SYNTHESIS

ECOLOGY LETTERS cnrs WILEY

Eco-evolutionary maintenance of diversity in fluctuating environments

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Abstract
Growing evidence suggests that temporally fluctuating environments are important in maintaining variation both within and between species. To date, however, studies of genetic variation within a population have been largely conducted by evolutionary biologists (particularly population geneticists), while population and community ecologists have concentrated more on diversity at the species level. Despite considerable conceptual overlap, the commonalities and differences of these two alternative paradigms have yet to come under close scrutiny. Here, we review theoretical and empirical studies in population genetics and community ecology focusing on the 'temporal storage effect' and synthesise theories of diversity maintenance across different levels of biological organisation. Drawing on Chesson's coexistence theory, we explain how temporally fluctuating environments promote the maintenance of genetic variation and species diversity. We propose a further synthesis of the two disciplines by comparing models employing traditional frequency-dependent dynamics and those adopting density-dependent dynamics. We then address how temporal fluctuations promote genetic and species diversity simultaneously via rapid evolution and eco-evolutionary dynamics. Comparing and synthesising ecological and evolutionary approaches will accelerate our understanding of diversity maintenance in nature.

KEYWORDS
balancing selection, Chesson's coexistence theory, eco-evolutionary dynamics, eco-evolutionary feedbacks, lottery model, negative frequency-dependence, rapid evolution, storage effect, temporally fluctuating environments, Wright–Fisher model

INTRODUCTION

Why is there so much variation in life on Earth? This has long been a central question in biology. Biological diversity is typically decomposed into several components including genetic variation within populations and species diversity in biological communities. The disciplines of population genetics and community ecology are both concerned with the maintenance of biological diversity in nature. In population genetics, the line of inquiry is typically framed in terms of asking why genetic variation within species is maintained despite fitness differences between genotypes (Crow & Kimura, 1970; Gloss & Whiteman, 2016). Similarly, community ecologists usually cast the problem as one of understanding how species diversity is maintained in spite of the competitive exclusion principle, which predicts that species using the same resources in the same way cannot coexist; one species will drive the other extinct (Gause, 1934; Hardin, 1960; Hutchinson, 1961; Tilman, 1982; Volterra, 1926).

To understand stable coexistence of genotypes or species, both disciplines have focused on mechanisms generating negative frequency-dependence (i.e. rare advantage). If rare types have higher growth rates than common types, extinction of alleles/species is unlikely to occur and genetic/species diversity is maintained. Among several mechanisms that promote negative frequency-dependence, previous empirical studies tended to focus on fluctuation-independent mechanisms, such as negative frequency-dependent selection (Ayala & Campbell, 1974) and resource partitioning (MacArthur & Levins, 1967), as well as spatially varying selection (Levene, 1953) and environments (Chesson, 2000a). More recently, an increasing number of empirical studies have demonstrated that temporally fluctuating selection/environments are important in maintaining both genetic variation (Bergland et al., 2014; Machado et al., 2021; Rudman et al., 2022; Yi & Dean, 2013) and species diversity (Angert et al., 2009; Ellner et al., 2019; Hallett et al., 2019; Letten et al., 2018; Sommer, 1985; Zepeda & Martorell, 2019). Although the topic itself has a long history in ecology (reviewed in Barabás et al., 2018; Chesson, 2000b; Ellner et al., 2019; Stump & Vasseur, 2023; Yamamichi & Letten, 2022) and evolutionary biology (reviewed in Felsenstein, 1976; Frank, 2011; Gillespie, 1991; Hedrick, 1986; Hedrick, 2006; Hedrick et al., 1976; Johnson et al., 2023: see also Figure 1 and Figure S1), the recent accumulation of empirical evidence has coincided with renewed theoretical interest into the role of temporally fluctuating environments in maintaining genetic variation (Bertram & Masel, 2019b; Dean, 2018; Dean et al., 2017; Gulisija et al., 2016; Kim, 2023; Novak & Barton, 2017; Park & Kim, 2019; Schreiber, 2020; Svardal et al., 2015; Wittmann et al., 2017, 2023; Yamamichi et al., 2019; Yamamichi & Hoso, 2017) and species diversity (Barabás et al., 2018; Chesson, 2018; Ellner et al., 2019; Fung et al., 2022; Johnson & Hastings, 2022a, 2022b; Meyer et al., 2022; Pande et al., 2020; Schreiber, 2021, 2022; Schreiber et al., 2019).

To date, however, genetic diversity maintenance has been largely studied by population geneticists in an evolutionary context, whereas understanding species diversity maintenance has primarily fallen within the domain of community ecology. Despite considerable conceptual overlap, the commonalities and differences of these two alternative paradigms have yet to come under close scrutiny (but see Dean & Shnerb, 2020). As Vellend (2016) pointed out, genetic variation within a population and species diversity in the same trophic level (i.e. horizontal communities) have many characteristics in common and it may be possible to accelerate our investigation on genetic and species diversity by considering analogies between population genetics and community ecology (see also Hairston et al., 1996). Despite the potential importance of this kind of synthesis, communication between disciplines is sometimes slow and findings made in one domain can take a long time to receive attention in another. For example, there was almost a 30-year

time-lag between the developments of neutral theory in population genetics (Kimura, 1968) and neutral theory in community ecology (Hubbell, 2001; see Leigh, 2007 for a detailed comparison of population genetics to community ecology in the context of neutral theory). Similarly, the maintenance of genetic variation in temporally fluctuating environments was first studied theoretically in population genetics in the 1950s (Dempster, 1955), but we needed to wait another quarter of a century before it was rigorously developed in community ecology (Chesson & Warner, 1981) despite earlier verbal arguments in the ecological literature (Hutchinson, 1941, 1961; Figure 1; Figure S1). Interestingly, it does not appear to be widely appreciated that one of the simplest haploid models used in population genetics (Seger & Brockmann, 1987; Turelli et al., 2001) is equivalent to the lottery model (Chesson & Warner, 1981), which is arguably the canonical model for demonstrating fluctuation-dependent coexistence in ecology (Box 1; but see Bertram & Masel, 2019a; McPeek & Gomulkiewicz, 2005).

Here we review studies in population genetics and community ecology and synthesise theories of diversity maintenance in temporally fluctuating environments across different levels of biological organisation. In ecology, researchers have focused on two broad classes of fluctuation-dependent coexistence mechanisms: the storage effect and relative nonlinearity (Barabás et al., 2018; Chesson, 1994, 2000b; Ellner et al., 2019). As the storage effect is more closely allied to treatments of temporal variability in population genetics, we focus on it here (see Yamamichi & Letten, 2022 for a recent review of relative nonlinearity). We identify various domain-specific concepts and tools that are well suited to broader cross-disciplinary adoption.

It should be noted, however, that there are many differences between genetic and species diversity: diploidy, allele dominance and recombination are genetic features, whereas niche differences are typically considered an ecological concept. In addition, even though the same factors such as competition, niches, fitness, mutation/migration and temporal variations govern both genetic and ecological systems, their relative importance may vary across the two disciplines. By comparing the similarities and differences between population genetic and ecological perspectives, we hope to advance the broader field of biodiversity research. We further address the possibility of eco-evolutionary dynamics (Hendry, 2016) that promote both genetic and species diversity simultaneously via fluctuations.

THEORIES IN POPULATION GENETICS

How do populations maintain genetic variation? If genetic variation is selected against, genetic diversity depends on migration or mutations that provide new variation into a population (i.e. mutation- or migration-selection balance). If genetic variation is selectively
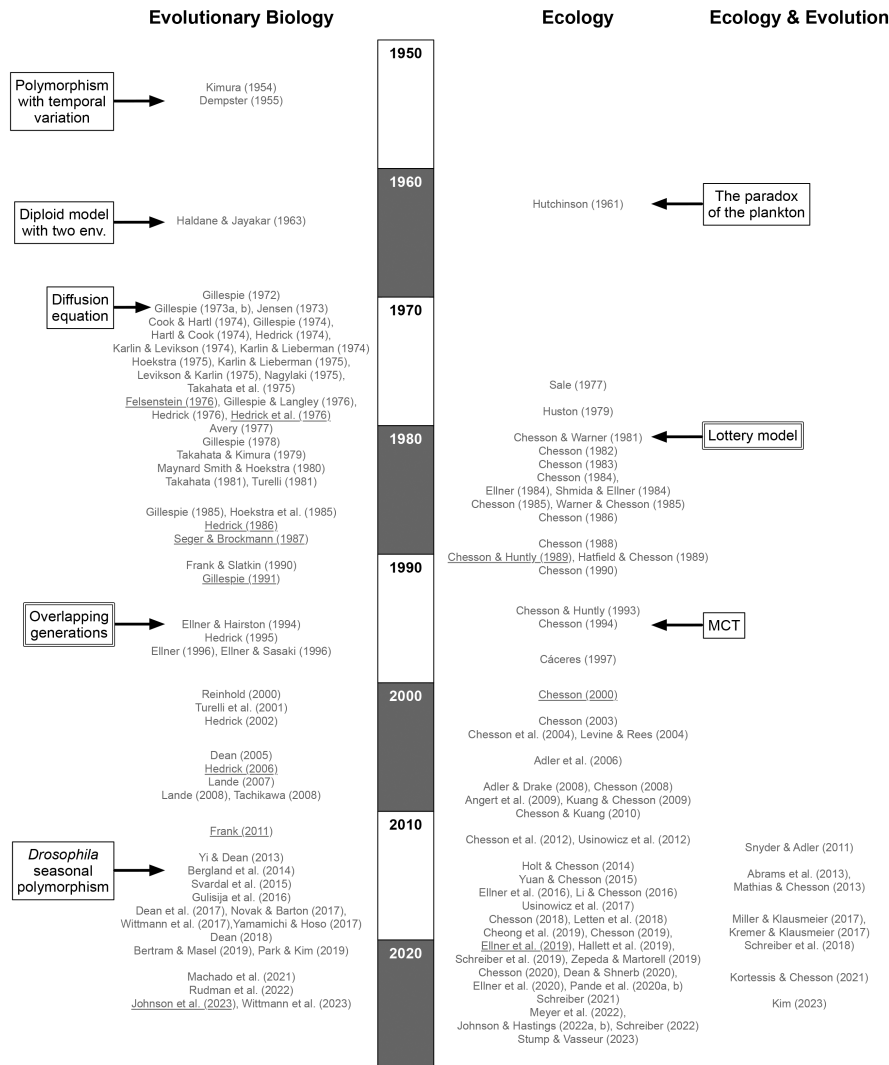
FIGURE 1　Papers on temporally fluctuating environments and the maintenance of diversity in population genetics, community ecology and eco-evolutionary studies. Underlined papers are reviews, arrows represent important concepts/findings, and the boxes with double lines for the 'lottery model' and 'overlapping generations' indicate that their coexistence mechanisms are equivalent. 'MCT' is modern coexistence theory. From the distribution of cited papers in this manuscript, it is clear that (1) population genetic studies on this topic are older than community ecology studies, (2) the number of papers is recently increasing in both research areas, and (3) eco-evolutionary studies combining the two disciplines are relatively new.

neutral, it will eventually be lost by genetic drift, albeit over longer time scales for larger populations. Selection pressure is therefore needed to actively maintain existing genetic variation in a population. In the 1950s, Dobzhansky hypothesised that some form of balancing (negative frequency-dependent) selection is maintaining genetic variation within populations by studying chromosomal inversion polymorphism in *Drosophila melanogaster* (Gloss & Whiteman, 2016). The idea that temporally fluctuating selection may promote the maintenance of genetic variation can be traced back to Dempster (1955) (cf. Kimura, 1954; Wright, 1948). Since then, various theoretical models have explored how temporally fluctuating selection can maintain genetic variation (reviewed in Felsenstein, 1976; Gillespie, 1991; Hedrick, 1986; Hedrick, 2006; Hedrick et al., 1976).

Using models of allele frequency dynamics in a population of constant size, population geneticists demonstrated that temporally fluctuating selection cannot maintain genetic variation in populations with discrete (non-overlapping) generations and haploid inheritance (Dempster, 1955; Gillespie, 1973; Haldane & Jayakar, 1963; Box 2; Figure 2). Researchers later demonstrated that there are various 'buffering' factors that can promote the maintenance of variation, including overlapping generations (Ellner & Hairston, 1994; Hedrick, 1995; Sasaki & Ellner, 1997; Seger & Brockmann, 1987; Turelli et al., 2001; Box 2; Figure 2) as well as complete allele dominance in diploid inheritance (Haldane & Jayakar, 1963), sex-limited traits (Gorelick & Bertram, 2003; Reinhold, 2000), epistasis and linkage disequilibrium (Gulisija et al., 2016; Novak

BOX 1   The lottery model is equivalent to the haploid population genetic model with overlapping generations

Consider a lottery model of competing species i (e.g. coral reef fish species competing for space: Sale, 1977) in ecology (Chesson & Warner, 1981):

$$N_i(t + 1) = \left\{ 1 - a_i + \left[\sum_{j=1}^{n} a_j N_j(t) \right] \frac{b_i(t)}{\sum_{j=1}^{n} b_j(t) N_j(t)} \right\} N_i(t), i = 1, 2, \ldots, n, \qquad (1.1)$$

where n is the number of competing species, N_i is the population density, a_i is the adult death rate and $b_i(t)$ is the number of juveniles produced by an adult of species i at generation t (but see Abrams et al., 2013 for an alternative form of the lottery model). When there are only two competing species ($n = 2$) and the two species have the same adult death rate ($a = a_1 = a_2$), the lottery model in Equation 1.1 can be simplified as

$$N_1(t + 1) = \left\{ 1 - a + a[N_1(t) + N_2(t)] \frac{b_1(t)}{b_1(t) N_1(t) + b_2(t) N_2(t)} \right\} N_1(t). \qquad (1.2)$$

From Equation 1.2, we can see $N_1(t + 1) + N_2(t + 1) = N_1(t) + N_2(t)$. Therefore, the total density in a competing community does not change over time, and thus we can consider the frequency dynamics by defining $p = N_1 / (N_1 + N_2)$ (i.e. by dividing Equation 1.2 by the total density):

$$p(t + 1) = \left\{ 1 - a + a \frac{b_1(t)}{b_1(t) p(t) + b_2(t)[1 - p(t)]} \right\} p(t). \qquad (1.3)$$

This is the haploid version of the population genetic model to track an allele frequency within a population, p, at generation t with generation overlap due to, for example, seed banks in plants (Turelli et al., 2001) where $b_i(t)$ is a temporally fluctuating selection coefficient (fitness) of an allele i. Thus, the haploid model in population genetics is a special case of the lottery model in community ecology. When the population size is finite (i.e. with genetic drift) and there is no selection (i.e. $b_1 = b_2$) or overlapping generations (i.e. $a = 1$), the model is identical to the Wright–Fisher model in population genetics, which has been analysed to understand neutral allele frequency dynamics (Crow & Kimura, 1970). As such, this model may also be useful for studying neutral dynamics in community ecology. Although the lottery model is often introduced as a model for the temporal storage effect, note that when each species has a different adult death rate ($a_1 \neq a_2$), relative nonlinearity may contribute greatly to coexistence (when sensitivity of recruitment to environmental variation is greater for species with larger adult death rates; Yuan & Chesson, 2015).

& Barton, 2017), temporal reversal of allele dominance (Bertram & Masel, 2019b; Wittmann et al., 2017), maternal effects (Yamamichi & Hoso, 2017) and additive contributions of alleles to fitness in diploid populations (Gillespie, 1978, 1991; Schreiber, 2020).

Despite the breadth of theoretical research, until recently, the general consensus held that temporally fluctuating selection was comparatively ineffective at maintaining genetic variation compared to spatially varying selection and other negative frequency-dependent selection mechanisms (Hedrick, 2006). However, more and more studies over the past two decades suggest that temporally fluctuating selection can greatly contribute to the maintenance of genetic variation (Bell, 2010; Johnson et al., 2023; Messer et al., 2016). Indeed, many SNPs in the *Drosophila* genome show persistent seasonal fluctuations (Bergland et al., 2014; Machado et al., 2021; Rudman et al., 2022) and genotype frequencies of *Daphnia* change in response to seasonal food availability

(Schaffner et al., 2019). These empirical findings show (at least transient) maintenance of diversity and have driven renewed theoretical interest into the role of temporally fluctuating environments in maintaining genetic variation (Bertram & Masel, 2019b; Dean, 2018; Dean et al., 2017; Gulisija et al., 2016; Novak & Barton, 2017; Park & Kim, 2019; Wittmann et al., 2017; Yamamichi et al., 2019; Yamamichi & Hoso, 2017). Interestingly, while classical studies tended to focus on stochastic temporal fluctuations, periodic (seasonal) fluctuations may be more efficient in maintaining variation because long sequences of unfavourable periods are unlikely.

THEORIES IN COMMUNITY ECOLOGY

Interest among community ecologists in the role of temporal fluctuations in maintaining species diversity has its

BOX 2   How diversity is maintained in the lottery model

Based on the population genetic model (Equation 1.3), when there is no generation overlap (no buffered growth: $a = 1$), $p/(1-p)$ can be represented as

$$\frac{p(t+1)}{1-p(t+1)} = \frac{b_1(t)p(t)}{b_2(t)\left[1-p(t)\right]}$$
$$= \frac{p(1)}{1-p(1)} \prod_{s=1}^{t} \frac{b_1(s)}{b_2(s)}. \tag{2.1}$$

This indicates that, depending on the geometric mean of $b_1(t)/b_2(t)$, there are three possible outcomes: when it is larger than one, the frequency ratio $p/(1-p)$ increases and eventually the frequency of allele 1, p, approaches one (Kimura, 1954); when it is smaller than one, the frequency of allele 2 approaches one; and when it equals one, the frequency ratio drifts randomly. Therefore, genetic variation is not maintained by temporal fluctuations. This indicates that the allele/species with the highest geometric mean fitness will win and the other alleles/species will go extinct. With overlapping generations (buffered growth), on the other hand, it is possible for two alleles/species to coexist (Figure 2).

If two species have positive invasion growth rates (IGRs), coexistence is stable (i.e. mutual invasibility; Grainger et al., 2019). When there is generation overlap ($a < 1$), we can consider the IGR as:

$$\bar{r}_{inv} \approx E\left\{ \log\left[1 - a + \frac{ab_1(t)}{b_2(t)} \right] \right\}. \tag{2.2}$$

This indicates that a model with discrete generations ($a = 1$) has a linear response to environmental variation: $\bar{r}_{inv} \approx E\{\log[b_1(t)] - \log[b_2(t)]\}$ (Figure 2a), which means that temporal variation in environments cannot affect IGR (Fox, 2013). In contrast, a model with overlapping generations ($a < 1$) has a convex response to environmental variation (Figure 2a), and thus increasing temporal fluctuations results in increasing IGR (cf. Jensen's inequality; McPeek, 2022) and stable coexistence (Figure 2b).

In addition to IGRs, we can calculate the stationary distribution of coexisting genotypes by utilising diffusion approximation analyses. When we consider a frequency change in one generation, Δp, Equation 1.3 can be rewritten as

$$\Delta p = p(t+1) - p(t)$$
$$= \frac{a\left[b_1(t) - b_2(t)\right]p(t)\left[1-p(t)\right]}{b_1(t)p(t) + b_2(t)\left[1-p(t)\right]}. \tag{2.3}$$

Thus, increasing generation overlap (by decreasing the parameter a) results in slower response to selection due to the fitness difference, $b_1 - b_2$ (Figure 2b). This means that slower responses of frequency dynamics to environmental changes make the maintenance of variation possible (Gillespie, 1991). Based on Equation 2.3, we can conduct diffusion approximation analyses and obtain an equilibrium frequency distribution (Figure 2c,d). The curves of the diffusion approximation show a similar pattern as the histogram from simulations (Turelli et al., 2001). Note that even when coexistence is stable, the frequency dynamics may spend long periods of time near zero or one (Figure 2c) and may be vulnerable to extinction due to demographic stochasticity. Also, it should be noted that bigger IGRs need not mean greater propensity to coexist (Pande et al., 2020) as larger IGRs do not necessarily equate to the stationary distribution being more concentrated away from extinction.

origin in Hutchinson's proposed solution to the paradox of the plankton (Hutchinson, 1961). Hutchinson argued that environmental fluctuations could prevent competitive exclusion of phytoplankton species competing for shared resources. This idea was formalised in the 1980s into a cohesive mathematical framework encompassing

two fluctuation-dependent coexistence mechanisms: the 'temporal storage effect' (Chesson & Warner, 1981) and 'relative nonlinearity of competition' (Armstrong & McGehee, 1980; Hsu et al., 1978; Koch, 1974). Empirical studies provide compelling evidence that the storage effect can promote species coexistence in zooplankton
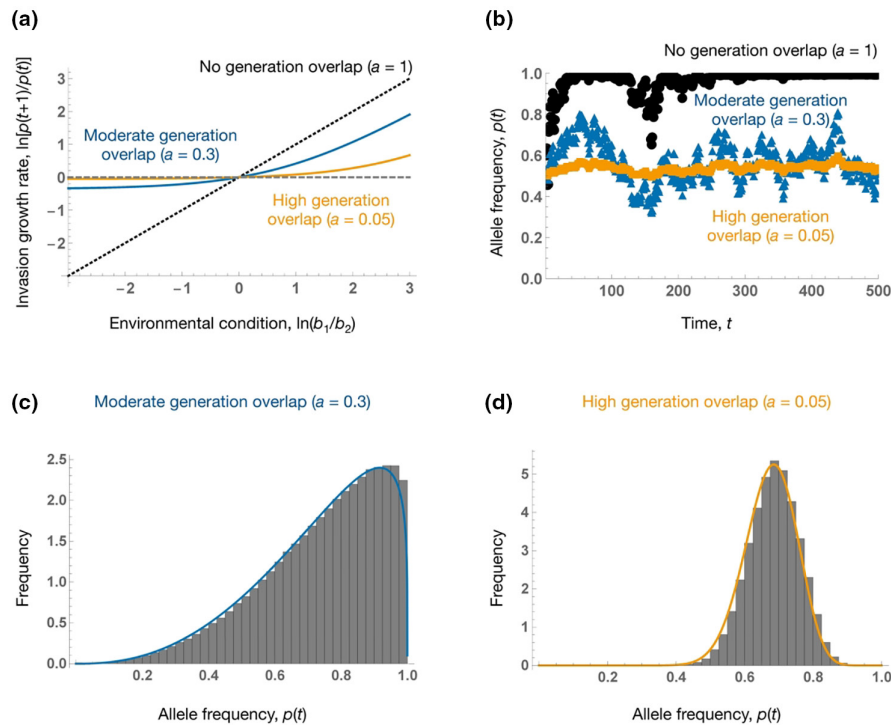
FIGURE 2 Effects of generation overlap on invasion growth rates (IGRs) and competition dynamics. (a) When there is no generation overlap ($a=1$: the dotted black line), the IGR, $\log[p(t+1)/p(t)]$, is a linear function of environmental variation, $\log(b_1/b_2)$ (Equation 2.2 of Box 2). With a moderate amount of generation overlap ($a=0.3$, the blue curve) the IGR is a convex function of environmental variation. Thus, environmental variation increases the IGR with generation overlap (cf. Jensen's inequality). With high generation overlap ($a=0.05$, the orange curve), the IGR becomes more convex. Positive values in the X-axis mean allele/species 1 is advantageous over allele/species 2. (b) Because of the positive IGRs of rare alleles/species, variation is maintained with a moderate amount of generation overlap ($a=0.3$, the blue triangles) while the allele frequency approaches one without overlapping generations ($a=1$: the black circles). With high generation overlap ($a=0.05$, the orange squares), the frequency dynamics is more stable. Here p is the frequency of allele/species 1 and the fitness of allele/species 1 (b_1) has a lognormal distribution with a mean of 1.05 whereas that of allele/species 2 (b_2) is 1. (c) Comparison of the simulation results with a moderate amount of generation overlap ($a=0.3$) in (b) (the histogram) and diffusion approximation (the blue line; see Turelli et al., 2001 for the diffusion approximation). Although coexistence is stable (i.e. the IGRs of two alleles/species are positive), the frequency dynamics are concentrated near $p=1$ and thus allele/species 2 is vulnerable to stochastic extinction. (d) Comparison of the simulation results with high generation overlap ($a=0.05$) in (b) (the histogram) and diffusion approximation (the orange line; see Turelli et al., 2001 for the diffusion approximation).

(Cáceres, 1997), grassland and desert plants (Adler et al., 2006; Angert et al., 2009; Hallett et al., 2019), trees (Usinowicz et al., 2012, 2017), phytoplankton (Descamps-Julien & Gonzalez, 2005; Ellner et al., 2019) and nectar yeasts (Letten et al., 2018). Assessing the storage effect in these empirical studies requires a diversity of investigatory approaches, including field surveys, experimental manipulations, mathematical model analyses and computer simulations.

While population geneticists have identified various genetic factors that promote the maintenance of genetic variation, community ecologists have tended to be more interested in decomposing species' invasion growth rates (IGRs) and understanding the relative importance of different fluctuation-dependent (i.e. the temporal and spatial storage effect, temporal and spatial relative nonlinearity, and fitness-density covariance) and fluctuation-independent coexistence mechanisms (e.g. resource partitioning, species-specific natural enemies). As a result, theoretical research in this area has largely crystallised around a framework referred

to alternately as *modern coexistence theory* (MCT), *Chesson's coexistence theory* or *quantitative coexistence theory* (Barabás et al., 2018; Chesson, 1994, 2000b; Ellner et al., 2016, 2019). The central tenet of coexistence theory is to decompose the contribution different mechanisms (e.g. the temporal storage effect) make to focal species' IGRs (Barabás et al., 2018; Chesson, 1994, 2000b; Ellner et al., 2016, 2019). Box 3 describes this procedure for evaluating the relative strength of the storage effect compared to inherent fitness differences between competing species.

SYNTHESISING THE TWO APPROACHES

Although ecologists and evolutionary biologists have used similar models to investigate diversity maintenance (Box 1), they have tended to employ different analytical approaches. For example, while both fields have used IGR to understand stable coexistence (Turelli, 1978a,

BOX 3   The storage effect in the Chessonian framework

To identify coexistence mechanisms for competing species in a fluctuating environment, Chesson (1994, 2018) assumes that each species is positively affected by some environmental factor E_i and negatively affected by the strength of competition C_i experienced by species i ($i = 1, 2$). For example, in the lottery model in Box 1, E_i can be chosen to be the per-capita birth rate, b_i, and C_i to be the total density of offspring, $b_1 N_1 + b_2 N_2$. When E_i and C_i are transformed the right way to the new variables $\mathcal{E}_i$ and $\mathcal{C}_i$, the per-capita growth rate $r_i(t)$ of species i can be approximated as a linear function of $\mathcal{E}_i$ and $\mathcal{C}_i$ with an interaction term:

$$r_i \approx \mathcal{E}_i - \mathcal{C}_i + \gamma_i \mathcal{E}_i \mathcal{C}_i, \tag{3.1}$$

where γ_i is an interaction coefficient. For example, when there is generation overlap ($a < 1$) in the lottery model, this interaction coefficient is negative as competition, $b_1 N_1 + b_2 N_2$, has less of a negative effect on per-capita growth rate when environmental conditions, b_i, are poor (*subadditivity*: Figure 4b). In general, this interaction coefficient can be negative or positive, and this nonlinearity represents 'buffered growth'. On the other hand, when there is no generation overlap ($a = 1$), there is only an additive effect of environment and competition (Figure 4a).

Taking the temporal averages of the per-capita growth rate yields the IGR for species i:

$$\bar{r}_i \approx \overline{\mathcal{E}}_i - \overline{\mathcal{C}}_i + \gamma_i \mathrm{cov}(\mathcal{E}_i, \mathcal{C}_i), \tag{3.2}$$

where the bars denote time averages, for example, $\bar{r}_i$ is the time average of $r_i(t)$. The first and second terms of the right-hand side corresponds to the average effect of environmental fluctuations and competition, respectively. Importantly, the third term, which lies at the heart of the storage effect, corresponds to the interaction between environment and competition, and its sign depends both on the sign of interaction coefficient γ_i and whether covariance between environment and competition is positive or negative. For example, in the lottery model, the covariance term is positive as better environmental conditions (larger b_i) immediately intensify competition (higher $b_1 N_1 + b_2 N_2$). As the interaction coefficient is negative, the third term in Equation 3.2 is negative. As the third term is negative for both species, its effect on coexistence depends on whether it is larger (i.e. less negative) for a species that has become rare in the community (the invader).

To determine the relative importance of the three terms in Equation 3.2, MCT compares the growth rates of rare invading species i and common resident species j. If the dynamics of the resident species j is stationary, its time-averaged per-capita growth rate is zero. Therefore, the difference is:

$$\bar{r}_i = \bar{r}_i - \bar{r}_j \approx (\overline{\mathcal{E}}_i - \overline{\mathcal{E}}_j) - (\overline{\mathcal{C}}_i - \overline{\mathcal{C}}_j) + [\gamma_i \mathrm{cov}(\mathcal{E}_i, \mathcal{C}_i) - \gamma_j \mathrm{cov}(\mathcal{E}_j, \mathcal{C}_j)], \tag{3.3}$$

which can be written as $\bar{r}_i \approx \Delta E - \Delta C + \Delta I$. When the first term of the right-hand side is positive, it means that species i benefits on average more from the environmental conditions than species j. For the lottery model, this term is positive when species i has the higher average per-capita birth rate ($\bar{b}_i > \bar{b}_j$). On the other hand, when the second term is positive, it indicates that species j is more impacted by competition on average than species i. For the lottery model, this term is zero. Finally, the third term can be positive if the product of the interaction coefficient and the covariance term of species i is larger than that of species j (i.e. density dependence in environment-competition covariance). In the lottery model this occurs as the interaction coefficient is negative, and the covariance between the environmental conditions, b_j, for the resident species j and the strength of competition, $b_1 N_1 + b_2 N_2 \approx b_j N_j$, is generally much stronger than the covariance between the environmental conditions, b_i, for the rare species i and the strength of competition (especially when a good environment for one species is a bad environment for the other species: Figure 4c). Then, the storage effect works as the rare species enjoys good environments with less competition (Figure 4d).

Traditionally, the storage effect is said to occur when (i) the covariance terms are positive and (ii) the interaction coefficients are negative. In words, (i) there is a positive covariance between the strength of competition and the environmental conditions, and (ii) species experiencing less favourable environmental conditions are less sensitive to competition. However, the third term in Equation 3.3 can also be positive when (i) there is a negative covariance between the strength of competition and environmental conditions and (ii) the interaction coefficients are positive (Schreiber, 2020). For example, this can occur in negatively autocorrelated environments when density-independent survival fluctuates differentially in the lottery model (Schreiber, 2021).

1978b, 1981), population geneticists have often utilised diffusion approximations by assuming weak selection (Gillespie, 1973, 1991; Turelli et al., 2001; Yamamichi & Hoso, 2017). IGRs correspond to the average per-capita growth rate of a species when rare in the community (Grainger et al., 2019). Intuitively, provided all species have positive IGRs whenever they are rare, one expects that all species can increase their densities when rare and, consequently, stably coexist (Grainger et al., 2019). Under suitable assumptions (e.g. no intransitivities), this heuristic is supported mathematically (Hofbauer & Schreiber, 2022). For a community with two competing genotypes or species, the IGRs determine three types of long-term outcomes: if both IGRs are positive, co-existence is stable. If one is positive and the other one is negative, one genotype or species may exclude the other. If both are negative, there are alternative stable states consisting of each species in isolation. It should be noted, however, that IGR approaches to coexistence require ability to recover from rare, which is a stronger notion of coexistence than the existence of a positive at-tractor (Grainger et al., 2019), and ecologists have also focused on the interplay between the attractiveness of a manifold (the equilibrium state) and the strength of sto-chasticity (Barbier et al., 2018; May & MacArthur, 1972). Both ecologists and population geneticists use IGRs to determine when species coexistence or protected poly-morphisms occur.

While using IGRs is a powerful first step for under-standing coexistence, they only tell part of the story (Ellner et al., 2020; Pande et al., 2020). Notably, IGRs do not provide information about how often environmental fluctuations drive species to low densities or genotypes to low frequencies. Population geneticists have used dif-fusion approximations to tackle this issue (see e.g. Karlin & Taylor, 1981; Otto & Day, 2007) as illustrated in Box 2 and Figure 2. Ecologists have used this approach as well, but less commonly (Hatfield & Chesson, 1989; but see Dean & Shnerb, 2020; Pande et al., 2020).

To foster a more synthetic treatment of diversity main-tenance in fluctuating environments between ecology and evolution, it may be valuable to investigate the recip-rocal utility of the two disciplines' analytical approaches and models. Indeed, Pande et al. (2020) utilised the diffusion approximation for understanding the effects of demographic stochasticity on species' coexistence. Similarly, the Chessonian framework of community ecology may be used to understand how stable coexis-tence of genotypes is maintained in population genetics.

Because of the popularity of the lottery model, there is a frequent misunderstanding that the storage effect needs generation overlap (via dormancy), but this is not the case (Li & Chesson, 2016; Yi & Dean, 2013). For the storage effect to increase the IGR and promote sta-ble coexistence, there are three necessary conditions: (1) species-specific responses to environmental fluc-tuations, (2) density-dependent covariance between environment and competition, and (3) lower sensitivity to competition in environmentally unfavourable time periods, or buffered population growth (Chesson, 1994; Box 3). We note that negation of conditions 2 and 3 can also allow for coexistence (Schreiber, 2020). In Box 3, the parameter γ represents a negative interactive effect of population buffering and the covariance term rep-resents conditions 1 and 2. As long as these conditions are satisfied, the temporal storage effect operates and promotes the maintenance of diversity (Box 4; Figures 3 and 4).

We can apply the decomposition approach of MCT based on the IGR to understand how the three conditions underpinning the temporal storage effect manifests in various population genetic models (Table S1). For exam-ple, when alleles contribute additively to fitness in diploid individuals, the storage effect occurs via heterozygotes buffering alleles through unfavourable environmental conditions (Schreiber, 2021). It should be noted, however, that additional work may be needed for some population genetic models. For example, in the diploid model with complete allele dominance (Haldane & Jayakar, 1963), the recessive allele tends to appear as a heterozygote with the dominant phenotype when rare. Thus, its IGR is zero because the heterozygote and a homozygote of the dom-inant allele have the same fitness, and thus one needs to determine whether this corresponds to a robust form of coexistence (see Dean & Shnerb, 2020 for a mathemati-cal formalism of this model). Still, stable coexistence in diploid models with partial dominance can be analysed by examining IGRs and it will be promising to highlight the different ways the γ and covariance terms show up in population genetic and ecological models in future studies.

DIFFERENCES AND UNDER-EXPLORED OVERLAP

Although the maintenance of biological variation in population genetics and community ecology are some-what similar, there remain important differences because certain processes only occur between individuals of the same species, while others are unique to species interac-tions within communities. For example, while the lottery model is similar to the haploid version of the population genetic model (as noted in Box 1) and it can be equiva-lent to models with genomic imprinting (Yamamichi & Hoso, 2017), there are no analogues of models account-ing for diploidy or recombination in community ecology models. Similarly, population geneticists have largely ignored the distinction between the storage effect and relative nonlinearity. Nevertheless, because one can view the lottery model with differential mortality as a haploid selection model (Box 1), the potential for relative nonlin-earity to regulate genetic diversity should not be over-looked in population genetics.

BOX 4   Simple density-based models with the storage effect

Based on the three necessary conditions for the storage effect, we can consider various models where the storage effect works. Previous studies have tended to focus on frequency-based (lottery) models (Boxes 1–3), but several recent studies have shown how the temporal storage effect operates under diverse density-based models (Bertram & Masel, 2019b; Li & Chesson, 2016; Yi & Dean, 2013). For example, Yi and Dean (2013) considered a serial transfer model with fluctuating environments (see also Dean, 2005; Table S1). Here growth rates of competing species are independent of densities, but the total population size is bounded because competitors cease to grow once the limiting resource is depleted. Population growth re-starts upon dilution to fresh medium. Because of this model construction, time available for growth depends on competitor frequencies. When there are two types of environments that promote growth of each species, a rare competitor spends more time in its favoured environment (because the other common competitor grows slowly) and less time in its less favoured environment (because the other competitor grows quickly). This results in negative frequency-dependence in community dynamics.

Yi and Dean (2013) concluded their results reflected a novel mechanism because the model does not incorporate any storage (e.g. through a seed bank or diapause) or any nonlinearities in competition. Li and Chesson (2016), however, noted that the model of Yi and Dean (2013) does in fact generate a negative interaction between environment and competition (i.e. buffered population growth). This example illustrates the difficulty of understanding the storage effect and its three conditions (Johnson & Hastings, 2022b).

We can also consider a new discrete-time model by modifying the Ricker model as arguably the simplest model that can exhibit a storage effect:

$$N_i(t + 1) = N_i(t)\exp\left\{c_i - d_i\left[N_i(t) + N_j(t)\right]\right\}, i, j = 1, 2, \tag{4.1}$$

where c_i and d_i are temporally fluctuating growth parameters of species i. Here, the invasion growth rate (IGR) of the rare species 1 can be written as:

$$\bar{r}_1 = \log\left[\frac{N_1(t+1)}{N_1(t)}\right] = \bar{r}_1 - \bar{r}_2 = \underbrace{\bar{c}_1 - \bar{c}_2}_{\text{fitness diff.}} + \underbrace{\overline{(d_2 - d_1)N_2}}_{\text{storage effect}}. \tag{4.2}$$

This is because the growth rate of the resident species 2, $\bar{r}_2$, is zero. The difference between the c parameters is called an average fitness difference in the framework of coexistence theory (Chesson, 2000b), whereas the remaining term is the storage effect. Thus, if mean parameters are the same between species, $\bar{c}_1 = \bar{c}_2$ and $\bar{d}_1 = \bar{d}_2$, then the IGR is $\bar{r}_1 = \text{cov}(d_2 - d_1, N_2)$ (because $\bar{r}_1 = \overline{(d_2 - d_1)N_2} = \text{cov}(d_2 - d_1, N_2) + \underbrace{(\bar{d}_2 - \bar{d}_1)\overline{N}_2}_{=0}$). When d_1 and d_2 are independent of one another, this simplifies to $\bar{r}_1 = \text{cov}(d_2, N_2)$ as d_1 is not correlated with N_2.

Under what conditions does the covariance become positive? Because the density of the resident species is determined as $N_2(t + 1) = c_2(t)/d_2(t)$, larger d_2 values leads to smaller N_2 values. However, the invading species at $t+1$ is affected by $d_2(t+1)$ and $N_2(t+1)$, not by $d_2(t)$ and $N_2(t+1)$ (Johnson & Hastings, 2022b). Because of this time-lag, negative autocorrelation in the d parameter makes this covariance positive and, consequently, a positive IGR and stable coexistence (Figure 3a,b). The storage effect is a sole driver for stable coexistence here. On the other hand, positive autocorrelation in d_2 would create a negative IGR, which causes stochastic bistability (i.e. either species is excluded depending on the initial condition: Figure 3c,d; Schreiber, 2021). It should be noted that there is no clear stage structure in this model, but the three conditions for the storage effect are satisfied.

Although tempting to ignore models and techniques that are tailored to processes that operate below the community level in community models, we propose that techniques used to understand diversity at one level of biological organisation may be transferable to other levels. Because alleles and species are equivalent in models of population genetics and communities, respectively, it may be possible to consider interspecific (higher-order) interactions (Levine et al., 2017) as epistasis (e.g. interactions between alleles at different
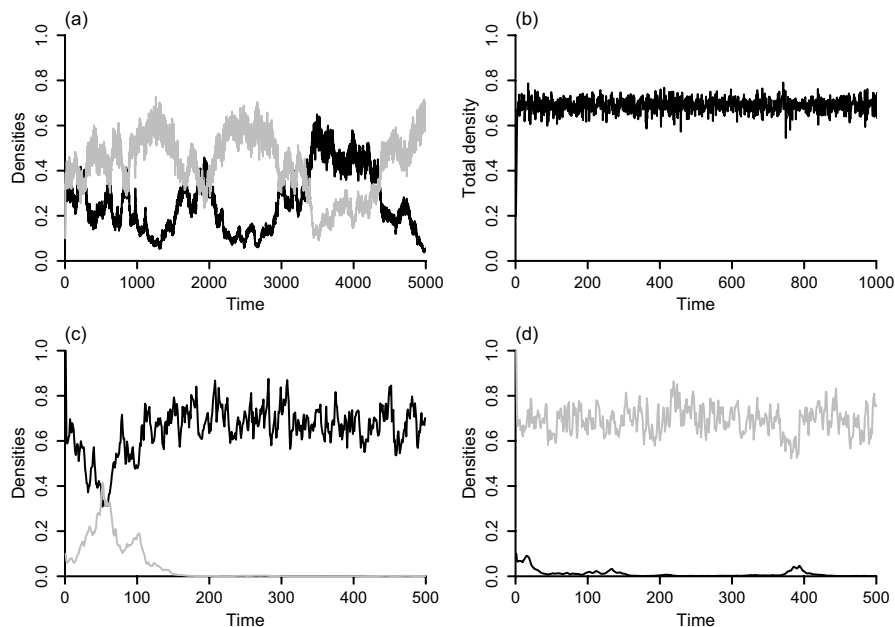
FIGURE 3 Stable coexistence and bistability in the modified Ricker model. (a) In the modified Ricker model (Equation 4.1 in Box 4), negative autocorrelation promotes stable coexistence. (b) The sum of two coexisting species in (a) shows smaller temporal fluctuations than the case with a single species in (c, d). (c, d) Positive autocorrelation results in bistability where the initial condition determines the surviving species. Here, in Equation 4.1, we assumed $\exp(c_i)=2$, $d_i(t)=\exp[m_i+\delta_i(t)]$ and $\delta_i(t) = \rho\delta_i(t-1) + \sqrt{1-\rho^2}s_ie_i$, where $m_i=0$, $s_i=0.1$ and e_i is a random variable of a normal distribution where the mean and variance are 0 and 1, respectively. The autocorrelation parameter $\rho=-0.5$ in (a, b) and $\rho=0.5$ in (c, d).
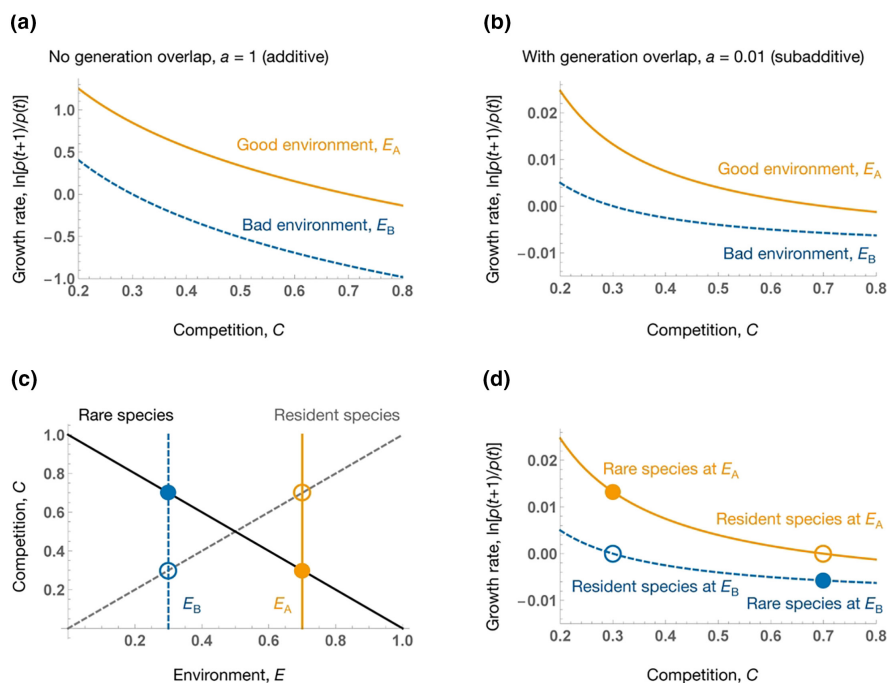

FIGURE 4 The storage effect in the lottery model. (a) When there is no generation overlap ($a=1$), environments have additive effects. The orange and blue curves indicate growth rates in good ($b_i=E_A=0.7$) and bad ($b_i=E_B=0.3$) environments, respectively, and competition is $b_1p+b_2(1-p)$. (b) With generation overlap ($a=0.01$), there is subadditivity. (c) When the good environment for a species is a bad environment for the other species ($b_i=1-b_j$, $i, j=1, 2$), competition for the rare species (the black solid line) and resident species (the grey dashed line) show contrasting patterns. (d) By combining (b) and (c), it is evident that the resident species experiences intense competition in good environments whereas the rare species enjoys weak competition in good environments.

loci on the same chromosome). For example, when two plant species are interacting with two types of soil microbiota and their associations are changing through generations, the plant–soil feedbacks (van der Putten et al., 2013) may be analysed by the two-allele-two-loci model with recombination (Gulisija et al., 2016). In this analogy, two alleles at the first locus represent two plant species, two alleles at the second locus are two types of soil microbiota, and recombination is a switch of the association between plants and soil microbiota (see also a recent study that shows the canonical plant–soil feedback model is equivalent to the special form of replicator equation studied in evolutionary game theory: Miller et al., 2022).

Other challenges to the incorporation of population genetic mechanisms into MCT and vice versa include allele dominance (Haldane & Jayakar, 1963), dominance reversal (Wittmann et al., 2017), maternal effects (Yamamichi & Hoso, 2017) and sex-limited traits (Reinhold, 2000) in population genetics. It is difficult to find an obvious ecological analogue for diploid inheritance. One possibility may be when pairwise interactions between individuals determine their performance. In which case, factors promoting the storage effect in diploid models (e.g. additive contributions of alleles to fitness) may also contribute to a storage effect in a two species model (e.g. resource exchanges between individuals contributing additively to fitness).

Recent studies also suggest that negative frequency-dependent selection not only maintains genetic variation, but also increases population-level performance (Takahashi et al., 2018). This effect is analogous to biodiversity-ecosystem functioning relationships where stable coexistence of diverse species due to niche partitioning enhances ecosystem-level productivity (Carroll et al., 2011). This raises the possibility that the storage effect may promote the portfolio effect, where biodiversity stabilises the biomass productivity of the community (Schindler et al., 2015). If temporal variation in the total biomass of communities is reduced by stable coexistence due to the storage effect, negative frequency-dependence through temporal fluctuations may affect ecosystem-level dynamics. This idea is not evident in classic frequency-based models (e.g. Figure 2) but may be tested by density-based models where total biomass in a community fluctuates temporally (e.g. Figure 3). For example, in the modified Ricker model (Equation 4.1 of Box 4), it is evident that coexistence results in more stable total biomass in the community (coexistence in Figure 3b results in ca. 30% of variance of total density of Figure 3c,d). Similarly, the diploid model of Schreiber (2020) shows that increasing genetic variation within a population results in a higher population density (Figure S2). It would be informative to examine how the temporal storage effect promotes coexistence of competing genotypes/species in systems that show the portfolio effect (e.g. salmon populations; Schindler et al., 2015).

ECO-EVOLUTIONARY DYNAMICS

So far, we have considered analogies between genetic and species diversity (Hairston et al., 1996; Vellend, 2016) and dynamics of genetic variation and competing species separately. However, recent studies suggest that ecological and evolutionary processes frequently operate on similar timescales (Hairston et al., 2005; Hendry, 2016; Messer et al., 2016; Schoener, 2011) and the maintenance of genetic variation and species coexistence may have eco-evolutionary feedbacks (Lankau, 2009, 2011; Lankau & Strauss, 2007; Schreiber et al., 2018; Vasseur et al., 2011; Yamamichi et al., 2022; Yamamichi & Letten, 2021). There is considerable scope for further exploration of an eco-evolutionarily mediated storage effect.

Consider a scenario where a competitively dominant species (species 1) that excludes two genotypes of the second species (species 2) when competing with either in isolation, but coexists with both genotypes when together through reversible mutations (Figure 5). This may be seen as a special case of Parrondo's paradox of game theory, where the combination of losing games results in a winning game (Cheong et al., 2019). For example, assume the number of juveniles at generation t, $b_i(t)$, in Equation 1.1 of Box 1 is determined by a normally distributed environmental variable $e(t)$ and the trait value of the species i, z_i, such that $b_i(t) = \exp\left\{ -[z_i - e(t)]^2 \right\}$. Then the species with the trait value that is equivalent to the mean value of $e(t)$, μ_e, has the highest fitness and can exclude other species (Figure 5a,b). However, even in the presence of a species with a higher fitness (species 1), if there are two genotypes with reversible mutations with a mutation rate m, then the species with two genotypes may be able to coexist with species 1 (Figure 5c,d):

$$N_i(t+1) = \left\{ 1 - a_i + \left[\sum_{k=1}^{n} a_k N_k(t) \right] \frac{b_i(t)}{\sum_{k=1}^{n} b_k(t) N_k(t)} \right\} N_i(t)$$
$$+ m[N_j(t) - N_i(t)], i, j = 2, 3.$$

$$(1)$$

Here we assumed that the trait values z_2 is on the opposite side of z_3 (Figure 5d), and thus the good environment for one genotype is a bad environment for the other genotype. Future work is needed to explore the conditions under which rapid evolution ensures stable coexistence via the temporal storage effect even in the presence of demographic stochasticity.

In addition, there are several studies that have considered the long-term evolutionary stability of the storage effect (Abrams et al., 2013; Kortessis & Chesson, 2021; Kremer & Klausmeier, 2017; Mathias & Chesson, 2013; Miller & Klausmeier, 2017; Snyder & Adler, 2011). Interestingly, these studies have come to different conclusions. Snyder and Adler (2011) showed
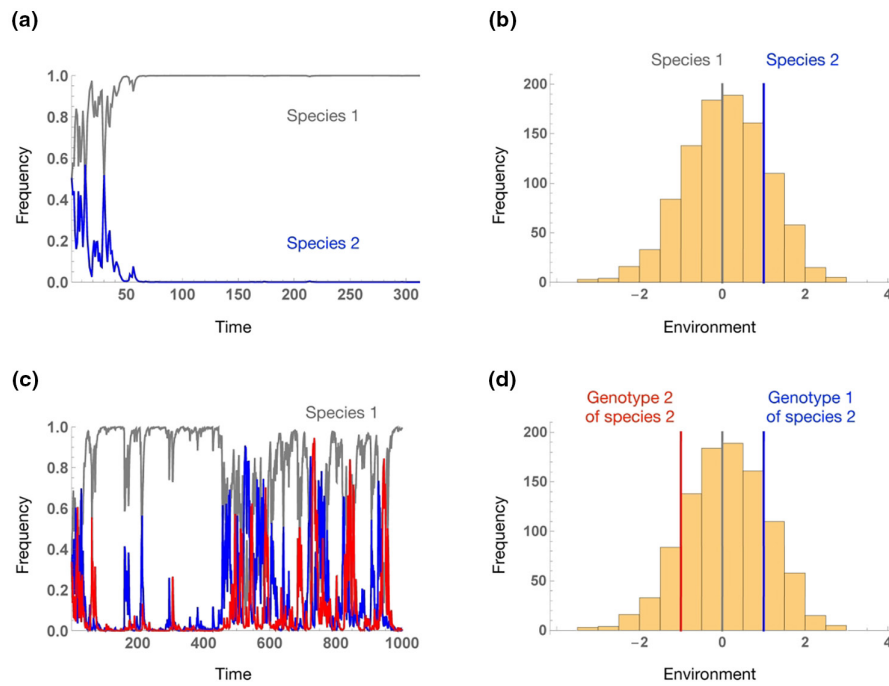
FIGURE 5 Intraspecific genetic variation can promote species coexistence via the temporal storage effect. (a) When species 1 (the grey line) has a higher fitness, it can exclude species 2 (the blue line). (b) Here we assume the environmental variable fluctuates according to a normal distribution with mean μ_e and standard deviation σ_e, and if the first species' trait value is closer to the mean of the environmental variable than the second species' trait, it has higher fitness. In this case, species 1's trait value is equivalent to the mean value of the normal distribution (i.e. $z_1 = \mu_e$). (c) When there are two genotypes in species 2 (the blue and red lines) and they are connected by reversible mutations (Equation 1), it can promote species coexistence with species 1 (the grey line). (d) We assumed that the trait values of species 2 is −1 (red) and 1 (blue). Parameter values are $n=3$, $z_1 = \mu_e = 0$, $\sigma_e = z_2 = 1$, $z_3 = -1$, $a_i = 0.5$ and $m = 0.01$.

that the storage effect is evolutionarily unstable, but other studies have demonstrated that the storage effect can arise via temporal character displacement (Abrams et al., 2013; Kortessis & Chesson, 2021; Mathias & Chesson, 2013; Miller & Klausmeier, 2017). It will be valuable to pursue a coherent theory on evolutionary stability of the storage effect with rapid evolution in future theoretical studies.

CONCLUSION AND FUTURE PERSPECTIVES

Despite considerable overlap in scope, theories in population genetics and community ecology have developed comparatively independent of each other (Figure 1). As a first step towards bridging this gap, we have shown that the lottery model in community ecology is equivalent to a classic population genetic model (with haploid inheritance and overlapping generations: Box 1). We have further argued that a synthetic treatment of community ecology and population genetics, leveraging underused techniques from each discipline, presents opportunities for novel insights. In particular, population genetics may benefit from analyses of IGRs and decomposition methods, while understanding how often species become rare in models of ecological communities may benefit from diffusion approximations and related techniques.

Although we have focused on the maintenance of variation in temporally fluctuating environments, there are many additional topics to be integrated in population genetics and community ecology. For example, it will be interesting to further develop theory of genetic/ecological drift in finite populations/communities resulting in transient neutral diversity with spatiotemporal fluctuations (e.g. O'Dwyer & Cornell, 2018). In addition, it should be possible to apply coalescent theory (Wakeley, 2009), sample-based theory of lineage convergence backward in time, to evolutionary community ecology with phylogenetics (Webb et al., 2002) to obtain null expectations under neutrality. Furthermore, we will be able to closely examine the similarities and differences between fixation indices (e.g. F_{ST}; Holsinger & Weir, 2009; Wright, 1951) and beta diversity (Anderson et al., 2011; Whittaker, 1960), as both of them are summary statistics of differentiation of local habitats. Also, it will be interesting to consider complex food web dynamics from a perspective of horizontal communities (Hofbauer & Schreiber, 2022) and how coexistence in large communities becomes possible with fine-tuning of the relevant interaction parameters (May, 1972). To this end, it should be possible to break the artificial border that has grown up between population genetics and community ecology. In conclusion, when it comes to understanding biodiversity, we have highlighted that community ecologists and population geneticists have much that they can learn from one another.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.