

CONCEPT

Extending the gleaner–opportunist trade-off

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Abstract

1. Species exhibit various trade-offs that can result in stable coexistence of competitors. The gleaner–opportunist trade-off to fluctuations in resource abundance is one of the most intuitive, yet also misunderstood, coexistence-promoting trade-offs. Here, we review its history as an ecological concept, discuss extensions to the classical theory and outline opportunities to advance its understanding.
2. The mechanism of coexistence between species that grow relatively faster than their competitors in a low-resource environment (i.e. a gleaner) versus a high-resource environment (i.e. an opportunist) was first proposed in the 1970s. Stable coexistence could emerge between gleaners and opportunists if the opportunist species (dominant in unstable environments) dampens resource fluctuations via relatively convex functional responses, while the gleaner species (dominant in stable environments) promotes fluctuations, or diminishes them less than the opportunist does, via relatively saturating functional responses.
3. This fluctuation-dependent coexistence mechanism has since been referred to by various names, including the Armstrong–McGehee mechanism and relative nonlinearity of competition. Several researchers have argued this mechanism likely plays a relatively minor role in species coexistence owing in part to the restricted range of conditions that allow it to operate. More recent theoretical research, however, suggests that relative nonlinearity can operate over wider conditions than previously thought.
4. Here, we identify several novel, or little explored, extensions to the gleaner–opportunist trade-off that can yield species coexistence under phenomena as diverse as fluctuations in predation/pathogen pressure, multiple resources, phenotypic plasticity and rapid evolution, amongst other phenomena.
5. While the original definition of the gleaner–opportunist trade-off may be imperfect as a collective for these extensions, we argue that a subtle reframing of the trade-off focusing on species' performance in equilibrium versus fluctuating conditions (irrespective of preferences for high or low resources, predation pressure or other competitive factors) reveals their fundamental commonality in stable coexistence via relative nonlinearity. An extended framing shines a light on the potential ubiquity of this canonical trade-off in nature and on the breadth of theoretical and empirical terrain that remains to be trodden.

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KEYWORDS

apparent competition, Armstrong–McGehee mechanism, Chesson's coexistence theory, exploitative competition, functional response, gleaner–exploiter trade-off, oligotroph–copiotroph trade-off, relative nonlinearity

1 | INTRODUCTION

Stable coexistence of competing species is predicated on trade-offs in how species utilize and are impacted by the environment around them (Chase & Leibold, 2003; Chesson, 2000). Competing species might preferentially consume different resources (i.e. resource partitioning) or be targeted more acutely by different predators or pathogens (i.e. species-specific enemies). Alternatively, species might make up for deficiencies in their competitive ability for resources (and/or vulnerability to predation) with superior capacity for dispersal and colonization (Skellam, 1951; Tilman, 1994), or segregate in space and time on the basis of variation and fluctuations in environmental conditions (Barabás et al., 2018; Chesson, 2018; Ellner

et al., 2019). We venture that many ecologists would agree these broadly capture the most prevalent trade-offs axes facilitating species coexistence in the natural world (Barabás et al., 2018; Chase & Leibold, 2003; Chesson, 2000, 2018; Ellner et al., 2019). What they are less likely to agree on is the relative importance of each.

One trade-off whose position is likely to prove particularly contentious in any hypothetical hierarchy of importance is the so-called gleaner–opportunist trade-off (Fredrickson & Stephanopoulos, 1981; Grover, 1990; Stewart & Levin, 1973) (Figure 1). The gleaner–opportunist trade-off traditionally describes a trade-off in species' relative growth rate when resources are either plentiful or scarce. Despite a long history of theoretical and empirical study, the prevalence of the gleaner–opportunist trade-off in natural systems and

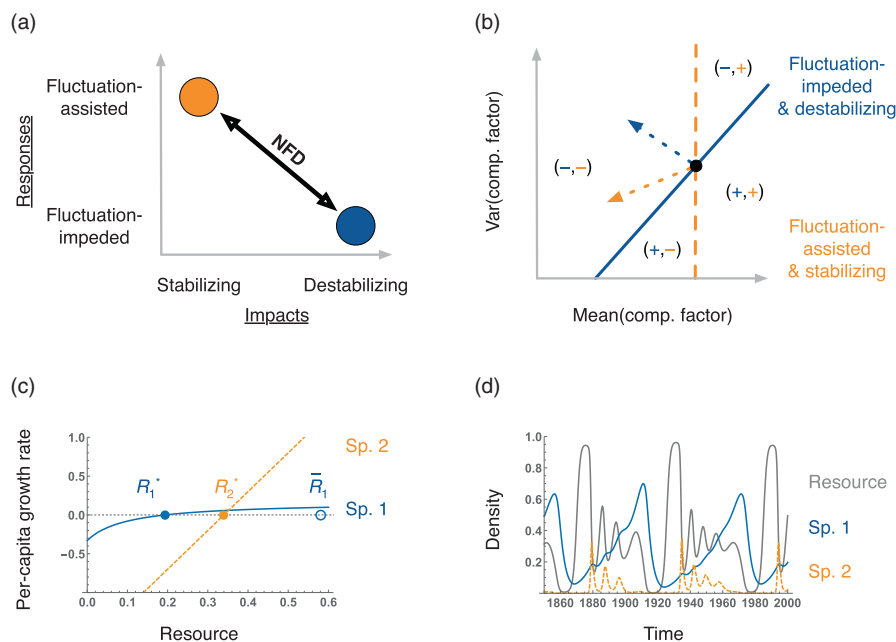


FIGURE 1 The gleaner–opportunist trade-off and fluctuation-mediated stable coexistence via relative nonlinearity. (a) Fluctuation-mediated stable coexistence is possible via negative frequency-dependence (NFD) when the orange species stabilizes population cycles and prefers fluctuating environments whereas the blue species promotes population cycles and prefers stable environments (Yamamichi & Letten, 2021). (b) A conceptual figure showing requirements (zero net growth isocline, ZNGI; solid and dashed lines) and impacts (dotted arrows) of two species on the mean and variance of a single resource (Chase & Leibold, 2003; Yamamichi & Letten, 2021). The fluctuation-impeded blue species has a higher growth rate when the variance in the limiting factor (e.g. resource) is low, but it increases the variance as shown by the upward impact vector. In contrast, the fluctuation-assisted orange species is neutral to the variance in this case, but it decreases the variance when abundant (i.e. ‘a consumer of variance’) (Levins, 1979). (c) Gleaner–opportunist trade-off where the orange species (Sp. 2) has a linear functional response and higher maximum growth rate whereas the blue species (Sp. 1) has a saturating functional response and lower resource requirement (R^*). When the orange species is absent, the blue species generates resource fluctuations (limit cycles) and the average resource abundance is shown by the blue circle, \bar{R}_1 . Because the orange species has a positive growth rate at \bar{R}_1 (i.e. $R_1^* < R_2^* < \bar{R}_1$), stable coexistence is possible (Abrams & Holt, 2002; Armstrong & McGehee, 1980; Klauschies & Gaedke, 2020). (d) Stable coexistence with the gleaner–opportunist trade-off via relative nonlinearity. Coexistence occurs with chaotic, intermittent cycles in (d). Although synchronous cycles may be more widely studied than intermittent cycles (Armstrong & McGehee, 1980), the latter provides a clearer illustration of the critical feedback dynamics underpinning fluctuation-dependent coexistence. Parameter values in (c)–(d) are from Abrams et al. (2003). See Appendix S1 and Figure S1 for details

its role in facilitating coexistence remains unclear. With a view to consensus building, here we review the historical background of the gleaner–opportunist trade-off and its conjugate coexistence mechanism—relative nonlinearity of competition—and propose a more inclusive definition that allows further explorations of various understudied extensions.

2 | HISTORICAL BACKGROUND

Understanding stable coexistence of competing species, in violation of the competitive exclusion principle (Hardin, 1960), has long been a central focus in community ecology (Hutchinson, 1961). To our knowledge, Stewart and Levin (1973) were the first to identify the potential for a seasonal resource supply to support the coexistence of species that grow optimally in low- versus high-resource environments, although Robert MacArthur distinguished ‘opportunistic’ and ‘equilibrium’ species as early as 1960 (MacArthur, 1960). Later researchers extended these findings to endogenous resource fluctuations generated by limit cycles (Armstrong & McGehee, 1976a, 1976b, 1980; Hsu et al., 1978a, 1978b; Koch, 1974; McGehee & Armstrong, 1977; Zicarelli, 1975) as well as exogenously fluctuating environments (Hsu, 1980; Smith, 1981). Among them, Armstrong and McGehee (1980) has been particularly influential in promulgating the concept of fluctuation-dependent coexistence, and thus, the coexistence mechanism arising from this trade-off is sometimes referred to as the Armstrong–McGehee mechanism (Xiao & Fussmann, 2013).

Although various researchers coined different terms to describe the trade-off, including the ‘gleaner–exploiter’ concept (Fredrickson & Stephanopoulos, 1981) and the ‘oligotroph–copiotroph’ trade-off (Koch, 2001), it was Grover (1990) who apparently first referred to it as the ‘gleaner–opportunist’ trade-off. Grover’s gleaner is characterized by a low-resource requirement (high-resource affinity), R^* , and a low maximum growth rate, while the opportunist has a high R^* and a high maximum growth rate (Figure 1c). Under equilibrium resource dynamics, the gleaner is expected to dominate (Tilman, 1982), but in the presence of resource fluctuations, the opportunist gains an advantage that can either lead to coexistence of the two strategies or exclusion of the gleaner.

Importantly, it was shown early on that the gleaner–opportunist trade-off alone is not sufficient to support coexistence. If all species have linear responses to resource abundance, resource fluctuations do not promote coexistence (Fox, 2013). Stable coexistence is contingent on negative frequency-dependence, that is, that competitor growth rate is a negative function of its own frequency in the community. For stable coexistence to emerge via a gleaner–opportunist trade-off, the gleaner (which is impeded by fluctuations) when dominant needs to exacerbate resource fluctuations, while the opportunist (which is assisted by fluctuations) needs to inhibit them (Figure 1a). In other words, we need to consider the impact niche alongside the requirement niche (sensu Chase & Leibold, 2003). Levins (1979) referred to this requirement–impact duality in terms of

one species consuming the mean and the other species consuming the variance of the resource (Figure 1b). This is evident in intermittent chaotic cycles in Figure 1d, where the blue species increases in relatively stable time periods but increases the amplitudes of resource cycles, while the orange species increases during fluctuating time periods but stabilizes resource cycles. Note that in the presence of externally driven resource fluctuations, where neither species can influence the amplitude of resource cycling, the opportunist can still reduce variance in resource concentration through time via rapid resource consumption, while the gleaner can increase the apparent variance in resource concentration due to slower resource removal.

Chesson (1994) later formalized these criteria under the banner of ‘relative nonlinearity of competition’—one of two broad coexistence mechanisms arising in temporally fluctuating environments (the other being the temporal storage effect). In Chesson’s schema relative nonlinearity refers to the requirement that species have differentially nonlinear growth responses to a shared limiting factor (e.g. a limiting resource). This is why many studies have focused on a gleaner with a saturating (Holling (1959)’s type II) functional response and an opportunist with a linear (type I) functional response (e.g. Armstrong & McGehee, 1980) (Figure 1c,d), but importantly coexistence is possible when both species have saturating functional responses (e.g. Hsu et al., 1978a) (Figure 2a,b) or when two species have concave and convex functional responses (Utida, 1957) (Figure 2c,d).

Despite substantial theoretical interests in the coexistence promoting role of the gleaner–opportunist trade-off since the 1970s (Abrams, 2004; Abrams et al., 2003; Abrams & Holt, 2002; Adler, 1990; Anderies & Beisner, 2000; Klauschies & Gaedke, 2020; Okuyama, 2015; Xiao & Fussmann, 2013) and some empirical studies (Grover, 1997; Hiltunen et al., 2008; Kirk, 2002; Litchman, 1998; Litchman & Klausmeier, 2001), a general perception emerged that the mechanism only operates under a restrictive set of conditions (Chesson, 1994; Grover, 1990; Xiao & Fussmann, 2013). Combined with logistical challenges in testing the trade-off experimentally, our understanding of its actual prevalence and importance in regulating community dynamics in natural systems has remained elusive. Nevertheless, as noted by Abrams (2004), given the ubiquity of nonlinear functional responses and seasonal/cyclical dynamic in nature, it seems unlikely to be a wholly rare phenomenon (particularly in the presence of large-amplitude fluctuations [cf. Chesson’s small variance approximation]: Kremer & Klausmeier, 2013; Litchman & Klausmeier, 2001). Moreover, in the following section, we identify several novel, or little explored, extensions to the original gleaner–opportunist concept that significantly expand its theoretical scope.

3 | EXTENSIONS

The perception that the gleaner–opportunist trade-off only facilitates coexistence under a narrow set of conditions stems, at least in part, from the correspondingly narrow set of assumptions and/or definitional constraints underpinning its original formulation.

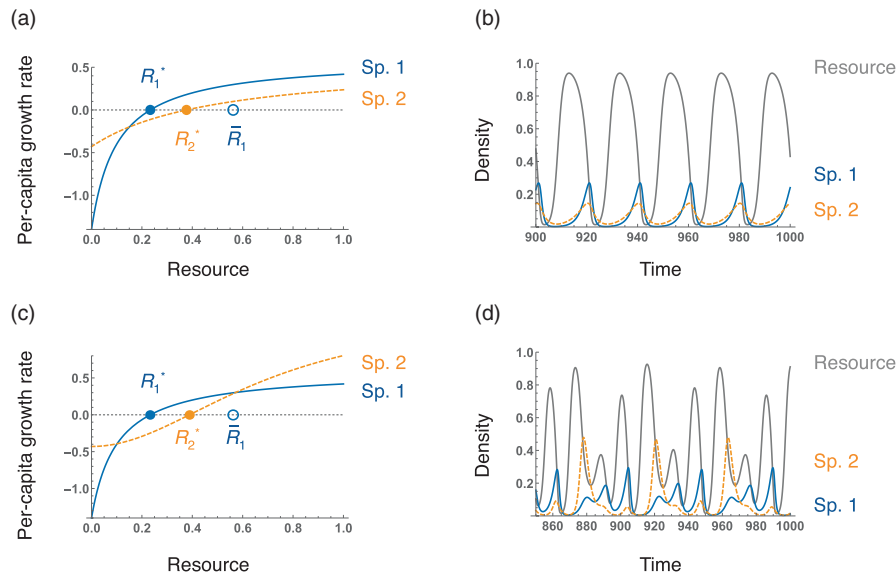


FIGURE 2 Fluctuation-mediated coexistence via relative nonlinearity without the canonical gleaner–opportunist trade-off. (a) In this example, there is no canonical gleaner–opportunist trade-off *sensu* Grover (1990) because the blue species is the ‘gleaner’ (with a lower R^*) and the ‘opportunist’ (with a higher maximum growth rate). (b) Despite the absence of the canonical gleaner–opportunist trade-off, two species stably coexist via relative nonlinearity. This is because NFD in Figure 1a still emerges here: the blue species (Sp. 1) has the lower R^* and a relatively concave functional response that promotes consumer–resource cycles whereas the orange species (Sp. 2) has a higher growth rate when the resource level is very low and a relatively linear functional response that stabilizes population cycles. (c) Here the orange species has a Holling type III (convex) functional response and there are two crossing points: it has a higher growth rate than the blue species when the resource concentration is either very low or very high. (d) Two species stably coexist via relative nonlinearity. The orange species increases when the resource fluctuates whereas the blue species increases when the resource is relatively stable. Note that $R^*_1 < R^*_2 < \bar{R}_1$ is no longer necessary for stable coexistence when the opportunist species has a nonlinear functional response (see Figure 3 as well). See Appendix S1 for details

Relaxing these constraints via various extensions to the original theory reveals a wider range of conditions under which the coexistence mechanism can potentially operate.

We show that coexistence is possible even when one species is, *sensu stricto*, a gleaner and an opportunist (after Grover, 1990) (Figure 2a,b; coexistence verified as stable via mutual invasibility analysis). Under this somewhat counterintuitive scenario, the blue species in Figure 2a has a lower R^* (i.e. the gleaner) and higher maximum growth rate (i.e. the opportunist). However, because the blue species has a more concave functional response and the competing orange species has a less negative growth rate when resource concentrations approach zero (Figure 2a), they can stably coexist with fluctuations (Figure 2b). The blue species drives resource fluctuations due to its more nonlinear (concave) functional response, which makes the orange species competitively superior in the region where the two species have negative growth rates. The orange species stabilizes fluctuations, making the blue species dominant and resulting in negative frequency-dependence (Figure 1a).

Based on the previous example, it may be tempting to redefine the gleaner as the species that performs best when the resource is scarce, even if it technically has a higher R^* (in contradiction of the original gleaner–opportunist definition). However, our second example shows that coexistence is possible when there are two crossing points in the per-capita growth rates (Figure 2c): Here, the orange species is better than its competitor in resource-poor and

resource-rich environments and stabilizes dynamics due to its convex functional response, whereas the blue species has a lower R^* and destabilizes dynamics (Figure 2c). This results in stable coexistence as the orange species benefits from fluctuating environments (Figure 2d).

One way to circumvent the inherent terminological ambiguity is to relax the definition of the gleaner–opportunist trade-off to allow the species that benefits from fluctuating environments to carry the ‘opportunist’ mantle and call a species that dominates in stable environments (e.g. with a lower R^*) a ‘gleaner’. Note that this terminology is focusing on species’ requirements (Y-axis of Figure 1a). If we focus on the impacts (X-axis of Figure 1a) instead, it might be better framed as a stabilizer–destabilizer trade-off, where the opportunist is the self-limiting stabilizer and vice versa.

An advantage of this subtle reframing of the gleaner–opportunist trade-off is that it provides a catch-all for a wider range of phenotypic trade-offs that can give rise to coexistence (or destabilization) via the mechanism of relative nonlinearity of competition, including species responses to fluctuations in top-down regulatory factors. Although research into the gleaner–opportunist trade-off has traditionally focused on coexistence mediated by bottom-up resource fluctuations, we can consider an analogous trade-off in the nonlinearity of sensitivity to predation or disease. Consider, for example, a scenario in which one species can tolerate higher predation pressure (i.e. higher P^*) but

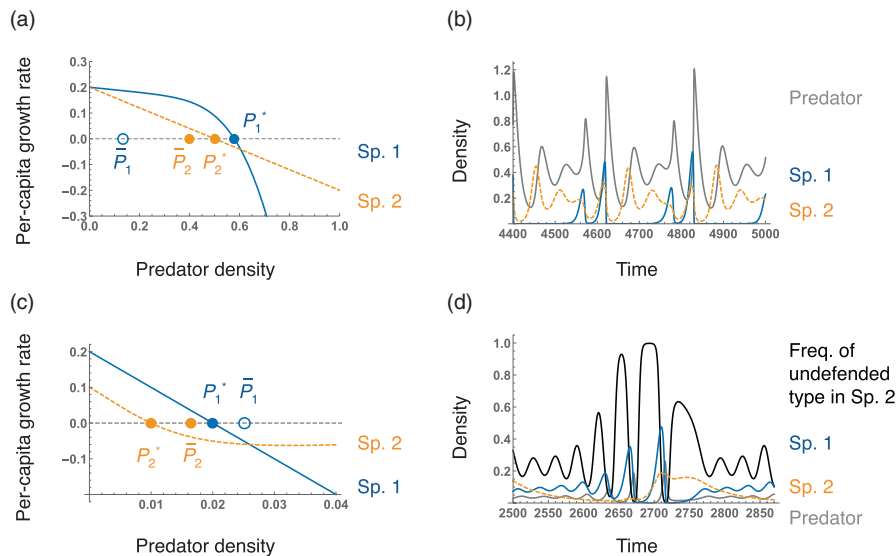


FIGURE 3 Stable coexistence via relative nonlinearity in apparent competition. (a) Per-capita growth rates when prey species are rare. The blue species (Sp. 1) has a higher P^* (more tolerant of predation) and thus is competitively dominant in stable environments. However, due to its concave response to predation, it causes predator–prey cycles. The orange species (Sp. 2) has a lower P^* but stabilizes population cycles due to its linear response to predation. Stable coexistence is possible because of mutual invasibility: the equilibrium predator density in the absence of the blue species (shown by the orange filled circle) is smaller than the blue species' P^* ($\bar{P}_2 < P_1^*$) and the average predator density when the orange species is absent (shown by the blue circle) is smaller than the orange species' P^* ($\bar{P}_1 < P_2^*$). Here, we assumed that the predator attack rate on the blue species increases as the predator density increases due to efficient group foraging. This situation may be seen, for example, in the context of mammalian prey species hunted by wolves: small species (e.g. hares) are more likely to be subject to a constant attack rate (i.e. group hunting by wolves does not increase the attack rate) while larger species (e.g. elk) are hunted more effectively by groups. See Appendix S2 and Figure S2 for details. (b) Two species stably coexist via relative nonlinearity. The orange species increases when the predator density fluctuates whereas the blue species increases when the predator density is relatively stable. (c) When we assume rapid induction of defense against predation of one prey species, two species may show a gleaner–opportunist-like trade-off. This may arise, for example, when two phytoplankton species are grazed by zooplankton, where one phytoplankton species (e.g. *Scenedesmus*) has inducible defense (predator-dependent cell clumping) while the other species is always unicellular (Verschoor et al., 2004). The blue species (Sp. 1) has higher predation tolerance (P^*) and a linear response to predation whereas the orange species (Sp. 2) has a higher growth rate when predation pressure is very high and a convex response to predation. Note that $\bar{P}_1 < P_2^*$ is not necessary for stable coexistence here because the opportunist species has a convex response to predation. (d) Fluctuation-mediated stable coexistence is possible when the blue species destabilizes population cycles and prefers stable environments (with higher P^*) whereas the orange species stabilizes population cycles via inducible defense and prefers fluctuating environments. Models and parameters are from Yamamichi and Letten (2021). We assume the prey densities are zero in the per-capita growth rates in (a) and (c). See Appendix S2 and Figure S3 for details

destabilizes dynamics, whereas the other species stabilizes dynamics but has a lower P^* (Figure 3a). In stable environments, species with the highest P^* will exclude other species via apparent competition (Holt, 1977), but two species can coexist via fluctuations in predator density (Figure 3b). Here, the blue and orange species are the 'gleaner' and 'opportunist' (or destabilizer and stabilizer) species, respectively.

The gleaner–opportunist trade-off (or its top-down analogue) may also be extended to spatial heterogeneity (e.g. the competition–colonization trade-off) (Abrams & Wilson, 2004; Pacala & Rees, 1998; Parvinen & Meszena, 2009; Wilson & Abrams, 2005) or to multiple fluctuating trade-off axes, where competitors might be gleaners for one resource and opportunists for another (Chesson, 2009; Levins, 1979). Levins (1979) showed how fluctuations across multiple competitive factors could yield coexistence of more than two species per resource with the emergence of covariance specialists. Nevertheless, this phenomenon has received remarkably little attention by theoreticians or empiricists alike. Chesson (2000, 2009)

has pointed to Huisman and Weissing (1999) as an example of species coexistence via multiple fluctuating competitive factors, but we note that none of the competitors in Huisman and Weissing (1999) exhibited a gleaner–opportunist trade-off for a single resource (Letten, 2022). This suggests that coexistence in Huisman and Weissing (1999) may have been exclusively a function of higher dimensional trade-offs.

So far, we have assumed that organismal traits are fixed (but see Grover, 1991; Sommer, 1985 for physiological flexibility via nutrient storage). However, an increasing number of studies have shown that adaptive trait changes are ubiquitous, especially in fluctuating environments, and can affect various ecological dynamics (Hendry, 2016). Recent studies have demonstrated that adaptive foraging of consumer species and inducible defence of prey species can greatly expand parameter conditions for fluctuation-mediated coexistence (Tan et al., 2020; Yamamichi & Letten, 2021; Yamamichi et al., 2011). For example, coexistence is possible due to rapid induction of defence resulting in the species with a lower P^*

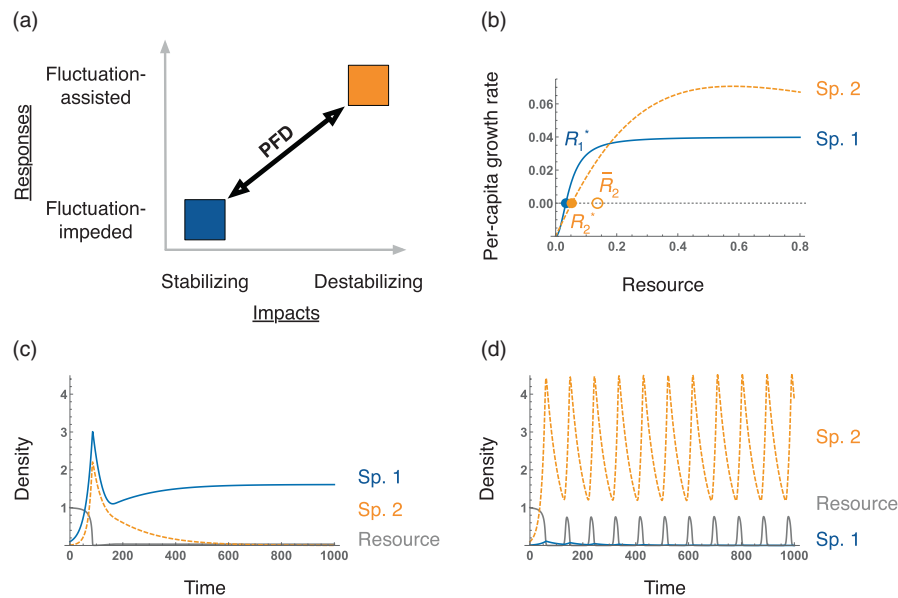


FIGURE 4 The gleaner–opportunist trade-off and fluctuation-mediated priority effects via relative nonlinearity. (a) Fluctuation-mediated priority effect arises via positive frequency-dependence (PFD) when the orange species promotes population cycles and prefers fluctuating environments whereas the blue species stabilizes population cycles and prefers stable environments (Yamamichi & Letten, 2021). (b) Gleaner–opportunist trade-off that induces a priority effect. Note that the orange species (Sp. 2) has the higher maximum growth rate whereas the blue species (Sp. 1) has the lower resource requirement (R_1^*). (c, d) Priority effect with the gleaner–opportunist trade-off via relative nonlinearity. (c) When the orange species is rare initially, the blue species reduces the resource abundance to the level where species 2 cannot grow. (d) When the blue species is rare at the beginning, the orange species causes population cycles and prevents the invasion of species 1. Note that $R_1^* < \bar{R}_2$ does not ensure invasion of the blue species because it has a saturating functional response. See Appendix S3 and Ke and Letten (2018) for details

having a convex response to predation (Yamamichi & Letten, 2021) (Figure 3c,d). In contrast, Kremer and Klausmeier (2013) found that rapid evolution undermined gleaner–opportunist coexistence. It will be important to clarify under what conditions rapid evolution promotes or hinders coexistence.

Questions also remain as to the maximum number of coexisting species via the gleaner–opportunist and analogue trade-offs. While Chesson (1994) found (via small variance approximations) that relative nonlinearity could only support coexistence of two species, others have shown coexistence of three or more species on a single fluctuating resource (Kremer & Klausmeier, 2013; Litchman & Klausmeier, 2001). Indeed, Zicarelli (1975) claimed that there was no constraint on the number of coexisting species under resource fluctuations. Nevertheless, Litchman and Klausmeier (2001) and Kremer and Klausmeier (2013) found that coexistence of three or more species via a gleaner–opportunist trade-off necessitated improbable trade-off curves. It remains to be seen whether the same constraints hold under the various extensions described above.

Finally, we also note that the gleaner–opportunist trade-off need not always result in negative frequency-dependence and therefore promote stable coexistence (Figure 4). Instead, under certain conditions, it can promote a fluctuation-mediated priority effect with positive frequency-dependence in community dynamics (Figure 4a) (Chesson, 2009; Ke & Letten, 2018; Klausmeier, 2010). When a gleaner species stabilizes population dynamics whereas an opportunist species

promotes temporal fluctuations (Figure 4b), the first species to a local habitat can induce a resource regime that favours its own growth and prevents colonization of the competing species (Figure 4c,d).

4 | FUTURE DIRECTIONS

It is apparent from the above extensions that there are numerous putative trade-offs that are closely allied with the gleaner–opportunist trade-off. For some of these extensions, the distinction between gleaner and opportunist strategists of Grover (1990) no longer fits comfortably (Figures 2 and 3). Nevertheless, any discussion of the gleaner–opportunist trade-off that excluded these phenomena would be incomplete.

Embracing a 'big tent' interpretation of the gleaner–opportunist trade-off does not negate the current dearth of existing empirical evidence, either for or against. The lack of empirical attention to either classical or extended interpretations of the gleaner–opportunist trade-off is disappointing, but it is understandable because measuring per-capita growth rates along resource abundance gradients (e.g. Letten et al., 2018) is time-consuming and often difficult, particularly for longer lived plants and animals (Kjørboe & Thomas, 2020; Letten & Yamamichi, 2021). However, it also presents an excellent opportunity for innovative experimental research: from pathogen fluctuations and multiple covarying resources to rapid evolution and phenotypic plasticity in

temporally variable environments, numerous hypotheses await empirical interrogation. Until such time, the importance of the gleaner-opportunist trade-off (and friends) will remain an 'animated question mark' (Kingsland, 1995).

AUTHOR CONTRIBUTIONS

Masato Yamamichi and Andrew D. Letten conceived the study and wrote the manuscript. Masato Yamamichi conducted simulations and produced figures.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

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