CONCEPTS AND SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Synthesizing the effects of individual-level variation on coexistence

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Abstract. Intraspecific trait variation (ITV) is a widespread feature of life, but it is an open question how ITV affects between-species coexistence. Recent theoretical studies have produced contradictory results, with ITV promoting coexistence in some models and undermining coexistence in others. Here we review recent work and propose a new conceptual framework to explain how ITV affects coexistence between two species. We propose that all traits belong to one of two categories: niche traits and hierarchical traits. Niche traits determine an individual's location on a niche axis or trade-off axis, such that changing an individual's trait makes it perform better in some circumstances and worse in others. Hierarchical traits represent cases where conspecifics with different traits have the same niche, but one performs better under all circumstances, such that there are winners and losers. Our framework makes predictions for how intraspecific variation in each type of trait affects coexistence by altering stabilizing mechanisms and fitness differences. For example, ITV in niche traits generally weakens the stabilizing mechanism, except when it generates a generalist–specialist trade-off. On the other hand, hierarchical traits tend to impact competitors differently, such that ITV in one species will strengthen the stabilizing mechanism while ITV in the other species will weaken the mechanism. We re-examine 10 studies on ITV and coexistence, along with four novel models, and show that our framework can explain why ITV promotes coexistence in some models and undermines coexistence in others. Overall, our framework reconciles what were previously considered to be contrasting results and provides both theoretical and empirical directions to study the effect of ITV on species coexistence.

Key words: annual plant model; functional traits; individual-level variation; intraspecific trait variation; Lotka-Volterra model; modern coexistence theory; storage effect.

INTRODUCTION

Intraspecific trait variation (ITV) is a ubiquitous feature of life. Although it has been long appreciated as the fuel for evolutionary change (Darwin and Wallace 1858), its relationship to ecological processes has only recently come into question (Clark 2010, Bolnick et al. 2011). Species exhibit variation in a variety of traits, from molecular-level physiology to whole-organism behavior and morphology (McGill et al. 2006, Litchman and Klausmeier 2008, Messier et al. 2010, D'Andrea

and Ostling 2016, Paine et al. 2018). This variation can lead to differences in the way that individuals interact with both conspecifics and heterospecifics (e.g., assortative mating due to differences in flowering phenology, trait-dependent competition, differential susceptibility to disease or predation; Weis and Kossler 2004, Lankau and Strauss 2007, Laine et al. 2011, Marden et al. 2017). Intraspecific variation can persist even when stabilizing selection is presumably strong (Bürger and Gimelfarb 1999), suggesting there may be underlying ecological forces favoring its maintenance. One idea that has gained traction is that ITV promotes or is essential for the coexistence of competing species (Jung et al. 2010, Violle et al. 2012). Given the longstanding challenge to understand how competitive communities support high species diversity (Hutchinson 1961), this idea provides an

attractive narrative that could align several open lines of inquiry. However, despite the attractiveness of this idea, a theoretical basis linking ITV to improved conditions for coexistence has yet to be established.

Theoretical studies have failed to provide general support linking ITV to coexistence; rather, the results have been inconsistent. For example, Hart et al. (2016) found that ITV generally promoted exclusion, except when it strengthened underlying stabilizing mechanisms. However, using a form of the Hart et al. model, with the addition of spatial environmental heterogeneity, Uriarte and Menge (2018) found that ITV sometimes (but not always) promoted coexistence amongst species that partitioned habitat. Some studies found that increasing ITV for all species helped coexistence (Crawford et al. 2019, Milles et al. 2020), while others found that it harmed coexistence (Courbaud et al. 2012, Barabás and D'Andrea 2016, Stump et al. 2020). Several studies have found that increasing ITV in one species promotes coexistence while increasing ITV in the other undermines coexistence; however, even then there are inconsistencies: in some cases, coexistence is promoted if the weaker species has higher ITV (Lichstein et al. 2007), in others, either species can be the high-ITV species (Barabás and D'Andrea 2016, Gomes et al. 2019). One study found that ITV had little to no impact on coexistence (Banitz 2019). Together, this body of work shows that ITV sometimes promotes coexistence, and sometimes undermines it. It is our goal here to synthesize this body of theory and distill the necessary conditions that would allow ITV to promote or impede coexistence.

The mix of findings are challenging to align because the multiple factors that can promote coexistence are rarely differentiated. Understanding how ITV modulates these factors could be instructive. Stable coexistence between two species requires that intraspecific competition be more intense than interspecific competition (Lotka 1932). In the framework of modern coexistence theory, any factor that impacts coexistence can be wholly considered via its impact on equalizing and stabilizing mechanisms (Chesson 2000a, Adler et al. 2007, Barabás et al. 2018). Stabilizing mechanisms (also called niche differences) give rare species an advantage, by strengthening intraspecific competition relative to interspecific competition. Equalizing mechanisms reduce competitive differences among species, allowing weaker competitors to coexist with stronger competitors (Chesson 2000a, Adler et al. 2007, Barabás et al. 2018). Species coexist if stabilizing mechanisms are substantial enough to overcome the fitness differences among species (with some caveats, see Schreiber et al. 2011, Barabás et al. 2018, Pande et al. 2020); however, the two effects are not mutually exclusive, and in fact most parameters in a model will alter both its stabilizing and equalizing components (Song et al. 2019). While modern coexistence theory has been used to examine the impact of many factors on coexistence (e.g., seasonal fluctuations [Miller and Klausmeier 2017], syntrophic nutrient exchange

[Stump and Klausmeier 2016], seed germination dynamics [Pake and Venable 1996], disease [Mordecai 2014], phylogenetic signal [Mayfield and Levine 2010, Godoy et al. 2014, Stump 2017], phenotypic plasticity [Turcotte and Levine 2016], functional traits [Adler et al. 2013]), there have been few attempts to examine how ITV affects these stabilizing and equalizing mechanisms (but see Hart et al. 2016, Uriarte and Menge 2018).

The factors producing stabilizing and equalizing mechanisms can be classified into one of four general processes that describe species interactions in terms of the means and variances of competition and environmental factors (Chesson 1994, 2000b, Barabás et al. 2018). First, variation-independent mechanisms (signified with $\Delta\rho$) describe processes where individuals of a resident species experience more competition than an individual of a rare invading species on average. This general process includes resource partitioning and predator partitioning (Chesson 2000a), and is the only general process that can occur in a spatially homogeneous system at equilibrium. Second, storage effects (signified with ΔI) describe processes that occur because species partition environmental conditions that fluctuate in time or space. For example, trees mast in different years, which reduces how much seedlings compete with heterospecifics in any given year (Usinowicz et al. 2012, 2017). Third, fitness–density covariances (signified with $\Delta\kappa$) describe processes that cause species to become segregated in space. Habitat partitioning (Stump and Chesson 2015) and intraspecific clustering (Ives 1988) are two classic examples of this general process. Last, relative nonlinearities (signified with ΔN) describe processes where competitive factors fluctuate, and species are affected differently by such fluctuations. For example, species can coexist by having different functional responses if resources fluctuate (Armstrong and McGehee 1980, Wilson and Abrams 2005). It is possible that ITV could affect any of these four processes.

Modern coexistence theory provides a theoretical structure that allows us to quantify how changes in the value of a trait (or more precisely a model parameter) affect the coexistence mechanism. Here, we utilize this basis to analyze how the introduction of ITV into particular traits can promote or impede the potential for coexistence in each of the four general processes described in the previous paragraph. In contrast to previous studies that investigate the impact of ITV using modern coexistence theory, we introduce a unified framework for interpreting the impact of ITV and apply it to models that we develop herein. We then evaluate how previous work on ITV and coexistence fits into our unified framework in order to understand, synthesize, and categorize the effects of ITV on coexistence.

To best organize our argument, we assume that traits are fixed at the individual level and have the potential to impact the demographic rates and parameters that underlie competition. We describe the relationship between a trait and a rate or parameter as a trait-

performance curve (though these may also be linear) and we assume that ITV changes symmetrically about a mean value. In this rather restrictive setting, a change in ITV will only yield a change in the population-level mean rate (or parameter) if the rate is a nonlinear or discontinuous function of the trait. Jensen's inequality states that if the input x of a nonlinear function $f(x)$ varies, and the second derivative of $f(x)$ is independent of x (and not equal to zero), then the mean of $f(x)$ over all values of x will differ from $f(x)$ evaluated at the mean of x. Most traits will likely have a nonlinear impact on demographic rates (Amarasekare and Savage 2012); if this is the case, then Jensen's inequality means that ITV will alter a species' average demographic rate (Fig. 1; Ruel and Ayres 1999). In particular, if the trait–performance curve is concave up, then increasing a species' ITV will increase its demographic rate and, if the trait-performance curve is concave down, then increasing a species' ITV will decrease its demographic rate (Fig. 1). Ultimately, disentangling the mapping of measured functional traits onto the parameters that govern theoretical models will be an important step in framing the influence of ITV on coexistence, but this is not the goal of the current paper. Nor is the goal to argue that anything is possible. Rather, we want to show that most models make one of a few reasonable assumptions about how traits affect demographic rates, and that if we know what those assumptions are, we can deduce a substantial amount about how ITV affects coexistence.

Here we synthesize the current literature and couple that synthesis to an organizing framework for how ITV affects pairwise species coexistence. We argue there are two categories of traits within which ITV can be embedded, *niche traits* and *hierarchical traits* (Fig. 2), and that these can be used to predict the impact of ITV on coexistence. We show that ITV in each type of trait is able to affect both the stabilizing mechanisms and fitness differences in a community, and outline when we expect each to occur. We then examine four models of coexistence, one for each general process, to illustrate how our framework can be used to understand the impact of ITV on coexistence. Additionally, we summarize the literature, and reinterpret previous results in terms of our framework. We show that our framework can explain previously contradictory results, and hope that it will aid in organizing and interpreting future studies of ITV and species coexistence.

Niche Traits and Hierarchical Traits

When considering the relationships between traits and the fitness of an individual, we find it practical to group traits into one of two categories: *niche traits* and *hierarchical traits* (Fig. 2). Note that these categories are specifically for how ITV affects between-species coexistence and therefore should not nullify other categorizations that may be useful in other contexts (e.g., effect vs. response traits (Lavorel and Garnier 2002). In this

section, we describe each category, including how ITV in each is expected to affect stabilizing mechanisms and fitness differences. We summarize this work by presenting flow charts for predicting how ITV in one species will affect the stabilizing mechanism (Fig. 3), and difference between species (Fig. 4) in the two-species community. These charts are meant to be both a guide for people thinking about ITV and to show where previous studies fall into the categories we define here.

Below we focus on how ITV affects fitness differences, rather than whether it is equalizing (i.e., making fitness differences smaller). We do this because ITV usually affects relative fitness independently of which species has the fitness advantage without ITV. We reserve the term equalizing for a few particular studies where the impact of ITV depends on fitness differences without ITV (Crawford et al. 2019, Milles et al. 2020).

Category 1: Niche traits

Niche traits affect a species' location on a niche axis or trade-off axis, such that changing an individual's trait will make it perform better under certain conditions, but at a cost to performance in other conditions (Fig. 2A, B). As such, at the species level, differences in niche traits are thought to stabilize coexistence. For example, beak size in Galapagos finches is a niche trait: finches with large beaks are better able to consume large seeds, but less able to consume small ones (Grant and Grant 1989). Thus, a species with high ITV will have some individuals that are well adapted to the dominant condition (i.e., the distribution of seed sizes) and many that are not. For example, ITV in beak size allows a population of a finch species to consume a greater variety of seeds but many individuals within that population may be poorly adapted to consuming the average seed. Therefore, ITV in a niche trait will widen and flatten a species' response curve to the environment (Fig. 2A), making it functionally more of a generalist.

We note that niche traits at the species level refer to stabilizing trade-offs, i.e., trade-offs that generate a stabilizing mechanism because the optimal trait is context dependent (Chesson 2000a, Adler et al. 2007). By contrast, some trade-offs are purely equalizing at the species level (Chesson 2000a, Adler et al. 2007). For example, a trade-off between seed production and density-independent seed survival would be equalizing: an individual that produces more seeds at the cost of seed survival does not capture a different niche, it simply makes a similar number of viable seeds (Muller-Landau 2008, Stump and Comita 2020). Traits that produce purely equalizing trade-offs should be seen as hierarchical traits (see Category 2: Hierarchical Traits).

We also note that different values of a niche trait need not be equally beneficial, even in the absence of competition (Fig. 2B). For example, if an island has mostly large seeds, then birds with large beaks would have an inherent advantage over birds with small beaks. However, beak
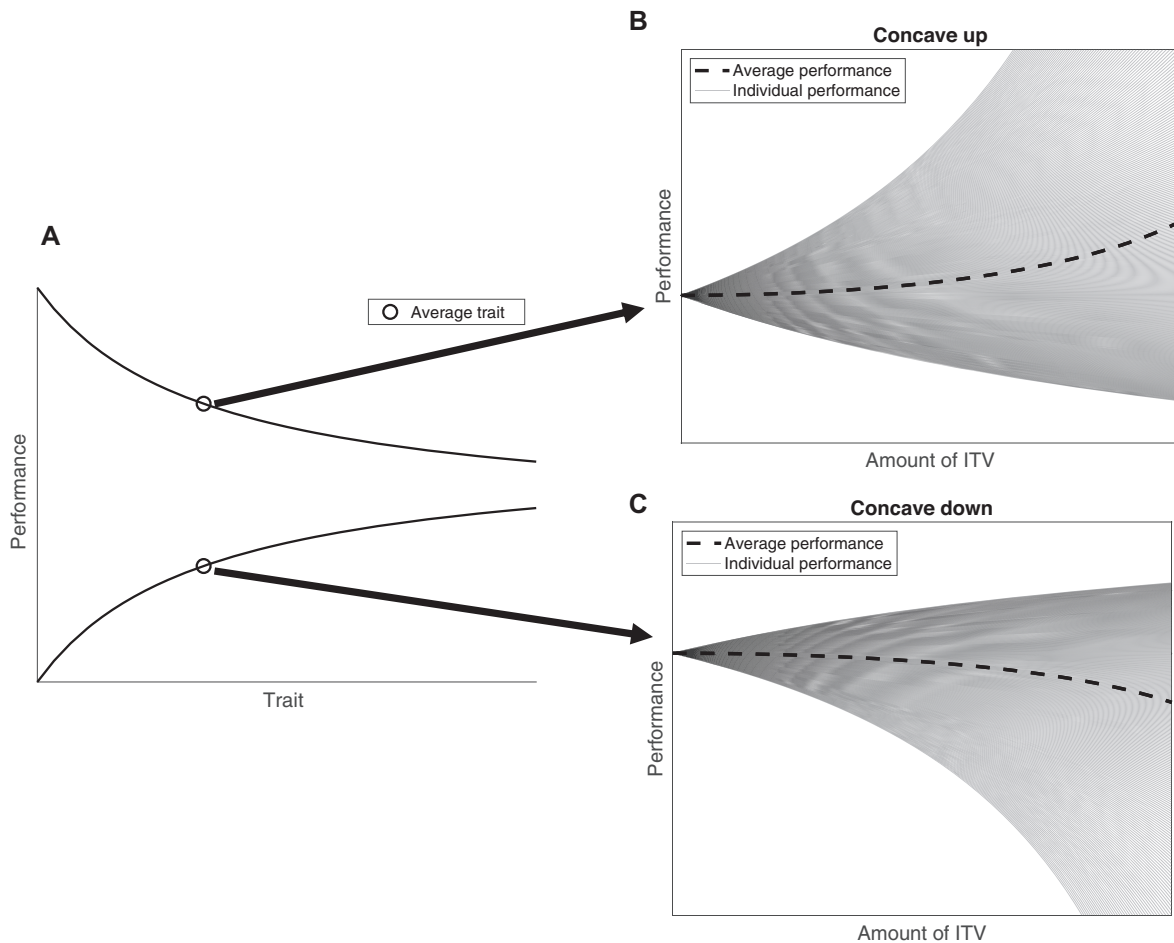
FIG. 1.   Jensen's inequality. (A) If a trait has a nonlinear impact on some ecological function, then the trait–performance curve can be categorized as concave up if it has a positive second derivative (the top line) or concave down if it has a negative second derivative (the bottom line). (B) If a trait–performance curve is concave up, then individual trait variation (ITV) will increase the species' average performance. This occurs because there will be a few individuals with extremely high performance. (C) If the trait–performance curve is concave down, then ITV will decrease the species' average performance, due to a few individuals with extremely low performance. Note that some curves are concave up in some places and concave down in others. If the range of traits occurs over areas where the trait–performance is entirely concave up or concave down (i.e., the sign of the second derivative does not chance), then the above holds. If the sign of the second derivative does change, however, then ITV could increase, decrease, or not change the average performance.

size would still be a niche trait, as increasing beak size would make an individual less able to consume the (albeit rarer) small seeds. In general, species better adapted to the common conditions may have a fitness advantage, but individuals or species adapted to the less common conditions may still find refuge from competition. For example, while small beaks would be maladaptive in the absence of competition, they could be adaptive if there is an excess of competition for large seeds. In the extreme case where only a single seed size is available for consumption, a certain trait value will be favored over all others, and beak size would effectively act as a hierarchical trait under these restricted conditions.

In general, ITV in a niche trait is expected to weaken stabilizing mechanisms (Fig. 3). ITV produces conspecific individuals that occupy different parts of niche space, reducing the average strength of intraspecific competition. Additionally, if species coexist by being at different locations on a niche axis, then ITV can produce heterospecifics with more similar traits, thus increasing niche overlap. For example, if two finch species coexist by consuming different seeds, then ITV in beak size would allow both species to consume a wide range of seeds. As a result, a given individual's diet is more likely to differ from many of its conspecifics as ITV increases while at the same time becoming more similar to some of its heterospecific competitors.

The one way that ITV can strengthen stabilizing mechanisms is if ITV is much greater in one species than the other, generating a generalist–specialist trade-off (Barabás and D'Andrea 2016). Under this situation, the
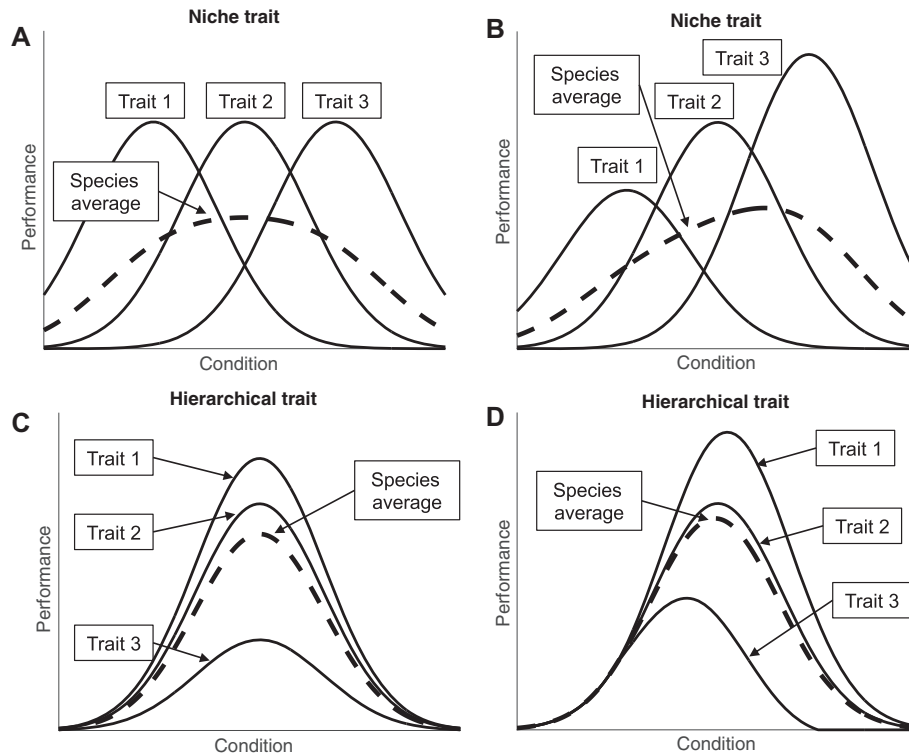
Fig. 2.   Our conceptual framework is that all traits can be placed into one of two categories (at least in terms of the impact of ITV on species coexistence). We show in Figs. 3, 4 how ITV in each type of trait is expected to impact stabilizing mechanisms and fitness differences, respectively. (A) First, niche traits are traits whose performance depends upon the condition. In the diagram, an individual with trait 1 will perform better than an individual with trait 3 under some conditions, but not others. For example, if a trait determines whether an individual is warm adapted or cold adapted, then this would be a niche trait. As a result, ITV causes species to have a more generalized niche, such that they have a moderate performance (at least on average) over a wide range of conditions. (B) This diagram also represents a niche trait. It differs from panel A because not all traits are inherently equal. However, it is still a niche trait: although the maximum performance of trait 3 is higher than the maximum performance of trait 1, there are some conditions where each performs the best (and thus there are costs and benefits to having either trait). For example, this could represent a trait that determines if an individual is warm adapted or cold adapted, and warm-adapted individuals perform far better in warm conditions that cold-adapted individuals perform in cold conditions. (C) Second, hierarchical traits, when some trait values are better (or worse) than others. In the diagram, an individual with trait 1 will always perform better than an individual with trait 3. For example, if a trait determines an individual's longevity (and there is no cost to higher longevity), then this would be a hierarchical trait. As a result, ITV does not change a species' niche, it simply changes the species' average performance (according to Jensen's inequality). (D) This diagram also represents a hierarchical trait. It differs from panel C because the different traits perform equally well under some circumstances. However, this is still a hierarchical trait, because trait 1 always performs at least as well as trait 3. For example, this could represent a trait that determines an individual's longevity in warm conditions and has no impact on longevity in cold conditions.

high-ITV "generalist" species has many individuals with extreme traits, and those individuals compete mainly with conspecifics, rather than with individuals from the low-ITV "specialist" species. The low-ITV specialist, however, must be a superior competitor for the narrower range of resources it can exploit. For example, if one finch species has higher ITV than the other, then the species with higher ITV could consume exceptionally large and small seeds, allowing the species to be, on average, sufficiently different. Generalist–specialist trade-offs are most likely to be stabilizing when species have similar mean traits; otherwise, ITV makes different species more similar.

Surprisingly, ITV in niche traits can also affect fitness differences. Two factors determine whether ITV in a

niche trait improves or reduces a species' fitness (Fig. 4). First, ITV can improve a species' fitness by giving it access to unexploited resources. For example, a Darwin's finch species with high ITV can consume more types of seeds than one with low ITV, giving it a fitness advantage. Second, ITV can reduce a species' fitness by producing maladapted individuals. As stated above, not all niche traits are equally adapted in the absence of competition. If traits values are not equally fit, then individuals with maladaptive traits will be at an inherent disadvantage. In this case, high-ITV species often suffer a fitness penalty because they have many individuals with maladapted traits. For example, a finch species with high-ITV would be at a disadvantage if seeds were all the same size, as many individuals would have beaks that

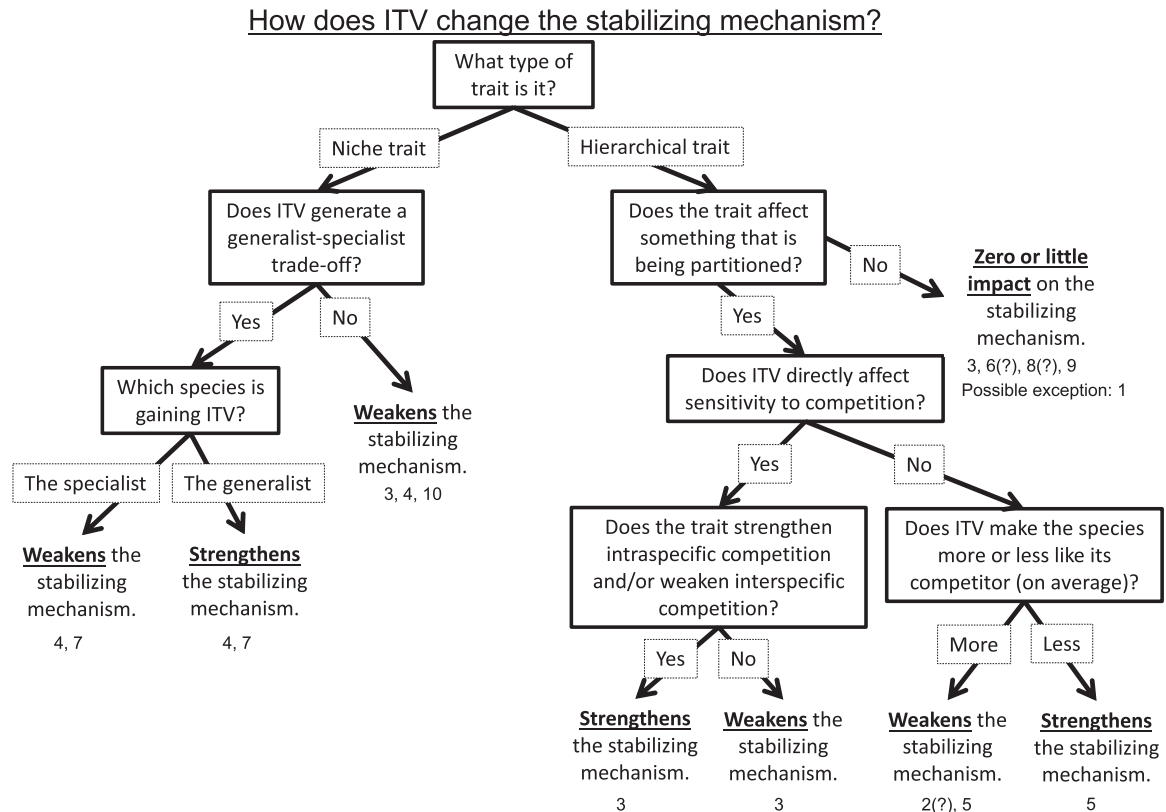## How does ITV change the stabilizing mechanism?

FIG. 3. Here we show a flow chart for predicting how ITV for a given species will affect the stabilizing mechanism in that community. We also list which studies have shown each of possible predictions, using the following: 1, Lichstein et al. (2007); 2, Courbaud et al. (2012); 3, Hart et al. (2016); 4, Barabás and D'Andrea (2016); 5, Uriarte and Menge (2018); 6, Crawford et al. (2019); 7, Gomes et al. (2019); 8, Banitz (2019); 9, Milles et al. (2020); 10, Stump et al. (2020). Note that 2, 7, and 9 represent a best guess, however, both models were complex enough that we are not sure how to classify them. Additionally, the study by Lichstein et al. (2007) (1) represents a possible exception, though we argue in the text why their result may belong with "Zero or little impact" on the stabilizing mechanism.

were either too large or too small to consume the seeds. However, if an individual with the average trait is maladapted, then ITV can improve a species' fitness by producing some individuals with adapted traits. For example, if a finch species has overly large beaks on average, then ITV will produce some individuals that can consume the common seeds. Whether ITV increases or decreases a species' fitness depends on the net impact of these factors.

Category 2: Hierarchical traits

Hierarchical traits make an individual more (or less) adapted to the environment, without changing its overall niche (Fig. 2C, D). For example, all else being equal, it is always better for an individual to be longer lived or more fecund. ITV in a hierarchical trait produces individuals that occupy the same niche, but with some individuals being superior to others (Fig. 2C). In some cases, the exact benefit of the trait will depend on the context; in these cases, the hierarchical trait does not incur a cost when outside of its functional context

(Fig. 2D). For example, cost-free disease resistance would be a hierarchical trait, as resistance would be as good as non-resistance in the absence of disease, and better in the presence of disease. Traits involved in equalizing trade-offs, which only affect an individual's ability to compete for a single resource (Chesson 2000a, Adler et al. 2007), are also hierarchical traits. For example, an equalizing trade-off between seed production and seed survival would be hierarchical, because the individuals that produced the most viable seeds would have an advantage over those who produced fewer viable seeds. We use the term hierarchical because at the species level, differences in hierarchical traits favor the exclusion of the inferior competitor.

ITV in a hierarchical trait affects fitness differences by altering the species' average performance. For example, if conspecific individuals are differently able to take up a resource, then what matters is the species' average resource uptake. The direction of the impact of ITV depends on Jensen's inequality: if a trait–performance curve is concave up, then ITV increases a species' average performance (Fig. 1B); if a trait–performance curve

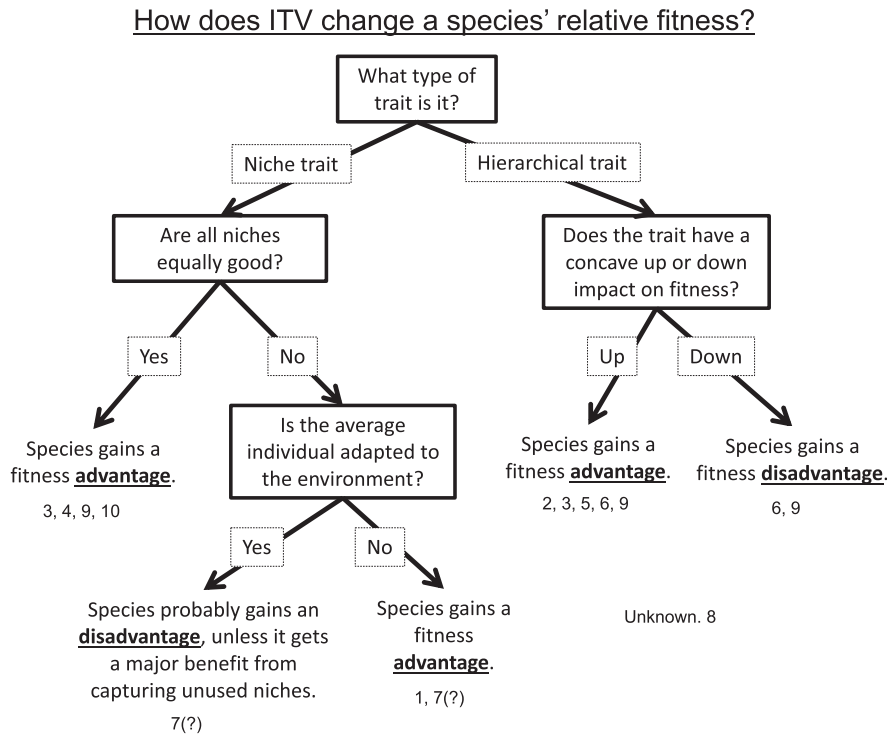## How does ITV change a species' relative fitness?

Fig. 4. Here we show a flow chart for predicting how ITV for a given species will affect that species' fitness. We also list which studies have shown each of possible predictions, using the following (this is the same as in Fig. 3): 1, Lichstein et al. (2007); 2, Courbaud et al. (2012); 3, Hart et al. (2016); 4, Barabás and D'Andrea (2016); 5, Uriarte and Menge (2018); 6, Crawford et al. (2019); 7, Gomes et al. (2019); 8, Banitz (2019); 9, Milles et al. (2020); 10, Stump et al. (2020). We believe that Gomes et al. (2019) (7) could be placed in either of two locations, depending on the parameters used. We are not sure where to place Banitz (2019) (8), and suspect that the traits have a nearly linear trait–performance curve.

is concave down, then ITV reduces a species' average performance (Fig. 1C); if a trait–performance curve is linear, then ITV has no impact; and if a trait–performance curve is concave up in some places and concave down in others, then the impact of ITV will depend on the mean trait and range of ITV (Ruel and Ayres 1999). ITV improves a species' fitness if it makes individuals more adapted to the environment on average. Thus, ITV on a trait with concave-up performance curve improves a species' fitness, and ITV on a trait with a concave-down performance curve decreases a species' fitness (Fig. 4). Interestingly, we have also found a few cases where ITV has a different impact on different species (Crawford et al. 2019, Milles et al. 2020); this appeared to occur because one has a mean trait in the concave-up part of the performance curve, while the other has a concave-down part of the performance curve.

Just as ITV in niche traits can influence fitness differences in addition to stabilizing mechanisms, ITV in hierarchical traits can influence stabilizing mechanisms in addition to fitness differences. In particular, this occurs if competitive imbalances play some role in the overall stabilization of the system. For example, imagine that species partition habitat, and each is the competitive dominant in one habitat; in this case, ITV that increases

the dominance of the locally superior species will stabilize coexistence at the larger scale (Uriarte and Menge 2018). We expect this to happen most often when there is a between-species trade-off that does not operate within species. For example, (Kasada et al. 2014) found a predation–fecundity trade-off between phytoplankton that was broken within each species and (Shiklomanov et al. 2020) found that several trade-offs predicted by the leaf economic spectrum across species did not occur within species.

Intraspecific trait variation in a hierarchical trait strengthens stabilizing mechanisms if it makes species more different on average along a niche dimension, and it weakens stabilizing mechanisms if it makes species more similar on average (Fig. 4). This often means that ITV in one species strengthens the stabilizing mechanism while ITV in the other species weakens it. For example, imagine two plankton species that coexist because one is more able to take up nitrogen and the other is more able to take up phosphorous. If ITV enables the nitrogen specialist to better take up nitrogen, it will strengthen the stabilizing mechanism by increasing niche differences, but if ITV makes the phosphorous specialist more able to take up nitrogen, it will undermine the stabilizing mechanism. Note that this example requires that the

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trait in question only affects nitrogen uptake, if the trait increased nitrogen uptake at the cost of phosphorus uptake this would represent a niche trait. The exact impact of ITV will thus depend on the trait, the curvature, and which species has higher ITV.

In our survey of the literature, we found two special cases of hierarchical traits that were initially unintuitive to us; we explain them here to show how they behave according to our expectations. First, some models used sensitivity to intra- or interspecific competition as a trait (Hart et al. 2016). These are hierarchical traits because individuals that are less sensitive to competition have higher fitness than individuals who are more sensitive to competition. In these cases, ITV will increase the stabilizing mechanism if it increases intraspecific competition or decreases interspecific competition on average and, conversely, ITV will weaken the stabilizing mechanism if it decreases intraspecific competition or increases interspecific competition on average. Second, some traits may not help species to partition their niches (e.g., Hart et al. 2016). For example, if species coexist by partitioning resources, and a trait affects fecundity or predator susceptibility (which they do not partition), then that trait would likely be hierarchical. This situation generally occurs when the trait does not impact part of a between-species trade-off. If a trait does not affect niche partitioning at the species level, then ITV will not directly affect the stabilizing mechanisms (though in some models, it has a small, indirect effect on stability due to a weakening of interspecific differentiation, e.g., Appendix S1: Figs. S3, S4).

Distinctions from previous frameworks

Many previous frameworks have attempted to categorize the world into a dichotomy and we wish to briefly explain how the niche vs. hierarchical trait dichotomy differs from other dichotomies. Our classification scheme is a required addition (not replacement) to these existing dichotomies.

Modern coexistence theory (Chesson 2000a, Adler et al. 2007, Barabás et al. 2018) categorizes processes as stabilizing niche differences and fitness differences. There are similarities to our framework; if conspecific individuals differ because of a niche trait, they are optimized for different contexts (just like species that have a stabilizing mechanism); if conspecific individuals differ because of a hierarchical trait, then one is better than all others (like species who have a fitness difference). If these traits were heritable (which we assumed they are not), then they would produce similar patterns at the within-species level, with niche traits producing diversifying selection and hierarchical traits producing directional selection. However, the framework we propose focuses on how within-species processes scale to affect interactions between species. This is why ITV in either type of trait can alter both stabilizing mechanisms and fitness differences.

Meszéna et al. (2006) proposed a different categorization of traits into those that impact coexistence as regulating factors, which produce density dependence, vs. external environmental factors, which change vital rates in a density-independent fashion. In our framework, both regulating and environmental factors can produce either a niche trait or a hierarchical trait. What is critical is whether changing a trait makes an individual better at everything, or better at some things and worse at others. For example, a trait that impacts how many eggs an individual lays at a given temperature is an environmentally regulated factor; however, it is a niche trait if increasing the trait made individuals more warm adapted and less cold adapted, or it is a hierarchical trait if increasing the trait only made individuals more warm-adapted (without altering how cold-adapted they are).

Lavorel and Garnier (2002) proposed categorizing traits as response traits, which describe how an individual is affected by resources and environmental factors, vs. effect traits, which describe how an individual affects ecosystem function. That framework was developed to study much different questions: if the environment changes, which traits will change because they caused populations to change, and which traits will change because the populations are changing? (The answer being response and effect traits, respectively.) Our framework mostly focuses on response traits, as these determine species interactions and community structure.

MODEL ANALYSIS

To explore the dynamical consequences of ITV in the two categories of traits, we examined four models: a MacArthur (1970) style model where species coexist by partitioning resources (generating a variation-independent mechanism, $\Delta\rho$), a lottery model where species coexist by partitioning temporal variation (generating mainly a storage effect, ΔI), an annual plant model where species coexist by partitioning habitat (generating mainly a fitness-density covariance, $\Delta\kappa$), and a Monod (1949) model where species coexist by partitioning their response to resource variation (generating mainly a relative nonlinearity, ΔN). These models generally represent the simplest set of assumptions necessary to generate each coexistence mechanism and together provide the basis for the mathematical study of coexisting competitors. Given that any pair of coexisting competitors relies on one of these four mechanisms (Chesson 2000), exploring the effects of ITV in this set of models should provide a complete catalogue of its potential effects in more complex models and in natural systems.

For each model, we consider different types of traits, T, which have mean 0 and within-species variance σ^2_{Tj} for species j. The trait affects a parameter in the model; for example, in the resource partitioning model, T determines an individual's optimum resource size. ITV is symmetric above and below 0, and we simulate it using a Gaussian or uniform distribution. Traits are not

heritable, and σ_{Tj}^2 and the mean of T are fixed for each species. We use a star to indicate the value of the parameter when $T = 0$. We calculate the growth rate of a species j, $\lambda_j(t)$, by integrating over individuals: if we write $\lambda_j(t, T)$ as the growth rate of an individual with trait T, and $p_j(T)$ as the probability distribution function of trait T, then

$$\lambda_j(t) = \int \lambda_j(t, T) p_j(T) dT$$

(Hart et al. 2016). We define $N_j(t)$ as the density of species j at time t.

To determine how ITV affects stabilizing mechanisms and mean fitness differences, we use invasion analysis (Turelli 1978, Armstrong and McGehee 1980). Each species in turn becomes an invader (indicated with subscript i; we write $\lambda_{i(1)}$ to indicate that species 1 is the invader). The invader's density is set to 0, and the competitor (the resident, subscript r) is allowed to reach its equilibrium density. We then calculate the expected growth rate of the invader, $E[\ln\{\lambda_i\}]$ (or $E[\lambda_i]$ for the fitness–density covariance model, [Chesson 2000b]). Species j's growth rates are normalized by their sensitivity to competition, β_j; we discuss β_j fully in Appendix S1, but it is generally used to scale growth rates to a per-generation time scale. The community-average stabilizing mechanism ($\overline{\Delta X}$ for general process X) is then

$$\overline{\Delta X} = \frac{1}{2}\left(\frac{E\left[\ln\{\lambda_{i(1)}\}\right]}{\beta_1} + \frac{E\left[\ln\{\lambda_{i(2)}\}\right]}{\beta_2}\right)$$

and the mean fitness difference between species 1 and species 2 is

$$\Delta X_1 - \overline{\Delta X} = \frac{1}{2}\left(\frac{E\left[\ln\{\lambda_{i(1)}\}\right]}{\beta_1} - \frac{E\left[\ln\{\lambda_{i(2)}\}\right]}{\beta_2}\right)$$

(Chesson 2003, Barabás et al. 2018). Species coexist if the stabilizing mechanism is stronger than the most negative fitness difference

$$\overline{\Delta X} > \left|\min\left(\Delta X_1 - \overline{\Delta X},\ \Delta X_2 - \overline{\Delta X}\right)\right|$$

(Chesson 2003, Schreiber et al. 2011, Barabás et al. 2018). For each model and each trait, we calculate the stabilizing mechanism and fitness difference as a function of each species' amount of ITV (σ_{T1}^2 and σ_{T2}^2). We explored several parameter sets for each model, and discuss when the outcome depended on the parameters chosen.

There are multiple definitions of fitness difference and stabilizing mechanism in the literature (Spaak and De Laender 2020). We chose the Chesson (2003) definition because it is best suited for studying models that vary in space and time. However, for the variation-independent mechanism, we also use a definition of fitness and

stability that was originally proposed in Chesson (1990), and is more commonly used for models that do not vary in space and time (e.g., Narwani et al. 2013, Godoy et al. 2014, Kraft et al. 2015, Kandlikar et al. 2019, Ke and Wan 2019).

Model 1: The variation-independent mechanism ($\Delta\rho$)

We first examine a model of resource competition. Populations grow by consuming resources. Each species has a Type 1 functional response, and species j captures resources h with attack rate $a_j(h)$. We assume that resources exist on an axis (x), and that each species has optimal resource utilization μ_j, and some dietary range σ_I^2. We will discuss the axis as prey size, though it could represent any one-dimensional axis. We generally model the attack rate using a Gaussian distribution, (though at times we model it using a uniform distribution, Appendix S1: Section S1.4). We then use the assumptions in MacArthur (1970), to take the limit of this model when there are an infinite number of resources. Under certain assumptions (e.g., resources do not go extinct), this model can be simplified to a Lotka-Volterra system

$$\frac{dN_j(t)}{dt} = r_j N_j(t)\left(1 - \sum_{k=1}^{2}\alpha_{kj}N_k(t)\right)$$

where r_j is the intrinsic growth rate, and α_{kj} is the competitive effect that species k has on species j,

$$\alpha_{kj} = \int a_j(h)a_k(h)dh,$$

(Appendix S1: Section S1.1). In the case of the Gaussian form of $a_j(h)$, the competition coefficient is

$$\alpha_{kj} = \frac{1}{\sqrt{4\pi\sigma_I^2}}exp\left\{-\frac{\left(\mu_j - \mu_k\right)^2}{4\sigma_I^2}\right\}$$

(MacArthur 1970).

We consider one case of ITV, by assuming that the trait affects an individual's optimal resource utilization, μ_j.

Results: Resource utilization, μ_j.—An individual with trait T has optimal resource utilization $\mu_j(T)$

$$\mu_j(T) = \mu_j^* + T$$

where μ_j^* is the mean optimal resource utilization for species j (Fig. 5A). This trait is a niche trait, as an individual with trait $T = 1$ is better at consuming larger resources, but worse at consuming smaller resources.

Under our assumption of a Gaussian resource uptake function and a Gaussian trait distribution, the competition term is

$$\alpha_{jk} = \frac{1}{\sqrt{2\pi\left(2\sigma_I^2 + \sigma_{Tj}^2 + \sigma_{Tk}^2\right)}} exp\left\{ -\frac{\left(\mu_j - \mu_k\right)^2}{2\left(2\sigma_I^2 + \sigma_{Tj}^2 + \sigma_{Tk}^2\right)} \right\}$$

(Appendix S1: Section S1.1). ITV reduces intraspecific competition, as expected for a niche trait. ITV will strengthen interspecific competition if ITV is weak and species have different mean traits (i.e., if $\sigma_{T1}^2 + \sigma_{T2}^2 + 2\sigma_I^2 < (\mu_1 - \mu_2)^2$), but will eventually weaken when ITV is strong (i.e., if $\sigma_{T1}^2 + \sigma_{T2}^2 + 2\sigma_I^2 > (\mu_1 - \mu_2)^2$, Appendix S1: Section S1.2).

As expected for a niche trait (Fig. 3), increasing ITV for both species always weakens the stabilizing

mechanism (Fig. 5B). This occurs because ITV always reduces intraspecific competition, and it either increases interspecific competition or decreases it a slower rate (Appendix S1: Section S1.2); thus, ITV reduces intraspecific competition relative to interspecific competition. Increasing ITV for just one species also generally weakens the stabilizing mechanism, for similar reasons. However, if ITV is much larger for one species than the other, then increasing the ITV of the high-ITV species even more can increase the stabilizing mechanism via a specialist–generalist niche (Appendix S1: Fig. S1).

Increasing a species' ITV increases its fitness (Fig. 5C). Species with more ITV have access to a wider range of resources (i.e., unused parts of niche space), and
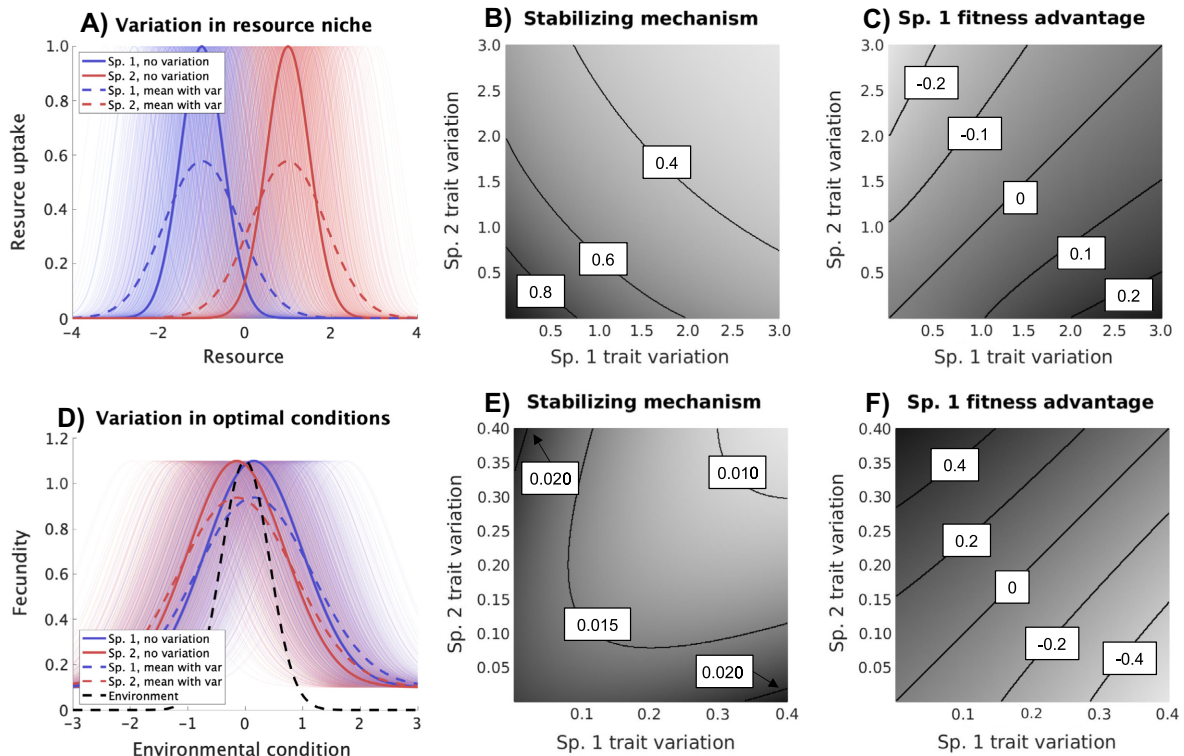

FIG. 5. Two examples of how ITV in a niche trait affects coexistence. (A) First, we consider model 1 (the variation independent mechanism, $\Delta\rho$), and assume that the trait impacts an individual's optimal resource. A species with high ITV will have individuals with many different optimal resources, which will cause the species as a whole to have a more generalized resource niche. (B) Because ITV causes a species to become more of a generalist, ITV in either species weakens the stabilizing mechanism. This occurs because it decreases intraspecific competition and increases interspecific competition. The parameters used to make this graph do not allow for a generalist–specialist trade-off to occur; however, it is possible under different parameters (Appendix S1: Fig. S2). (C) In this model, all resources have the same dynamics and the same caloric benefit, and therefore all niches are equivalent in the absence of competition. As such, a species will gain a fitness advantage if it has more ITV, as it has access to an unused part of niche space. (D) Next, we show model 2 (the storage effect, ΔI), and assume that the trait impacts an individual's optimal conditions for reproduction. As with variation in a species' resource niche, ITV in this model causes a species to have a more generalized niche, as they tend to have a more moderate level of reproduction over many environmental conditions (at least on average). (E) As with the previous model, ITV reduces the stabilizing mechanism in the model, is it reduces the amount that species partition their temporal niche. However, under certain conditions, this can generate a generalist–specialist trade-off, where the low-ITV specialist has an advantage during its optimal years, and the high-ITV generalist has an advantage during non-optimal years. (F) Unlike the previous model, not all niches are created equal. Rather, environmental conditions close to $E(t) = 0$ occur much more often than those with $|E(t)| \gg 0$. Both species have a mean trait that is well adapted to the community. As such, ITV causes them to produce many mal-adapted individuals, and therefore reduces that species' fitness. Parameters for model 1: $\sigma_I^2 = 0.25$, $\mu_1^* = -1$, $\mu_2^* = 1$. Traits varied according to a normal distribution. Parameters for model 2: $\delta = 0.4$, $\mu_1^* = 0.15$, $\mu_2^* = -0.15$, $w = 0.7^{1/2}$, $Y_{gain-j} = 1$, $Y_{min-j} = 0$. $E(t)$ was normally distributed with mean 0 and variance $0.5^{1/2}$. See sections "Model 1" and "Model 2" for definitions of parameters. The trait varied using a normal distribution.

therefore experiences less intraspecific competition. ITV also changes interspecific competition; however, this ends up having the same effect on both species, and therefore does not affect fitness differences. Also, we assumed that all resources are equally common, and therefore individuals with extreme traits do not suffer from being maladapted (Fig. 4).

To validate the generality of these results, we found that the above results hold qualitatively for uniform uptake functions other than the specific form of α_{jk} (Appendix S1: Fig. S2). Additionally, we analyzed coexistence in this model by determining how it impacted the stabilizing niche difference and fitness ratio (measures of fitness and stability proposed in Chesson [1990]). We found that the results were qualitatively the same (Appendix S1: Section S1.3).

Model 2: The storage effect (ΔI)

Next we examine the lottery model, originally developed to study coral reef fish (Chesson and Warner 1981). Each time step represents one year, and $N_j(t)$ is the frequency of species j adults at the start of the year. Every year, adult individuals produce a large number of offspring, $Y_j(t)$. Those offspring will not survive to the next year unless they can capture a territory, and they cannot outcompete adults for territories. However, each adult dies with probability δ, vacating its territory. Each offspring is equally likely to capture a territory; thus, a given offspring of either species will capture a site with probability $\delta/C(t)$, where

$$C(t) = Y_1(t)N_1(t) + Y_2(t)N_2(t)$$

(note: it is $\delta/C(t)$ because if there are K total territories, then there will be δK vacant territories, and $C(t)K$ offspring competing for each territory). Thus, the growth rate of species j at time t is

$$\lambda_j(t) = 1 - \delta + \frac{\delta Y_j(t)}{C(t)}.$$

Fecundity depends on some environmental condition, $E(t)$, which varies from year to year. For simplicity, we assume $E(t)$ has mean 0. Each species has some optimal condition, μ_j, such that its fecundity in year t is.

$$Y_j(t) = Y_{\text{gain}}\exp\left\{-\frac{\left(E(t) - \mu_j\right)^2}{w}\right\} + Y_{\text{min}}$$

where Y_{min} is the minimum fecundity, Y_{gain} is the maximum amount that fecundity can increase in a given year (i.e., so $Y_{\text{gain}} + Y_{\text{min}}$ is the maximum fecundity), and w is a scaling constant (Fig. 5D).

In this model, species can coexist by partitioning their best years for reproduction (Chesson and Warner 1981). The general process driving coexistence is a storage effect: rare species gain an advantage because there is

less competition during their high-fecundity years. This is a necessary but not sufficient condition for coexistence: if one species has much lower average $Y_j(t)$, then it will lose more during its bad years than it gains during its good years and be excluded. The stabilizing mechanism is stronger when δ is small (because this limits how much a species can lose during a bad year) and when species strongly partition temperature (i.e., $Y_1(t)$ and $Y_2(t)$ differ in most years, which occurs when their means are different, $|\mu_1^* - \mu_2^*| \gg 0$); the fitness differences are large if one species has a much higher mean fecundity (i.e., the mean of $Y_j(t)$, which will be large when a species' average optimal condition, μ_1^*, is close to the community average of 0; Chesson and Warner 1981).

Here we consider two types of traits: fecundity (Y_{gain} and Y_{min}), and optimal conditions for fecundity (μ_j^*). We chose these traits because the former represents a hierarchical trait and the later a niche trait.

Result: Variation in fecundity.—First, the trait T affects an individual's fecundity according to some nonlinear function $f(T)$,

$$Y_{\text{gain}}(T) = Y_{\text{gain}}(1 + f(T))$$

$$Y_{\text{min}}(T) = Y_{\text{min}}(1 + f(T)).$$

We assume that $f(0) = 0$ and $f(T) > -1$ for all T, and that $f(T)$ is concave down (our results are similar if $f(T)$ is concave up, except that ITV has the opposite impact on fitness differences). Therefore, an individual with trait T at time t produces

$$Y_j(T, t) = (1 + f(T))$$

$$\times \left(Y_{\text{gain}}\exp\left\{-\frac{\left(E(t) - \mu_j\right)^2}{w}\right\} + Y_{\text{min}}\right)$$

$$= (1 + f(T))Y_j^*(t)$$

offspring, where $Y_j^*(t)$ is the fecundity an individual with trait $T = 0$ at time t (Appendix S1: Fig. S3a). Fecundity is a hierarchical trait: an adult with high $f(T)$ always produces more offspring than a conspecific adult with low $f(T)$. As a hierarchical trait, what matters is how it affects a species' performance on average (Fig. 4). A species with a trait variance of σ_{Tj}^2 will produce an average of about

$$\int Y_j(T, t)p_j(T)dT \approx \left(1 + \sigma_{Tj}^2\frac{\partial^2 f(0)}{\partial T^2}\right)Y_j^*(t)$$

offspring (Appendix S1: Section S1.4). Because the function is concave down (i.e., $(\partial^2 f(0))/(\partial T^2) < 0$), ITV will cause the population to produce fewer offspring on average. This has a clear effect on fitness differences: this trait is a concave-down, hierarchical trait; thus, the species with more ITV has lower fecundity, and therefore a fitness disadvantage (Appendix S1: Fig. S3c), as expected (Fig. 4).

Intraspecific trait variation in this trait has little impact on the stabilizing mechanism, as it is a hierarchical trait that does not affect a between-species trade-off (Appendix S1: Fig. S3b), as expected (Fig. 3). Species coexist by partitioning which years they have relatively high fecundity. If ITV increases fecundity, then the high-ITV species produces more offspring in both optimal and suboptimal years; this causes neither more nor less temporal partitioning, and therefore has little impact on the stabilizing mechanism (Appendix S1: Fig. S3b). We note that the impact is non-zero, however, due to an indirect effect of altering variation in fecundity (Appendix S1: Section S2.3).

Result: Variation in optimal conditions for reproduction.—Next, the trait T affects an individual's optimal conditions for reproduction,

$$\mu_j(T) = \mu_j^* + T.$$

Therefore, an individual with trait T produces

$$Y_j(T, t) = Y_j^* \exp\left\{ -\frac{\left(E(t) - \mu_j^* - T\right)^2}{w} \right\} + Y_{\min -j}$$

offspring (Fig. 5D). This trait is a niche trait: increasing an individual's T increases its fecundity during high-$E(t)$ years but lower its fecundity during low-$E(t)$ years. ITV thus widens and flattens a species' response curve: ITV decreases a species' average fecundity when $E(t)$ is close to μ_j^*, and increases its average fecundity when $E(t)$ far from to μ_j^* (Fig. 5D). Thus, ITV increases a species' niche breadth, while making it less specialized on a particular condition (Fig. 5D).

As expected with a niche trait (Fig. 3), increasing ITV generally weakens the stabilizing mechanism (Fig. 5E). Storage effects promote coexistence if each species has some years when it has high fecundity and its competitor has low fecundity. When ITV is high for both species, fecundity for both species will be similar in most years, weakening the mechanism. However, if both species have similar μ_j^*, then increasing ITV for one species can increase the stabilizing mechanism by producing a generalist–specialist trade-off (Fig. 5E), as expected (Fig. 3). In this case, the low-ITV specialist has a fecundity advantage during years that are optimal for both species (i.e., when $E(t) \approx \mu_j^*$), and the high-ITV generalist has a fecundity advantage during nonoptimal years (i.e., when $E(t)$ differs from μ_j^*).

The main impact of ITV on fitness differences is that it changes how adapted a species is to the environment. An individual will have peak fecundity during years when $E(t) \approx \mu_j(T)$; therefore, an individual with an extreme value of $\mu_j(T)$ is maladapted, as $E(t) \approx \mu_j(T)$ may never occur in that individual's lifetime. A population with high ITV will have some well-adapted individuals (i.e.,

those with $\mu_j(T) \approx 0$, since the mean of $E(t)$ is 0) and some maladapted individuals (i.e., those with large $|\mu_j(T)|$). If the average individual is well adapted to the community (i.e., μ_j^* is close to 0), then ITV reduces that species' fitness, as it increases the number of maladapted individuals in the population (Fig. 5F), as expected (Fig. 4). However, if the average individual is maladapted (i.e., $|\mu_j^*|$ is large), then ITV can increase the species' fitness, as it increases the number of adapted individuals (Appendix S1: Fig. S4), as expected (Fig. 4).

ITV could also impact fitness differences by allowing a species to capture unused niches (Fig. 4); in this case, that would occur if some individuals have peak years that differ from all other individuals. Individuals with a very high or low trait would reproduce the most during years where most of its conspecifics had low fecundity, thus reducing intraspecific competition (Appendix S1: Section S2.2). However, we considered many parameter sets and, under the parameter sets we examined, this impact on fitness tended to be much weaker than the impact of changing how adapted a species is to the environment (data not shown).

Model 3: The fitness–density covariance ($\Delta\kappa$)

Next, we examine competition between annual plants in a two-patch model. Here $N_j(x,t)$ is the number of seeds of species j in patch x at the start of year t. Every seed germinates at the beginning of each year. In the absence of competition, each plant would produce $Y_j(x)$ seeds; this number varies with patch x and species j. Competition lowers seed production to $Y_j(x)/C_j(x)$, where the effect of competition $C_j(x)$ is a Beverton-Holt model

$$C_j(x) = 1 + \alpha_j(N_1(x, t) + N_2(x, t))$$

where α_j is an individual's sensitivity to competition (i.e., how much that individual's fecundity declines in the presence of competitors). A fraction $(1 - d)$ of seeds remain in the site where they were produced, and the remaining d disperse to the other site. Thus, the number of seeds of species j in site x at time $t + 1$ is

$$N_j(x, t + 1) = N_j(x, t)\frac{Y_j(x)(1 - d)}{C_j(x)} + N_j(y, t)\frac{Y_j(y)d}{C_j(y)}$$

(where the second term is seed production in site $y \neq x$). If we define $\nu_j(x)$ as species j's proportion of seeds at site x (i.e., $\nu_j(x, t) = (N_j(x, t)/N_j(x, t) + N_j(y, t)))$, then growth rate of a species across both sites is

$$\lambda_j(t) = \sum_{x=1}^{2} \nu_j(x, t)\frac{Y_j(x)}{C_j(x)}.$$

Species can coexist if $Y_1(x) > Y_2(x)$ in one patch and $Y_1(x) < Y_2(x)$ in the other. The main general process driving coexistence is a fitness-density covariance:

species become partially segregated, and therefore a rare species experiences less competition where it grows best (Appendix S1: Section S3.2). Like with the storage effect, a difference in patch preference is a necessary but not sufficient condition for coexistence – a rare species can still be excluded if it loses more in its worst patch than it gains in its best patch. The stabilizing mechanism is stronger when dispersal is low (as this leads to more segregation) and when species strongly partition patches. The fitness differences are stronger when species have large differences in their sensitivity to competition, α_j, or their average fecundity, $Y_j(x)$.

We consider two types of traits: sensitivity to competition, α_j, and fecundity in patch 1, $Y_j(1)$. We chose these traits to contrast two forms of hierarchical traits, one that is involved in a between-species trade-off, and one that is not. Additionally, in the appendix we examine a niche trait that determines an individual's optimal conditions for reproduction (similar to the optimal conditions for reproduction in the storage effect model); we find that the results are nearly identical to the storage effect model (Appendix S1: Fig. S5 and Section S3.2).

Result: Variation in sensitivity to competition.—First, a trait T affects an individual's sensitivity to competition,

$$\alpha_j(T) = (1 + T)\alpha_j^*$$

(where $T > -1$). Sensitivity to competition is a hierarchical trait: high-T individuals produce more offspring in both patches. Our definition of $C(t)$ causes sensitivity to competition to have a concave up impact on fitness (Appendix S1: Fig. S6a); as such, ITV increases a species' average reproductive output. Therefore, as a hierarchical trait that is concave up, ITV improves a species' fitness (Appendix S1: Fig. S6c), as expected (Fig. 4).

Sensitivity to competition is a hierarchical trait that is not part of a between-species trade-off; therefore, as expected (Fig. 3), it has only a small, indirect impact on the stabilizing mechanism (Appendix S1: Fig. S6b). Decreasing sensitivity to competition increases an individual's ability to compete across both patches, and as such, does not cause a species to become more specialized in a particular patch. The small impact is due to species' shifting slightly in their distribution.

Result: Variation in fecundity in patch 1.—Next, the trait T affects an individual's fecundity in patch 1, such that

$$Y_j(T, 1) = \left(Y_{gain}\exp\left\{-\frac{(E(1) - \mu_i)^2}{w}\right\} + Y_{min} \right)$$
$$\times (1 + f(T))$$
$$= Y_j^*(0, 1)(1 + f(T))$$

where $f(T)$ is concave up, $f(0) = 0$, and $f(T) > -1$, and $Y_j^*(0, 1)$ is $Y_j(T, 1)$ for an individual with trait $T = 0$ (Fig. 6A). Fecundity in patch 1 is another hierarchical

trait: an individual with high $f(T)$ will produce more off-spring than a conspecific with low $f(T)$ in patch 1, and the same number of offspring in patch 2. This hierarchical trait has a concave-up impact on fecundity; therefore, ITV will increase a species' average fecundity, giving it a fitness advantage (Fig. 6C), as expected (Fig. 4).

Unlike with sensitivity to competition, fecundity in patch 1 is involved in a between-species trade-off; therefore, ITV in this trait has a large impact on the stabilizing mechanism (Fig. 6B). ITV can have a positive or negative impact on the stabilizing mechanism, depending on who experiences it. Imagine that in the absence of ITV, species 1 had lower sensitivity in patch 1, and species 2 had lower sensitivity in patch 2 (as is the case in Fig. 6A); thus, they could coexist because species 1 is the better competitor in patch 1 and species 2 is the better competitor in patch 2. In this case, ITV in species 1 would increase its advantage in patch 1. This would make species more different in their performance in patch 1, thereby increasing the amount that the species partition habitat, and therefore increasing the stabilizing mechanism (Fig. 6B). However, ITV in species 2 would decrease its disadvantage in patch 1. This would make the species have more similar fecundity in patch 1, thereby decreasing the amount that they partition habitat, and weakening the stabilizing mechanism (Fig. 6B). Thus, like with many hierarchical traits (Fig. 3), each species' ITV impacts the stabilizing mechanism in a different way.

Model 4: Relative nonlinearity (ΔN)

Last, we consider the Monod model, which models microbes competing in a chemostat (Monod 1949). The microbes compete for a single resource $R(t)$, which is fed into the chemostat at rate $R_{in}(t)$ (which varies with time). $R_{in}(t)$ has a mean of $\overline{R_{in}}$, and fluctuates by an amount A and with period τ

$$R_{in}(t) = \overline{R_{in}} + A\sin\left(\frac{2\pi t}{\tau}\right).$$

Media is removed from the chemostat at rate δ, and with it, any microbe or resources; thus, resources are removed at rate $\delta R(t)$, and microbes are removed at rate $\delta N_j(t)$. Microbes take up resources according to a Type II functional response

$$f_j(R(t)) = \frac{a_j R(t)}{1 + a_j R(t)h_j}$$

where a_j is species j's attack rate, and h_j is its handling time. For simplicity, we assume a perfect conversion rate. Therefore, the growth rate of species j is

$$\frac{1}{N_j(t)}\frac{dN_j(t)}{dt} = f_j(R(t)) - \delta$$

and the equation governing the resource is

$$\frac{dR(t)}{dt} = R_{in}(t) - N_1(t)f_1(R(t)) - N_2(t)f_2(R(t)) - \delta R(t).$$
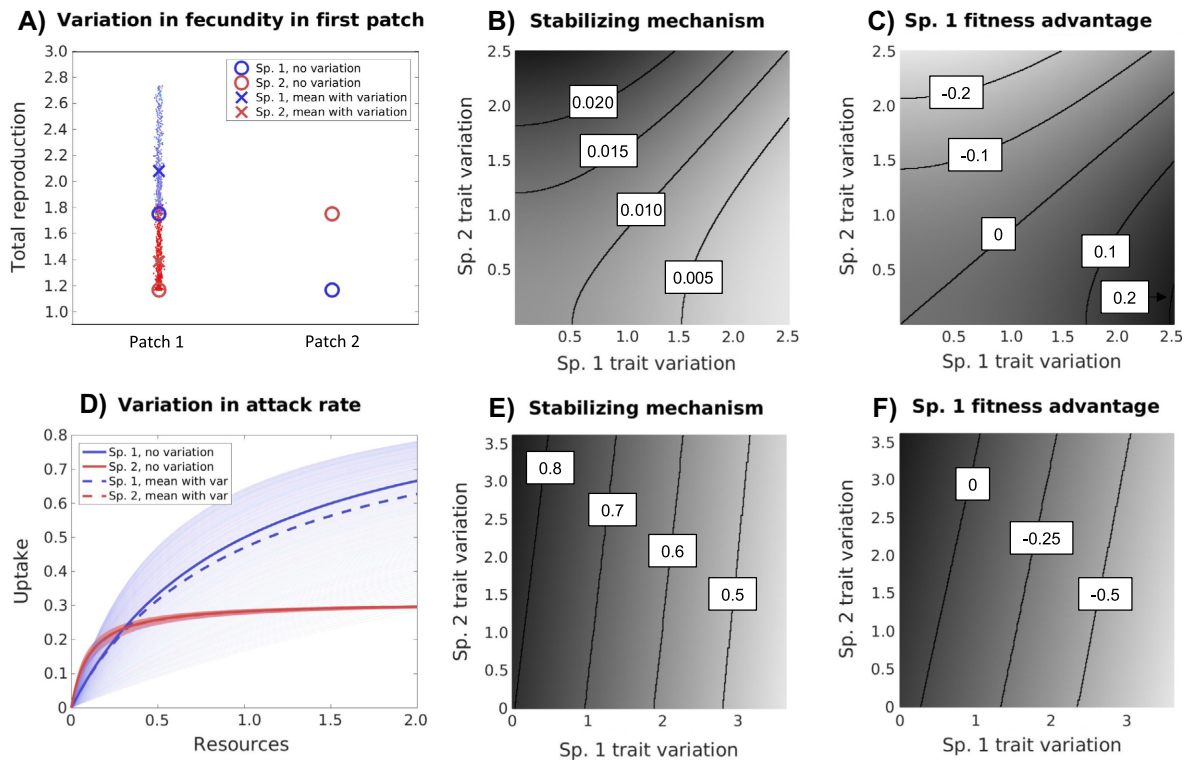
Fig. 6. Two examples of how ITV in a hierarchical trait affect coexistence. (A) First, we show model 3 (the fitness–density covariance, $\Delta\kappa$), and assume that the trait impacts a species' fecundity in habitat 1. Here we show the amount the expected fecundity of an individual in each patch when there is a moderate amount of competition. The trait has a concave-up impact on fecundity, and as such, ITV will increase a species' ability to compete in patch 1. (B) Species can coexist because species 1 is a better competitor in patch 1, and species 2 is a better competitor in patch 2. ITV in species 1 will increase that species' advantage in its preferred habitat. This will strengthen habitat partitioning, and therefore boost the stabilizing mechanism. Conversely, ITV is species 2 will reduce that species' disadvantage in its non-preferred habitat. This will reduce habitat partitioning, and therefore weaken the stabilizing mechanism. (C) Increasing a species' ability to reproduce in patch 1 will always help that species. As such, ITV gives both species a fitness advantage. (D) Second, we show model 4 (the relative nonlinearity, ΔN), and assume that the trait impacts an individual's attack rate. Both species have a Type 2 functional response. Attack rate has a concave-down impact on resource uptake, because individuals with high attack rates are handling time limited (and thus gain little benefit from an increased attack rate). Thus, ITV will reduce a species' average resource uptake, particularly when resources are abundant. (E) Species can coexist because species 1 uptakes resources faster when they are abundant, whereas species 2 uptakes resources faster when they are rare. ITV in species 1 makes it less able to take up abundant resources, which makes it more like species 2, and therefore reduces the stabilizing mechanism. Similarly, ITV in species 2 makes it slightly less able to take up abundant resources, which makes it less like species 1, and therefore increases the stabilizing mechanism. Note, in panel D, that ITV has less of an impact on species 2 than on species 1, and as such, the stabilizing mechanism is less sensitive to ITV in species 2. (F) Because the trait has a concave-down impact on resource uptake, ITV will reduce both species' fitness. ITV has a stronger impact on species 1's resources uptake, so ITV will harm species 1 more than species 2. Parameters for model 3: $d = 0.2$, $\alpha_1^* = \alpha_2^* = 0.5$, $Y_1(1) = 27.6$, $Y_1(2) = 17.6$, $Y_2(1) = 17.6$, $Y_2(1) = 27.6$, $f(T) = T^2$. The trait varied using a uniform distribution. Parameters for model 4: $a_1 = 1$, $a_2 = 3$, $h_1^* = 1$, $h_2^* = 3.2$, $\delta = 0.2$, $\overline{R}_{in} = 6$, $A = 5.5$, $\tau = 0.5$. See sections "Model 3" and "Model 4" for definitions of parameters. The trait varied according to a uniform distribution.

Species can coexist if there is a gleaner–opportunist trade-off (Armstrong and McGehee 1980, Grover 1997), such that the gleaner has a higher resource uptake when resources are low (i.e., a high a_j and h_j), and the opportunist has a higher resource uptake when resources are high (i.e., a low a_j and h_j; Fig. 6D). The stabilizing mechanism in this system is relative nonlinearity. Here, the gleaner benefits from resources being at a constant, low amount; however, because it has such a high handling time, it has trouble dampening resource fluctuations (Armstrong and McGehee 1980, Grover 1997). Conversely, the opportunist benefits from fluctuating resources, because it benefits from periods of high

resource density; however, its low handling time means that it will shorten any periods of abundant resources (Armstrong and McGehee 1980, Grover 1997). Levins (1979) described this situation as one species consuming the variance (as if it was a resource): the opportunist is a variation specialist, and resource variation is low when it is common (because it is consuming it so effectively), but high when it is rare (because the gleaner cannot consume it effectively). Thus, species can coexist under the appropriate trade-off between a_j and h_j.

We consider two traits: attack rate, a_j, and location on an $a_j - h_j$ trade-off axis. The first trait is a hierarchical trait, and the second is a niche trait. In the appendix, we

also examine ITV in a trait affecting just handling time, h_j; the results are similar to variation in attack rate (Appendix S1: Fig. S7).

Result: Variation in attack rate, a_j.—First, the trait T affects an individual's attack rate,

$$a_j(T) = a_j^*(1 + T)$$

(where $T > -1$). This is a hierarchical trait, as high-T individuals are always more able to take up resources. A Type II functional response is concave down, because an individual with a high a_j will become handling time limited. As such, ITV lowers the species' average resource uptake (Fig. 6D). Thus, as a concave-down, hierarchical trait, ITV lowers a species' fitness (Fig. 6F), as expected (Fig. 4).

Intraspecific trait variation in this hierarchical trait affects the stabilizing mechanism, as it affects one element of a between-species trade-off (the $a_j - h_j$ trade-off). ITV in the gleaner strengthens the stabilizing mechanism, whereas ITV in the opportunist weakens the stabilizing mechanism (Fig. 6E). Under the parameter sets we analyzed, increasing a species' ITV had the biggest impact on its resource uptake at higher resource levels (i.e., when most individuals are handling-time limited; Fig. 6D). Because of this, increasing a species' ITV reduces its ability to take advantage of periods of high resource levels, and makes it less able to reign in resource variation. The opportunist's niche is that it can quickly take up abundant resources, but it is self-limiting because it reduces those fluctuations. ITV weakens both of these effects, making it more like the gleaner, and weakening the stabilizing mechanism. The gleaner, on the other hand, persists by taking up scarce resources. The gleaner is quite handling-time limited, and when the gleaner is abundant, resource fluctuations increase. ITV strengthens both of these effects, making the gleaner less like the opportunist, and therefore stabilizing the system. Thus, ITV promotes coexistence if it makes resource uptake functions more different on average and undermines coexistence if it makes the functions more similar on average (Fig. 3).

Result: Variation in attack-rate–handling-time trade-off.—Second, we assume that all individuals are constrained by a universal trade-off axis, such that an individual at location μ_j has an attack rate of

$$a_j = a_1 + \frac{a_2}{1 + e^{\mu_j}}$$

and a handling time of

$$h_j = h_1 + \frac{h_2}{1 + e^{\mu_j - h_3}}$$

where a_1, a_2, h_1, h_2, and h_3 are scaling constants (Appendix S1: Fig. S8). We assume that $a_2 > 0$ and $h_2 > 0$, such that increasing an individual's μ_j makes it more of an

opportunist. The trait T affects an individual's location on the trade-off axis

$$\mu_j(T) = \mu_j^* + T.$$

This is a niche trait: an individual with a high T will take up more resources when resources are scarce, but fewer resources when resources are abundant. As such, ITV changes a species' average performance under both situations, though the exact effect depends on where the mean individual is (Appendix S1: Fig. S8).

Like other niche traits (Fig. 3), ITV in the position along the trade-off axis tends to be destabilizing (Appendix S1: Fig. S8c). In all the cases we considered, it appears that a species with high ITV produces many individuals who are more like their competitor, and therefore, the species is less able to partition the gleaner/opportunist niche. Interestingly, when both species have very similar average traits, ITV in one species could increase the stabilizing mechanism; however, it also increases the fitness differences, such that the species are unable to coexist.

The main impact of ITV on fitness differences was that it changed how adapted individuals were to the environment on average. It appears that for any set of parameters, there is one (or possibly two) locations of trait space that are optimal. ITV makes the species' average performance more like that optimal performance, it increases that species' fitness; however, if ITV makes its performance less optimal, then it decreases that species' fitness. In some cases, it could be different for both species, where ITV hurts the more adapted species and benefits the less adapted species (Appendix S1: Fig. S8c). This model only had two niches (gleaner vs. opportunist); and as such, ITV did not appear to benefit a species by giving it access to unused niches.

Synthesis with Previous Studies

Several previous models have examined how ITV affects coexistence. We have summarized them in Table 1, and show how they fit within our framework in Figs. 3, 4. In this section, we review them, and reinterpret their results in terms of our framework. We first describe models that incorporated ITV in niche traits, and then models that used hierarchical traits. In several models, we have transformed the variables in those studies to make the models look more similar to the ones here. We did not consider studies where the impact of ITV was driven by evolution (e.g., Maynard et al. 2019). Most published studies were of competition between two species, though we examine below whether the predictions of our framework apply also to multispecies models.

Niche traits

Hart et al. (2016) studied how ITV affects coexistence by contrasting the impact of three different traits. Their model for coexistence that was similar to our annual plant model (model 3: the fitness–density covariance). It

CONCEPTS AND SYNTHESIS

TABLE 1. A summary of previous studies of individual trait variation (ITV) and coexistence.

Paper	Model type	Trait	Results
Lichstein et al. (2007)	lottery model	competitive ability of offspring (a hierarchical trait)	ITV in the weaker species made species more likely to dominate. ITV created a very weak stabilizing mechanism.
Courbaud et al. (2012)	lottery model, with a fecundity–competition trade-off	competitive ability of offspring and adult fecundity (both hierarchical traits)	Increasing ITV in both species made coexistence less likely, and made the lower-competition species more likely to dominate.
Hart et al. (2016)	annual plant model with Beverton-Holt competition	sensitivity to competition (a hierarchical trait)	ITV in both species made the dominant species stronger.
Hart et al. (2016)	annual plant model with Beverton-Holt competition	sensitivity to intra- or interspecific competition (a hierarchical trait)	ITV in sensitivity to intraspecific competition made species less likely to coexist. ITV in sensitivity to interspecific competition made species more likely to coexist.
Hart et al. (2016)	annual plant model with Beverton-Holt competition	location on a one-dimensional niche axis (a niche trait)	Increasing ITV for both species reduced coexistence.
Barabás and D'Andrea (2016)	Lotka-Volterra model, with a one-dimensional niche axis	location on the niche axis combined with intrinsic growth (a niche trait)	ITV reduced coexistence, except when it produced a generalist–specialist trade-off.
Uriarte and Menge (2018)	annual plant model in a two-patch system with habitat partitioning	sensitivity to competition in a particular habitat (a hierarchical trait)	The species with higher ITV in any patch was more likely to dominate. ITV in a species' best habitat helped coexistence, and ITV in a species' worst habitat hurt coexistence.
Crawford et al. (2019)	individual-based model of a grassland community	functional traits, such as specific leaf area (we think a hierarchical trait)	ITV in the weak species promoted coexistence, and ITV in the dominant species was either harmful or had no effect.
Banitz (2019)	individual-based model of competition–colonization trade-offs	adult mortality, seed competitive ability, seed production, and mean dispersal distance (all hierarchical traits)	ITV usually had no effect on coexistence, and sometimes undermined it.
Gomes et al. (2019)	Monod model with variable resource inputs	location on a longevity-resource uptake trade-off (a niche trait)	ITV in one species (but not the other) could allow the species to coexist.
Stump et al. (2020)	model of trees with pathogen partitioning	resistance gene profile (a niche trait)	ITV in a single species gave that species a competitive advantage. ITV in all species weakened the stabilizing mechanism.
Milles et al. (2020)	individual-based model of foraging	an individual's location on a slow-fast continuum (a hierarchical trait)	ITV increased persistence times, but never lead to coexistence.

had two differences from ours: it occurred in one patch, and sensitivity to interspecific competition (α_{ij}) could be different than sensitivity to intraspecific competition (α_{ii}). Thus, their model was

$$\lambda_j(t) = \frac{Y}{1 + \alpha_{jj}N_j(t) + \alpha_{kj}N_k(t)}.$$

They analyzed two hierarchical traits (described in the next section), and one niche trait. For the niche trait, they assumed that each individual has some niche location μ, competition between two individuals is determined by difference is niche location

$$\alpha\left(\mu_j, \mu_k\right) = \alpha^* \exp\left\{ -\frac{\left(\mu_j - \mu_k\right)^2}{4\sigma_I^2} \right\}$$

and the trait T determines an individual's niche

$$\mu_j(T) = \mu_j^* + T.$$

This is a niche trait because a high-T individual competed more with high-T individuals and less with low-T individuals. They analyzed the case where species had different mean traits but the same variance in ITV, and they found that ITV always undermined coexistence (Hart et al. 2016). This is as expected, because if species had the same amount of ITV, then a specialist-generalist trade-off was impossible; therefore, ITV in this niche trait undermined coexistence (Fig. 3).

Barabás and D'Andrea (2016) examined coexistence in a Lotka-Volterra model in both two-species and multispecies communities. Their model was similar to ours (model 1: variation-independent mechanism), except that their trait determined both an individual's location along a one-dimensional niche axis, and its intrinsic growth rate. This trait determined how strongly an individual competed with others and is therefore a niche trait. As with our model, they found that ITV tended to undermine coexistence, unless species had similar average traits but one had far more ITV: the conditions required for a generalist-specialist trade-off (Fig. 3). They also found that multispecies communities with ITV tended to be less diverse than those without ITV (Barabás and D'Andrea 2016). This goes beyond what we showed in our two-species model but is perhaps not surprising: ITV in a niche trait is expected to weaken

stabilizing mechanisms; therefore, we should expect communities with ITV to be less diverse than those without it.

Gomes et al. (2019) studied the impact of ITV in several models of bacterial growth. They analyzed a Monod model, similar to ours (model 4: relative nonlinearity). In their model, resources varied, and both species had the same Type II functional response. Microbes died both from being removed from the chemostat, and from natural cause (at rate μ_j)

$$\frac{1}{N_j(t)}\frac{dN_j(t)}{dt} = f_j(R(t)) - \delta - \mu_j.$$

The trait in their model was an organisms' longevity factor, which decreased an individual's death rate.

$$\mu_j(T) = \frac{\mu_j^*}{T}$$

but also decreased its resource uptake rate

$$f_j(R(t),\,T) = \frac{a_j}{T}\frac{R(t)}{1 + R(t)}.$$

Longevity is thus a niche trait, as a high T was beneficial when resources rare, but not when they were common. The authors found that when resource inputs varied, ITV in one species could help species coexist (Gomes et al. 2019). This makes sense under our framework, as it likely generated a generalist-specialist trade-off (Fig. 3).

Stump et al. (2020) studied how variation in plant resistance (R)-genes affected the ability of pathogens to promote coexistence. They examined a model of competition between trees, similar to a spatially explicit lottery model. They assumed that many pathogens were genotype-specific, and that an individual could protect itself from a particular strain of pathogens by having a corresponding R-gene allele. For example, an individual with R-gene alleles A and B would be protected against the corresponding pathogen strains A and B, but susceptible to strain C. Thus, R-genes diversity was a form of ITV, as a species' number of R-genes determined the number of phenotypes it could be. In this model, R-gene alleles were a niche trait: an individual with a given allele became protected against one pathogen strain, but susceptible to others. As a result, a species with more ITV experienced less intraspecific competition, as two conspecifics were less likely to share pathogens. Thus, species with higher ITV had a fitness advantage, as it gave them access to unused niches (i.e., diseases that they could protect themselves against; Fig. 4). They also found that increasing every species' ITV weakened the stabilizing mechanism by weakening intraspecific competition, which is to be expected for a niche trait (Fig. 3).

Hierarchical traits

Lichstein et al. (2007) studied how ITV in seedling competitive ability impacted coexistence. They analyzed competition using a lottery model, similar to ours (model 2: the storage effect). However, the chance that an individual captured a site was not based on a random draw from a lottery. Instead each individual had a competitive ability, and the most competitive individual always captured the site. ITV determined the width of a species' distribution of competitive abilities. We felt that competitive ability best represented a hierarchical trait, as more competitive individuals could outcompete less competitive individuals. Fitness changed from 1 to 0 as an individual's competitive ability changed from the most competitive to the second-most competitive; thus, we expect the trait–performance curve to be sigmoid-like (concave up at the low end and concave down at the high end). The authors mainly examined ITV in the weaker species, and saw that ITV helped it; this makes sense, as that is probably where the trait–performance curve was concave up (Fig. 4). They found that if the species with the lower mean competitive ability had higher ITV, that coexistence was possible. This is arguably an exception to our expectations. That said, the coexistence region was brought about by an indirect effect (a species with higher ITV was harmed more by variation in competitiveness, but tended to increase it, generating a relative nonlinearity), which was extremely weak (as the coexistence region was quite small); thus, this result is arguably in line with our expectations (Fig. 3).

Courbaud et al. (2012) studied how intraspecific variation in a competition–colonization trade-off would impact coexistence. They analyzed a model similar to Lichstein et al. (2007), except that they parameterized species with two values: the number of offspring produced by each adult, and their mean competitive ability. They found that without ITV, coexistence was possible through a trade-off in fecundity and competitive ability, which we believe generated a relative nonlinearity (i.e., the less competitive species benefitted if there was variation in the number of open sites, but their high fecundity decreased this variation when they were dominant). Like Lichstein et al. (2007), they modeled ITV as variation in competitive ability, and assumed that both species had the same variance. The traits varied independently, and therefore were both hierarchical traits (if they varied along a trade-off axis, they would have been niche traits). They found that ITV shrank the region of parameter space where species coexisted, likely by increasing the fecundity-specialist's fitness (as it benefitted more from variation; Courbaud et al. 2012). It may have weakened the stabilizing mechanism as well, by making both species more variation adapted (and therefore more similar, Fig. 3).

As stated above (see "Niche Traits"), Hart et al. (2016) studied three simple models of ITV. They

analyzed a model for coexistence between annual plants, where sensitivity to interspecific competition (α_{ij}) could be different than sensitivity to intraspecific competition (α_{ii}). They analyzed two forms of hierarchical traits. In the first form, they considered the case where inter- and intraspecific competition coefficients were equal, and the trait T determined sensitivity to both,

$$\alpha_{jj}(T) = \alpha_{jk}(T) = (1 + T)\alpha_j^*.$$

Like in our model, sensitivity to competition is a hierarchical trait, and one that does not correspond to a species level trade-off (and indeed, there was no general process in that case that allowed species to coexist). And, as expected, they found that ITV affected fitness differences (Fig. 4), but could not create a stabilizing mechanism (Fig. 3). In the second form, Hart et al. (2016) they assumed that there were two traits: sensitivity to inter- and intraspecific competition.

$$\alpha_{jj}(T_1) = \alpha_{jj}^* + T_1$$

$$\alpha_{jk}(T_2) = \alpha_{kj}^* + T_2.$$

Thus, each trait is hierarchical, as an individual with a high T_1 and T_2 can produce more offspring in the presence of competitors. This is a special case of a hierarchical trait, as it directly impacts inter- and intraspecific competition. In both cases, the trait has a concave-up impact on growth; therefore, ITV reduced a species' average sensitivity to competition. Thus, as expected by our framework, ITV in sensitivity to interspecific competition reduced the average impact of interspecific competition, and therefore made species more likely to coexist (Fig. 3). Similarly, ITV in sensitivity to intraspecific competition reduced average intraspecific competition, and therefore made species less likely to coexist (Fig. 3).

Uriarte and Menge (2018) showed that the results of Hart et al. (2016) would change if species had different competitive abilities in in different habitats. They explored competition in a two-patch annual plant model, much like ours (model 3: the fitness-density covariance). Their model had one subtle difference, however, which is that sensitivity to competition ($\alpha_j(x)$) varied over space, rather than fecundity (Y). Thus, their model was

$$\lambda_j(t) = \sum_{x=1}^{2} \nu_j(x, t) \frac{Y}{1 + \alpha_j(x)(N_1(x, t) + N_2(x, t))}.$$

Coexistence in their model was similar to ours: a stabilizing mechanism was generated if each species had a relative competitive advantage in one habitat (i.e., $\alpha_1(1) < \alpha_2(1)$ and $\alpha_1(2) > \alpha_2(2)$), and each became partially segregated in its own habitat (Uriarte and Menge

2018). In their model, a trait T affected an individual's sensitivity to competition in a given site

$$\alpha_j(T, x) = \alpha_j(x)^* + T.$$

Thus, T was a hierarchical trait, as a high-T individual produced more offspring in habitat x. The trait had a concave-up performance curve, so ITV increased a species' average fecundity in a particular habitat. They found that the species with more ITV was more likely to dominate (Uriarte and Menge 2018). This result makes sense in our framework: the trait is a hierarchical trait that is concave up; therefore, ITV would give a species a fitness advantage (Fig. 4), potentially allowing it to outcompete its competitor. They also found that ITV helped coexistence if it occurred in the patch where the species had the advantage, but ITV hurt coexistence if it occurred in the patch where the species had the disadvantage. This result also makes sense in our framework. Here, species coexist by partitioning how sensitive they are to competition in each patch, and each trait would impact one part of this species-level trade-off. ITV in the habitat where a species was less sensitive to competition makes that species even less sensitive to competition in that habitat, thereby making it less like its competitor and increasing the stabilizing mechanism (Fig. 3). However, ITV where a species was more sensitive to competition makes the species makes it more like its competitor, thus weakening the stabilizing mechanism (Fig. 3).

Crawford et al. (2019) used an individual-based model to study how ITV in several functional traits changed species richness and evenness in a grassland community. Their model was based on a previously studied simulation known as the IBC-grass model (May et al. 2009), but altered so that conspecifics could have different functional traits. They modeled competition for light and belowground resources, along with herbivory. Plants differed in this model by having different functional traits (e.g., specific leaf area, maximum resource utilization, palatability). ITV was modeled by randomly varying these traits, with some built-in correlations between traits (e.g., maximum size correlated with seed mass). Additionally, individuals experienced conspecific negative density dependence via reduced resource uptake. The complexity of their model made it difficult to tell how to classify these traits. Most of the traits on their own would be hierarchical— all else being equal, plants will benefit by being less palatable, more able to utilize resources, and taller—though the correlations meant that they were involved in trade-offs. We expect, however, that most of these trade-offs were equalizing, rather than stabilizing, as they mainly affected an individual's ability to take up resources; if this is the case, then those traits could be classified as hierarchical. Crawford et al. (2019) found that ITV helped weak species to coexist, but it either harmed or had no effect on the dominant species. We suspect that

this result mainly was due to changes in fitness, and that the trait–performance curve was concave up in some regions and concave down in others. Specifically, we suspect that dominant species had traits near the optimum, in a region where the trait–performance curve was concave down, so ITV reduced their ability to take up resources (Fig. 4). We also suspect that the weaker species' performance curve was concave up, such that ITV allowed it to produce a few highly adapted individuals that brought up the species average (Fig. 4).

Banitz (2019) used an individual-based model to study species coexisting via competition–colonization trade-offs. Their model contained four traits: adult mortality, seed competitive ability, seed production, and mean dispersal distance. These traits were allowed to vary randomly, and as such, likely represented hierarchical traits (e.g., all else being equal, individuals benefitted from lower mortality). Species did not coexist in most parameter sets (Banitz 2019). They found that ITV did not lead to coexistence, and in a couple cases, undermined it. This is not surprising, as ITV in a hierarchical trait that is not part of an underlying trade-off should not generate a stabilizing mechanism (Fig. 3), and likely produced fitness differences (Fig. 4). In some cases, traits varied spatially as well, in essence a form of habitat partitioning. They found that random ITV in addition to habitat partitioning had little impact on diversity (Banitz 2019). We were slightly surprised that fitness-differences did not have more of an impact, though our understanding of the model leads us to think that the traits had a nearly linear impact on fitness; if this is the case, then ITV would be expected to have no effect.

Milles et al. (2020) used an individual-based model to study how individual variation in foraging affected coexistence between foragers. The trait was an individual's location on a slow-fast continuum, i.e., whether individuals explored areas thoroughly or quickly moved to new patches. Their model did not appear to generate a stabilizing mechanism, as long extinction times only seemed to occur when both species had similar traits (Milles et al. 2020). Therefore, we think that the slow-fast continuum was equalizing, and thus the trait was a hierarchical trait. It appeared that the optimal trait value was an intermediate value, suggesting that the trait-function relationship was concave-down around that point. Their Fig. 5 also suggests that the trait–function relationship was more linear (or perhaps concave up) at extreme values of the trait. They found that ITV tended to have an equalizing effect. This is what our framework would expect: the hierarchical trait was concave-down for species with high fitness (those with an intermediate trait), therefore ITV reduced the fitness of those species; the trait was linear or concave-up for those with low fitness (those with an extreme trait), therefore ITV increased the fitness of those species (or perhaps just did not change them; Fig. 4).

DISCUSSION

Rarely are two individuals in a species identical, and what this means for coexistence has drawn much recent debate. Some studies have shown that ITV undermines coexistence (Barabás and D'Andrea 2016, Hart et al. 2016), while others have shown that ITV promotes coexistence (Uriarte and Menge 2018, Gomes et al. 2019). Here we have put forward a novel framework for how ITV affects coexistence. It is perhaps intuitive that ITV should promote coexistence if it causes species to be regulated by different factors, or if it reduces mean competitive differences. Our framework goes beyond that: we showed that every previous model of ITV made one of a few core sets of assumptions and explored what those assumptions mean for coexistence. We argue that there are two categories of traits: niche traits and hierarchical traits (Fig. 2). We note that these categories are specifically usefully for understanding how ITV affects coexistence, and that other categories will be useful for different problems. We show that ITV in both categories of trait has the potential to affect both stabilizing mechanisms and fitness differences (Figs. 3 and 4, respectively), at least between two species. It is possible that other trait categories may exist, or that there will be exceptions to the rules. However, we have examined every model of ITV and coexistence that we know of, and developed several new models here, and there was at most one small exception to this framework (i.e., ITV generating a very small stabilizing mechanism in [Lichstein et al. 2007]).

Key findings

ITV in niche traits has a clear and general impact on stabilizing mechanisms: ITV undermines coexistence unless it creates a generalist–specialist trade-off. The impact of hierarchical traits on stabilizing mechanisms is harder to generalize. ITV in a hierarchical trait will promote stability if it makes species more different along the key niche dimension, and it will weaken stability if it makes species more similar. Thus, understanding whether ITV affects stability requires knowing two things. First, one must know the curvature of the trait-function relationship, to know whether ITV will increase or decrease a species' average performance. Second, one must understand how the performance maps to the stabilizing mechanism, and thus whether increasing the average performance of a given species will make it more or less like its competitor. Indeed, we suspect that there are many traits that are unrelated to the important niches that species partition; in these cases, ITV will not impact the stabilizing mechanism at all.

We also note that ITV that strengthens a stabilizing mechanism does not always make species more likely to coexist, because it may also affect fitness differences. In some of the models we examined, ITV had little impact on the stabilizing mechanism (Appendix S1: Figs. S3,

S6); however, ITV in both niche and hierarchical traits always altered fitness differences. In fact, ITV generally had a larger impact on the fitness difference than the stabilizing mechanism (e.g., Fig. 5E, F, Appendix S1: Fig. S5). Thus, when ITV does promote coexistence, we would not be surprised if it most often does this by acting as an equalizing mechanism (but see the specialist–generalist trade-off). It may be worth noting that equalizing mechanisms would not be seen in most simple models, as most models (including most of ours) assumed that species were competitively identical in a system without ITV.

We focused here on a two-species system, though we think our results can be used as a foundation for work in multispecies systems. Multispecies systems are notoriously complicated: the location of species in niche space impacts both its fitness and the community-average stabilizing mechanism (Stump 2017), a change in the ratio of intra- to interspecific competition may actually undermine coexistence (Barabás et al. 2017), and intransitive competition can cause invasion analysis to fail (Schreiber et al. 2011, Saavedra et al. 2017). Thus, the extension of our results to multispecies systems will not be straightforward. However, we would conjecture that some of the basic principles shown here will apply to multispecies systems. Our categorization of niche and hierarchical traits does not depend on the number of species (Fig. 2), and therefore could be used to inform multispecies studies. We found that, in two-species systems, ITV in a hierarchical trait that is concave-up improves a species' fitness; we have no reason to believe that this result will change in a multispecies system. Similarly, in two-species systems, ITV in a niche trait increases a species' fitness if individuals experience less competition but reduces a species' fitness if it leads to maladapted individuals; we also have no reason to believe that this result will change in a multispecies system.

However, we expect that some of our two-species results may not hold in multispecies systems. For example, we found that in a two-species system, ITV in a hierarchical trait that is not part of a between-species trade-off has little impact on coexistence (Fig. 3); this result is unlikely to hold in many multispecies systems, as changes in competitor abundances can propagate through the competitive network, in ways the stabilize the system (Barabás et al. 2017, Stump 2017). That said, we wish to note that three previous studies have examined multispecies systems, and their results could be predicted from our two-species framework: Barabás and D'Andrea (2016) found that ITV in a niche trait lead to lower diversity, Stump et al. (2020) found that ITV in a niche trait weakened the stabilizing mechanism and Banitz (2019) found that ITV in a hierarchical trait (one that species did not partition) had little impact on diversity. Thus, on the one hand, we are confident that ITV will affect multispecies communities in unique and interesting ways, and sometimes in ways that run contrary to the predictions laid out in this paper. On the other hand,

just as two-species Lotka-Volterra models laid the foundation for work on multispecies coexistence, we think that our work here lays the foundation for future work of ITV and multispecies coexistence.

Challenges in mapping niche and hierarchical traits onto functional traits in nature

An additional benefit of our classification system is that, once categorized as niche or hierarchical traits, the potential effects of ITV on coexistence are restricted to the outcomes we have described. Categorizing traits as niche or hierarchical will require detailed observations on individual performance across a gradient of conditions. A rule of thumb is that those traits for which the optimal value changes with conditions are niche traits while those that are always superior or inferior (over the spatial and temporal domain of interest) are hierarchical traits (Fig. 2). The challenge in classifying traits in natural systems arises from the need to describe "conditions" in a meaningful way. In our examples, "conditions" tend to be defined as purely environmental factors (e.g., temperature, precipitation, etc.) or purely ecological factors (e.g., heterospecific or resource density) but, in practice, "conditions" could represent a correlated change in two or more factors that jointly affect performance (e.g., a PCA axis). If two or more of these factors are uncorrelated in space and/or time, there is a possibility that traits could be interpreted as niche traits under certain conditions and hierarchical traits under others. For example, body size may represent a niche trait if, for example, smaller individuals are better equipped to forage on smaller resources; however, during cold periods, body size may represent a hierarchical trait if temperature has a large size-dependent impact on performance that dominates over the differentiation due to foraging. We might conceptualize this example as a continuous transition between panels A and D of Fig. 2, mediated by temperature. For this reason, a trait that is hierarchical for one population or species may be better represented as a niche trait in another. In addition, like correlations among environmental factors, traits may be correlated with one another, leading to linkages among niche and hierarchical traits. For example, a single trait itself can be hierarchical, but if it is correlated with a niche trait, its effect may resemble those of the (unaccounted for) niche trait when viewed in its natural context. Moreveor, many traits are determined by combining multiple measurements into a single measure (e.g., root-to-shoot ratio); our framework should work with such composite traits, as long the composite trait is meaningful (e.g., as long as root-to-shoot ratio matters more than root mass or shoot mass alone).

Whether a trait is a niche trait or a hierarchical trait will always depend on the community and the general process being studied. For example, consider specific leaf area (SLA) in annual plant communities. Work in the

Arizona desert showed that a trade-off between growth rate and water use efficiency, combined with annual variation in rainfall, generated a storage effect (Angert et al. 2009). That work showed that SLA correlates with an individual's location on the growth–efficiency trade-off axis (Angert et al. 2009), and as such, we believe that SLA is a niche trait in this context. Work in a California grassland examining within-year competition for resources, showed that SLA mainly contributed to a species' fitness (Kraft et al. 2015); as such, we believe SLA is a hierarchical trait in this context. Note that a key difference is the general process and temporal domain under study: temporal partitioning vs. within-year competition. As such, we predict that SLA could be a niche trait for any between year storage effects operating in the California system, and a hierarchical trait for any within-year resource partitioning occurring in the Arizona system. Similar patterns should occur in other systems. For example, we expect that wood density would be a niche trait for coexistence via gap dynamics (as low wood-density trees have a growth advantage in high light and high wood-density trees have a survival advantage in low light, Loehle 1988, Visser et al. 2016), and a hierarchical trait for coexistence via predator partitioning (as dense wood is more enemy resistant; Clark et al. 2018). In addition, mathematical models can also provide some insight into which traits might function at niche traits. Under Lotka-Volterra competition, only the competition coefficients contribute to the stability of coexistence, thus if ITV in a niche trait is important for coexistence, that trait should be associated with competitive ability. Similarly, when competition is modulated by a storage effect, stable coexistence depends on differences in fecundity rather than mortality. Thus, if ITV in a niche trait impacts coexistence, the trait should be associated with fecundity.

A basic postulate of trait-based ecology is that traits affect vital rates, and vital rates affect ecological outcomes (McGill et al. 2006). In this paper, we modeled traits as having a direct effect on vital rates. We feel that our framework has helped build a good understanding of how variation in vital rates affects coexistence, though we also recognize that this is only half of the picture. If traits have a nonlinear impact on vital rates, then there is another avenue for ITV to impact coexistence. In particular, if the relationship between a measurable trait and the vital rate it impacts is nonlinear, then even symmetric variation in the trait would lead to asymmetric variation in the vital rate, an aspect that we did not consider here. E. M. Holdridge and D. A. Vasseur (unpublished data) recently considered ITV in uptake rates of non-substitutable resources in an R^* model of exploitative competition. Because uptake rates are bounded on a finite interval in their model, mapping a continuous distribution of traits (e.g., a normal distribution) requires a nonlinear or discontinuous mapping of traits onto rates. They used a sigmoid trait-rate mapping and found that this enhanced the parameter space supporting coexistence. Future studies that explore the complete range of connectivity between trait variation, vital rate variation, and coexistence will thus provide a broader context for the role of ITV in community ecology.

Additionally, most of the modeling studies we examined considered traits that only functioned as niche or hierarchical traits, but not both. However, many functional traits in nature are likely to function as both; for example, in phytoplankton, cell size impacts an individual's ability to reproduce, take up resources, and avoid predators (Litchman and Klausmeier 2008). It is possible that ITV in a single trait will impact some processes like a niche trait, and others like a hierarchical trait. It is not clear how such "hybrid" traits would impact our framework. It is possible that hybrid traits are really just niche traits, as changing an organism's trait makes it better at some parts of its niche and worse at others. There is some evidence for this in the literature: the trait in Barabás and D'Andrea (2016) impacted both intrinsic growth (in a hierarchical way) and the competition kernels (in a niche way); yet when we treated the trait as a niche trait, their results lined up with our predictions. It may be necessary to break hybrid traits into their constituent parts and analyze those parts separately. Finally, it is possible that our niche/hierarchical dichotomy may represent extremes of a spectrum, like most dichotomies in ecology (e.g., generalist/specialist); in this case, our framework will work best for traits that are mostly niche or mostly hierarchical. We did not examine the impact of hybrid traits, mainly because there are so few cases of them in the literature. Thus, future work should examine the ecological impact of hybrid traits.

Relationship to other ITV frameworks

Bolnick et al. (2011) described six mechanisms whereby ITV could impact the ecology of communities; however, it is worth noting that in the absence of plasticity, these are extensions of ITV's effect that require Jensen's inequality. For example, the idea that increasing ITV could change the number of interspecific interactors ("increased degree") is contingent upon ITV expanding the reach species' interactions across some threshold that delimits resource overlap with a heterospecific. The existence of the threshold generates a nonlinearity upon which Jensen's inequality operates to then change the number of interactors. Similarly, a phenotypic subsidy (where individuals with traits yielding higher fitness subsidize the trait space with lower fitness) requires a nonlinearity, otherwise symmetric variation about the mean trait ensures that between-individual differences simply cancel out. For tractability and to isolate the effects of ITV, we have assumed here that ITV is non-heritable and that population sizes are inherently large enough to be described by continuous distributions. Where traits are heritable or plastic within individuals, adaptation will generate emergent trait distributions whose shape will depend upon many factors, including the rate of

adaptation and the context under which interspecific competition plays out. Similar to ITV, plasticity has been shown to both promote and inhibit coexistence (Miner et al. 2005) and it has been suggested that modern coexistence theory could be used (like we do in this paper) as a framework for organizing these disparate results (Turcotte and Levine 2016).

Clark (2010) and Clark et al. (2010) are often cited as the source of the hypothesis that ITV promotes coexistence (e.g., Jung et al. 2010, Violle et al. 2012, Funk et al. 2017). From our understanding, that is not what these papers claimed. Rather, they argued that species coexist via high-dimensional niches and proposed a test that used variability in growth and reproduction between individuals to detect such species-level differences. Indeed, the test they proposed (that the correlation between two conspecifics is usually greater than between two heterospecifics; Clark 2010, Clark et al. 2010) is more likely to be significant when there is *less* not *more* ITV in the system. This is not to say that the individual level differences are unimportant, rather, in this case, they simply reveal species-level differences in the response to environmental variation. To see the difference between the coexistence consequences of these two sources of ITV, consider our model of annual plants (model 3: the fitness-density covariance). In that model, conspecific individuals would have different fecundities, even in the absence of ITV, because they were in different patches. If a researcher wandered through this theoretical ecosystem and did not know about the underlying habitat differences, then differences in fecundity could be interpreted as ITV; and in that case, the environmentally driven differences would be contributing to coexistence, but not the ITV per se. Previous work showed this explicitly: in the model by Banitz (2019), random ITV had essentially no impact on coexistence, whereas ITV that was the result of habitat partitioning strongly promoted coexistence. However, the key is that this latter ITV does not reflect inherent differences between individuals; rather, it reflects underlying environmental heterogeneity, and it is the species' difference in their response to environmental heterogeneity that drives the coexistence. Future empirical studies of ITV should attempt to determine whether apparent ITV is caused by species experiencing different environmental conditions (i.e., differences that would disappear in a common garden), or if it is caused by differences between individuals that would remain in a common garden.

Promising directions

Our review exposes several limitations of the current modeling literature, that present fertile ground for future studies. First, ITV is generally modeled as variability in a vital rate parameter. Indeed, we only found three models that explicitly modeled traits from first principles, based specifically on how they affect the organism

(Crawford et al. 2019, Milles et al. 2020, Stump et al. 2020). Many models have been produced that use specific traits as parameters, and explore how between-species trait differences affect competition and diversity (e.g., Miki and Kondoh 2002, May et al. 2009, Hartvig and Andersen 2013, Amarasekare and Coutinho 2014, Falster et al. 2017). However, those models assume that conspecifics are identical and thus do not contribute to the discussion of how ITVs affect coexistence. Thus, we argue that the biggest gains could be made by explicitly modeling functional traits, rather than continuing to model ITV using abstract model parameters. Additionally, most models have assumed that there is one trait, which affects the niche that species are partitioning (with the exceptions of Banitz [2019] and Crawford et al. [2019]). However, species are characterized many traits, and it is widely believed that multiple stabilizing mechanisms are operating in most systems (Wright 2002). It is likely that ITV in one trait will affect one (or a few) niches out of many. Additionally, as we stated above, we believe that many traits will be niche traits for some mechanisms while being hierarchical traits for others, we are interested in what impact this would have on coexistence. Thus, an important future problem will be to examine how traits affect coexistence in a system with multiple traits and multiple stabilizing mechanisms.

In summary, our synthesis provides a conceptual framework for how ITV affects coexistence. We show that traits can be categorized as niche or hierarchical (Fig. 2), and that this categorization can be used to predict when stabilizing mechanisms and fitness differences will be impacted by ITV (Figs. 3, 4). We show that breaking the impact of ITV into its stabilizing and fitness components helps clarify why some studies found that ITV promotes coexistence and others found ITV undermine it. We hope that this framework will be helpful in guiding future empirical and theoretical work.

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