the number or biomass of missing competitors.
Density inflation: an increase in abundance per unit area which, unlike density compensation, does not assume a specific underlying mechanism.
Ecological character displacement: competition-driven niche and morphological divergence among species when in sympatry relative to when in allopatry.
Ecological opportunity: availability of ecologically accessible resources that may be evolutionarily exploited.
Ecological release (original definition): population-level niche expansion in response to reduced interspecific competition.
Ecological release (proposed definition): population-level niche expansions and shifts when a constraining interspecific interaction is reduced or removed.
Interspecific competition: competition between populations of different species.
Intraspecific competition: competition within a species; correlates positively with population density if resources are limited.
Niche: distribution of habitats and resources used.
Niche expansion: an increase in niche width, as measured by an increase in the variance of habitats or resources used.
Niche shift: a change in the mean position along a resource axis.
Sympatry: the state of having no spatial separation such that organisms may interact regularly during normal activity.

Evolution of Ecological Release: Current Conceptions Are Highly Varied

In keeping with the dominant paradigm of ecology at the time [32], ecological release was initially conceived as a response – niche expansion, primarily – to reduced interspecific competition. To determine how researchers have recently defined and contextualized ecological release, we surveyed peer-reviewed publications containing the phrase ecological release (105 studies; Table S1 in the supplemental information online) in the period November 8, 2018 to March 24, 2020.

We found that recent studies varied substantially in what was accepted as a potential identifier of ecological release. The most frequently mentioned signal was niche expansion (44.8% of studies; Figure 1A). However, some studies considered density compensation (22.9%) and morphological change (including both increased variation and mean shifts; 23.8%) as potential evidence for ecological release. Lineage diversification (i.e., speciation), although seldom taken as direct evidence for ecological release, was mentioned in 17.1% of studies. In addition, 28.6% of studies accepted multiple potential identifiers of ecological release (e.g., both niche expansion and morphological change) and 13.3% specified none.

Current definitions of ecological release have also expanded to include multiple underlying mechanisms. Only 28.6% of studies aligned with Wilson [2] in their narrow focus on release from interspecific competition (Figure 1B). Other studies tended to focus on release from predation or herbivory (11.4%) or from interspecific antagonists in general, including competitors but also predators, parasites, and pathogens (29.5%; Figure 1B). This broadened definition was common among the substantial portion of studies that described ecological release in the context of anthropogenic environmental change (36.2%; Table S1 in the supplemental information online). For example, several studies explored whether ecological release explained invasion success of some non-native species (i.e., the enemy release hypothesis; [33]). Additionally, multiple studies either acknowledged or directly investigated ways in which other anthropogenic changes, including habitat modification, climate change, and overhunting or overfishing, might alter community composition and lead to ecological release (Table S1 in the supplemental information online). One study [34] associated ecological release with positive interspecific interactions, such as facilitation and mutualisms, which can drive niche expansion via amelioration of environmental stressors [35,36]. In its broadest conception, ecological release was described as a relaxation of constraining selective pressures [37].

Defining Ecological Release in the 21st Century

That the definition of ecological release varies widely depending on whom you ask is problematic. To facilitate communication and effective hypothesis testing, we propose the following definition for **ecological release (proposed definition)**: niche expansions and shifts when a constraining interspecific interaction is reduced or removed.

Moving Beyond Interspecific Competition

In the days of Lack and Wilson, interspecific competition was seen as the primary force structuring ecological communities, and thus it makes sense that the idea of ecological release was presented in that context. Researchers now widely accept that other biotic factors can constrain a population’s resource use, resulting in acknowledgement that niche expansion may occur during ecological release from predation or ecological release from parasitism.

One could expand the idea even further, as there are many additional ecological mechanisms that can promote niche changes. These include positive interspecific interactions such as facilitation and mutualisms [34–36], an increase in the local supply of resources [38,39], and changes in

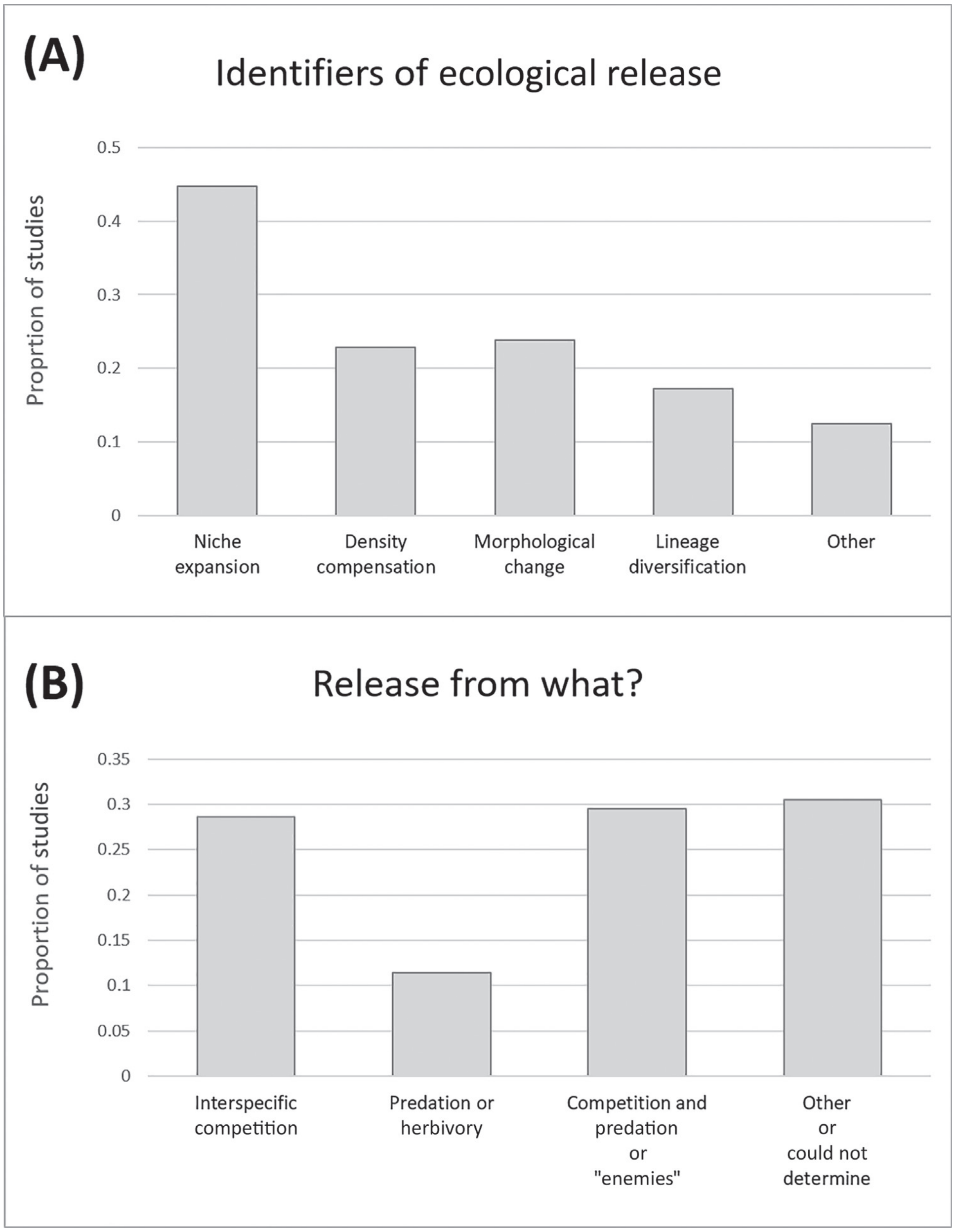

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Figure 1. According to 105 Recent Studies, What Is Ecological Release? (A) Studies varied in what they accepted as identifiers that ecological release had occurred, though in corroboration with Wilson's definition [2], niche expansion – an increase in resource use breadth - was the most mentioned identifier. Note that the proportions do not add to 100%, as some studies accepted multiple indicators (e.g., both niche expansion and morphological change) while others mentioned no specific indicators of ecological release. See Table S1 in the supplemental information online for details. (B) Studies varied in the mechanisms they identified as underlying ecological release. Most authors implied or stated that ecological release resulted from a relaxation of pressures imposed by antagonists, including competitors, predators, parasites, pathogens, or some combination thereof.

abiotic (e.g., climatic) conditions that provide access to previously inaccessible resources [40]. We suggest that, rather than broaden the possible mechanisms underlying ecological release so much that its original meaning becomes unrecognizable, we use the term only to describe the direct release from constraining, negative interspecific interactions (i.e., competition, predation, parasitism, and pathogenicity). We acknowledge that this release itself can have different proximal causes, including but not limited to establishment in a new geographic area, extinction of an antagonist, or a surge in local resource availability.

What Should Count as Potential Evidence That Ecological Release Has Occurred?

The term density compensation reflects its traditional association with interspecific competition (the increased density compensates for the number or biomass of reduced competitors; [20]). As we propose extending the definition of ecological release to include additional negative interspecific interactions, the term **density inflation**, which describes an increase in density without assuming a specific mechanism, is an appropriate substitute for density compensation [23]. However, we have already discussed the historical precedent for and rationale behind distinguishing niche expansion (and ecological release) from density responses. Thus, there are two outstanding issues which we explore in the following text: (i) why we break from tradition in accepting both population-level niche expansions (increases in resource use variance) and niche shifts (changes in mean resource use) as potential evidence for ecological release; and (ii) why many authors have subsumed distinct evolutionary phenomena (namely, morphological evolution and diversification) into ecological release, and why we choose not to.

Niche Dynamics of Ecological Release: Population- and Individual-Level Responses

We favor a framework for describing niche changes during ecological release which evaluates means and variances, jointly, at the levels of both populations and individuals (Figure 2). Using this framework, we can generate specific predictions about how ecological release might affect the evolution of traits other than the niche itself (see next section).

First, we suggest that during ecological release, a population may undergo a niche expansion, niche shift, or both. For example, if a species of consumer were introduced to a new community with similar prey resources but fewer competitors, the population may expand resource use to consume both larger and smaller prey without changing its mean niche position. However, if new resource availability is asymmetrically distributed, then a shift in population mean niche position may occur as resource use broadens. Several of the ecological release patterns described in the 1960s and 1970s, including Wilson's original description of niche expansion in Melanesian ants [2], were also accompanied by such directional niche shifts [25,27,29], although this did not prevent the term ecological release from becoming almost exclusively associated with variances. That niche shifts without expansion (e.g., [41,42]; Figure 2A) have not historically qualified as ecological release may reflect semantic tradition more than biological reality (Box 2). Alternatively, niche shifts without expansion may be rare and ephemeral; even if many individuals switch to preferred, newly available resources, some individuals will still benefit from using old resources, especially if the preferred resources become depleted [43].

Second, we acknowledge that population-level niche expansion during ecological release can be the result of several different patterns at the individual level. One possibility is that population-level niche expansion proceeds via a widening of individual-level niches to include newly available resources (parallel release; [44]). Another possibility is that population-level niche expansion proceeds via individuals diverging in their mean niche position while maintaining relatively narrow individual niche widths, resulting in a population of individuals specializing on different parts of the

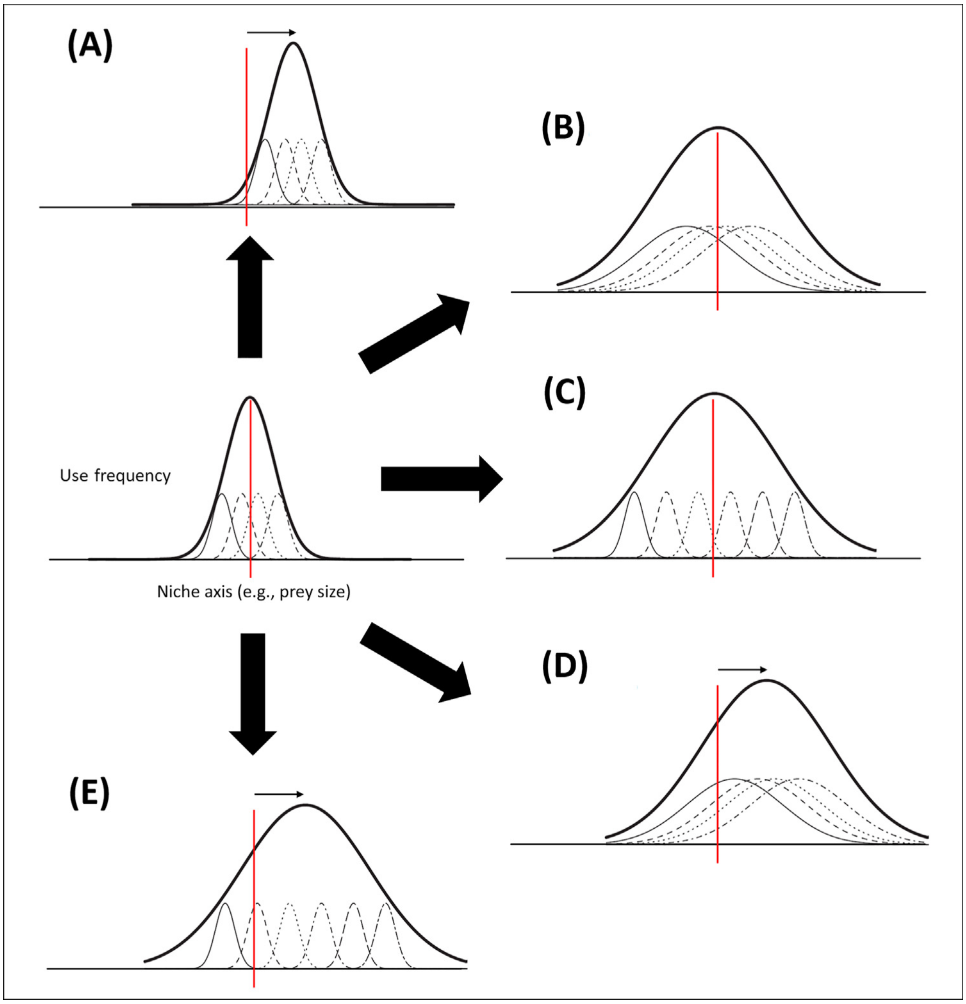

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Figure 2. Five Scenarios Illustrating Niche Responses during Ecological Release from the Same Hypothetical Initial State. Broken black lines are the niches of individuals within the population (unbroken black line). The vertical red line represents the mean niche position in the initial state. (A) Although population-level niche shifts without expansion did not historically qualify as ecological release, we recognize this scenario as a potential response to a reduction in biotic constraints. A population may also experience ecological release via (B) within individual niche expansion and with no population-level niche shift (C) between individual niche expansion and with no population-level niche shift (D) within individual niche expansion along with a population-level niche shift (E) between individual niche expansion along with a population-level niche shift.

resource spectrum (the niche variation hypothesis; [45]). These possibilities, which can manifest from behavioral plasticity in a single generation or individual-level niche evolution over multiple generations [44,46], represent opposite extremes but are not mutually exclusive. Furthermore, either can lead to population-level expansion around a stable mean (Figure 2B,C) or accompanied by a niche shift ([47]; Figure 2D,E).

Evolutionary Consequences of Ecological Release

Morphological Evolution (Formerly Known as Character Release)

Ecological release has long been hypothesized to have multiple potential evolutionary consequences. For example, MacArthur and Wilson [3] introduced the term character release to describe

Box 2. Mean-Variance Distinction between Ecological Character Displacement and Ecological Release

Ecological character displacement and ecological release each represent responses to changes in the intensity of interspecific competition. Given their historical ties (having both been formally introduced by Wilson) as well as their conceptual overlap, it may be tempting to assume that the two phenomena are, in a way, opposite. However, we argue that this is not strictly true.

Ecological character displacement refers to niche divergence resulting from interspecific competition that leads to evolutionary shifts in other (mostly morphological) traits (reviewed most recently in [10]; the role of plasticity in these shifts has also been recently discussed [64]). Studies of character displacement focus mostly on means, explicitly predicting that trait shifts represent an evolutionary response to interspecific competition. A classic example is mean beak size divergence between the large ground finch (*Geospiza magnirostris*) and medium ground finch (*G. fortis*) on Daphne Major driven by competition for limited seeds [65].

Historically, ecological release referred to increases in niche breadth, rather than shifts in mean niche position, and focused primarily on resource use. For example, the Cocos finch (*Pinaroloxias inornata*), isolated from confamilial competitors on its own remote island, exhibits multiple foraging behaviors across a wide range of microhabitats [66]. In contrast to ecological character displacement, the evolutionary consequences of ecological release were not inherent to the term. Therefore, classic conceptions of ecological character displacement and ecological release were distinct in at least two ways: the former focused on mean niche position and encompassed explicit evolutionary predictions, whereas the latter focused on resource-use variances and represented a purely ecological phenomenon.

The mean-variance distinction between ecological character displacement and ecological release is at least partly historical artifact; it was implicit in the concepts as they were originally described [1,2], and early empirical studies mostly followed suit by focusing on either means (ecological character displacement) or variances (ecological release), but not both. Yet as we demonstrate, shifts in mean niche position sometimes occur during ecological release (see main text). More generally, the mean and variance of a trait can jointly determine how the trait distribution changes in response to selection [67,68]. In this way, the mean-variance distinction between ecological character displacement and ecological release may ultimately obscure our understanding of how populations respond to changes in biotic pressure. Thus, we embrace the possibilities that ecological release may drive niche shifts as well as niche expansions and that either may accompany or lead to evolutionary change.

morphological evolution exhibited by populations assumed to have undergone ecological release. As originally envisioned, character release can manifest in two ways: (i) an increase in morphological variation, for example, if a bird population experiencing ecological release has a broader diet and also exhibits increased bill size variation [45]; or (ii) a morphological mean shift, for example if a bird population experiencing ecological release with a directional bias toward consuming larger prey items also exhibits an increase in average bill size [30,48].

With the potential for ecological release to take many forms (Figure 2), it is unsurprising that associated morphological changes can also vary. For example, we might expect shifts in morphological means only when ecological release is accompanied by a niche shift (Figure 2A,D,E). Additionally, increases in morphological variation may be more common when niche expansion proceeds via individuals diverging in their mean niche position, as the population will ultimately comprise individuals that specialize on different and relatively narrow segments of the resource spectrum (Figure 2C,E). If instead, individuals simultaneously broaden their resource use such that their individual niches overlap substantially (Figure 2B,D), selection may not favor increased morphological variation.

Yet, these scenarios are hypotheses to be tested. Morphological evolution, even that which is consistent with patterns originally described by MacArthur and Wilson [3], should not be accepted as prima facie evidence that ecological release has occurred because other processes may cause the same evolutionary outcome. As use of the term character release has mostly stopped (Table S2 in the supplemental information online), we ask that the field take care to distinguish morphological evolution from ecological release, which should be reserved for describing niche changes.

Adaptive Speciation

In recent years ecological release has become an essential component of conceptual models that posit how **ecological opportunity** – loosely defined as the availability of ecological resources that can be evolutionarily exploited – can ultimately promote adaptive diversification [4,49–51]. By and large, these models posit that if ecological release leads to increased and heritable trait variation on which selection can subsequently act, a species may be primed to diverge into distinct forms that later become reproductively isolated. If this process occurs repeatedly within a lineage across time or space, it manifests as adaptive radiation.

Conceptual and theoretical models may propose links between ecological release and adaptive speciation, but they do not equate them – the former can occur without the latter. Indeed, there may be conditions under which ecological release precludes rather than prompts speciation, such as when it promotes gene flow between populations that might otherwise remain distinct [52]. Ecological release is one of many potential primers of diversification but remains a hypothesis to be evaluated against other contenders.

Experimental microbial systems are perhaps the most amendable to direct tests of the proposed mechanistic links between ecological release and adaptive diversification [53], as empirical studies in nature must often infer whether ecological release in the past is responsible for present diversity. However, it may be possible to bridge this process–pattern divide by exploring whether ecological release in extant clades is more likely to occur along some niche axes (e.g., microhabitat, macrohabitat, or diet) than along others, and whether these are the same axes that tend to define patterns of adaptive diversification [54]. Theoretical studies that explicitly investigate the relationship between niche width evolution and diversification [55] should inform the design and interpretation of empirical work. Additionally, more studies of all types should simultaneously consider the effects of ecological release along multiple niche axes, as expansion along one axis may alter evolution along another [56,57].

Concluding Remarks

There is a rich collection of outstanding conceptual questions, spanning topics in ecology and evolution, related to how populations respond to a reduction in biotic constraints (see Outstanding Questions). Tackling them will require collaboration and clear communication.

By investigating ecological release with a critical lens, we discovered a lack of consensus around exactly what it represents. We hope that our proposed definition for ecological release – niche expansions and shifts when a constraining interspecific interaction is reduced or removed – along with the discussion we have provided, will ultimately lead us to a sharper understanding of what ecological release is and, by extension, how it might be studied.

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Supplemental Information

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Outstanding Questions

Multiple biotic interactions during ecological release. How do changes in interspecific competition and intraspecific competition interact to drive niche changes during ecological release? What are the relative effects of decreased interspecific competition versus predation on the magnitude of ecological release?

Exploring the niche dynamics of ecological release. How frequently and under what conditions is ecological release accompanied by a niche shift? How frequently and under what conditions does ecological release occur within versus between individuals within a population?

Understanding the ecoevolutionary dynamics of ecological release. What is the role of plasticity in ecological release? How does natural selection operate during ecological release? Is evolutionary change more likely to accompany ecological release along certain niche axes (e.g., macrohabitat, microhabitat, and diet)? Under what conditions does ecological release lead to speciation?

Ecological release and a multidimensional niche. Does ecological release along one niche axis tend to promote or inhibit ecological release along others? How do the common niche axes along which ecological release occurs differ across taxa, and do these axes of release correlate with the niche axes along which taxa tend to diversify?

Ecological release in the Anthropocene. Is ecological release more common in human-altered environments? To what extent is ecological release responsible for the success of invasive species?

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