ENVIRONMENTAL PERTURBATIONS AND TRANSITIONS BETWEEN ECOLOGICAL AND EVOLUTIONARY EQUILIBRIA: AN ECO-EVOLUTIONARY FEEDBACK FRAMEWORK

Tim Coulson

Department of Zoology, University of Oxford, The Zoology Research and Administration Building, 11a Mansfield Road, Oxford, OX1 3SZ, UK

Email: tim.coulson@zoo.ox.ac.uk

Abstract

In this paper I provide a general framework for linking ecology and evolution. I start from the fact that individuals require energy, trace molecules, water, and mates to survive and reproduce, and that phenotypic resource accrual traits determine an individual's ability to detect and acquire these resources. Optimum traits, and their values, are determined by the dynamics of resources, aspects of the environment that hinder resource detection and acquisition by imposing risks of mortality and reproductive failure, and the energetic costs of developing and maintaining the traits – part of an individual's energy budget. These budgets also describe how individuals utilize energy by partitioning it into maintenance, development and/or reproduction at each age and size, age and size at sexual maturity, and the size and number of offspring produced at each reproductive event. The optimum energy budget and body size is consequently determined by the optimum life history strategy that maximizes fitness by trading off size- and age-specific mortality and development rates with any reproductive gains due to extending development and delaying the onset of reproduction. An eco-evolutionary feedback loop occurs when resource accrual traits evolve impacting the quality and quantity of resources that individuals accrue, leading to a new optimum body size and life history strategy and altered population dynamics that, in turn, impact the resource base. These feedback loops can be complex, but can be studied by examining the eco-evolutionary journey of communities from one equilibrium state to another following a perturbation to the environment.

KEYWORDS: body size evolution, dynamic energy budgets, global environmental change, integral projection models, life history theory, paradox of stasis, quantitative genetics, stochastic demography, Trinidadian guppy.

Introduction

In the lowland streams of Northern Trinidad, guppies (*Poecilia reticulata*) live in complex, stable, communities. They predominantly feed on abundant stream invertebrates of high nutritional quality that are also food for a number of other fish species. Guppies themselves are prey for predatory fishes, such as wolf fish (*Hoplias malabaricus*) and pike cichlids (*Crenicichla frenata*). Predation is the primary cause of death for guppies living in these communities, such that their populations are limited by predation. In response to this limitation, guppies have evolved streamlined bauplans, live in shoals, have high maximum swimming speeds, fast metabolic rates, are rather dully colored, have small sizes and low ages at sexual maturity, large litters of small offspring, and fast life histories (Reznick and Endler 1982, Reznick and Bryga 1987, Reznick and Yang 1993, Reznick et al. 2001, Travis et al. 2014). These traits have evolved to enable guppies to optimally detect, acquire, and utilize food in an environment where the risk of death in the jaws of a predator is near constant and high.

Above waterfalls, on the same streams where high-predation guppies are found, predatory fish are largely absent. Guppies in these streams live at high density in simpler, stable, communities, with only one major competitor, Hart's killifish (*Rivulus hartii*), which is also an intra-guild predator. The guppy populations are food-limited, the limiting resource is therefore food availability, and the primary cause of death and failure to breed is starvation. A consequence of this is that high-quality invertebrates are rapidly consumed and are largely absent, so that guppy diets contain a high percentage of low-quality food such as algae and bacteria, that are largely absent from the diets of high-predation guppies. Guppies adapted to these low predation environments have evolved a greater age and larger size at sexual maturity, brighter male coloration, a less-streamlined bauplan, reduced shoaling behaviour, altered mouth morphology, a lower metabolic rate, smaller litter sizes, larger offspring and a slower life history (Reznick and Endler 1982, Reznick and Bryga 1987, Reznick and Yang 1993, Reznick et al. 2001, Travis et al. 2014). These traits have evolved to enable guppies to detect, acquire, and utilize food in

a relatively safe environment compared to the high predation one, but where the major challenge is securing enough resources to thrive.

When high predation guppies are introduced to low predation environments, their population increases in size, the age, sex and phenotypic trait structure of the population changes, and they rapidly evolve, with the community moving from the high predation equilibrium to the low predation one. Because these changes are repeated across streams, they are predictable in that we know what will happen when guppies are released from predation (Reznick and Endler 1982, Reznick and Bryga 1987, Reznick and Yang 1993, Reznick et al. 2001, Travis et al. 2014).

What characterises the Trinidadian freshwater ecosystems when they are at ecological and evolutionary (quasi)-equilibrium in either the high- or low-predation state? The structure and genetic, phenotypic trait, size, age, and sex structure of all populations in the community show no persistent temporal trends with time. I consequently use the term 'equilibrium' to describe a stochastic but stationary state of populations and the community. This means there may be temporal fluctuations in the sizes and structures of populations within the community, but none will exhibit a long-term temporal trend (Lundberg, Ranta, and Kaitala 2000). If they did, some species would go extinct, and this does not happen. I use the prefix 'quasi' to acknowledge that some slow temporal patterns in genotype frequencies may occur in cases of slow co-evolution between species, but, that in general, natural systems frequently achieve states where statistics describing the state of each population with the community remains within bounds for protracted periods of time (Figure 1; Lewontin 1969, Bronstein, Dieckmann, and Ferrière 2004). A consequence of this is there will also be no persistent temporal trends in community size and structure, or energy and nutrient flows.

The existence of a (quasi)-equilibrium state raises a paradox. When systems are in (quasi)-equilibrium states, the means of all heritable phenotypic traits in all species are expected to be

at, or very close to, their optimal values, as otherwise evolution would be expected to occur and the system would not be at an evolutionary equilibrium. Phenotypic traits are defined as any attribute that can be characterised at the individual level, ranging from molecules within cells to lifetime reproductive success. In the wild, many traits including those that describe the timing of events such as birth, measures of body size, and lifetime reproductive success are under directional selection, are heritable, but do not evolve as predicted (Merilä et al. 2001, Estes and Arnold 2007, Haller and Hendry 2014, Rollinson and Rowe 2015, Bonamour et al. 2017). Instead they exhibit stasis that is consistent with the system being at equilibrium. The paradox is why do we predict phenotypic evolution but not see it? I address this paradox later in the paper.

An environmental perturbation, such as the loss of a predator species, leads to a period of transience within a community as population sizes and structures change (Hastings 2004; Georgelin, Kylafis and Loeuille 2015). In time, the system will achieve a new (quasi)-equilibrium state (Figure 1) (Brown and Vincent 1992, Lundberg, Ranta, and Kaitala 2000, Johansson and Dieckmann 2009). The observation of almost immediate evolution following a biotic or abiotic shift raises a second paradox. Evolution requires additive genetic variation within a population, but if phenotypic traits are at their optimum values, they are subject to stabilising selection, which should have eroded additive genetic variation (Crow and Kimura 1970). The evolutionary equilibrium attained by a system should consequently exhibit very low, or zero, levels of additive genetic variance. Yet populations in ecosystems in the wild in (quasi)-equilibrium states express substantial amounts of additive genetic variance for many traits (Crow and Kimura 1970, Kruuk et al. 2000). The maintenance of genetic variance is a second paradox that requires a solution if we are to understand why perturbed systems move from one evolutionary equilibria to another. I also consider this paradox.

The genetic diversity paradox has similarities with another problem that has long interested biologists – why do so many species coexist when they appear to share niches and rely upon the same resources (Chesson 1986, Wright 2002)? The coexistence problem is also relevant to the problems I address in this paper, and in particular why the ecological and evolutionary (quasi)-equilibria contain so many coexisting species.

Before reviewing properties of ecological and evolutionary equilibria, and considering ways to predict the ecological and evolutionary transients between contrasting stationary states following a biotic or abiotic change, I do two things. First, I consider how the different levels of biological organisation – alleles, genotypes, phenotypes – are linked by a number of fundamental processes (Figure 2) (Coulson et al. 2017). Second, I introduce the concept of resource accrual traits.

Parental alleles combine, through patterns of mate choice, to generate the distribution of offspring genotypes, which in turn develop into a distribution of offspring phenotypes traits. These traits determine individual abilities to acquire resources as a function of the environment in which they find themselves, which in turn determines continued rates of development and chances of survival, reproduction and dispersal at each age and size. Both the population dynamics, and the strength of selection that can alter the distribution of phenotypic traits, genotypes and alleles, are inevitable emergent properties of these rates. Recombination and mutation determine the distribution of alleles among individuals selected to be parents. The fundamental biological processes of mate choice; development; survival, reproduction, and dispersal; and mutation, can all be influenced by aspects of the biotic and abiotic environment. The biotic environment experienced by an individual consists of the numbers and attributes of all individuals it interacts with whether they are con- or hetero-specifics. These interacting individuals include its parents, who can use their attributes to influence offspring phenotypes via controlling the developmental environment via non-genetic inheritance.

Resource accrual traits are the set of traits associated with the detection and acquisition of resources required for life (Abrams and Chen 2002): energy, trace molecules and water required for survival, and mates necessary for reproduction (at least in sexually reproducing diploid species) (Brown et al. 2004). Within the set of resource accrual traits are resource detection traits such as the size and structure of sense organs and the brain, and resource acquisition traits such as foraging behaviours and aspects of morphology. I will argue that these traits are likely to be subject to stabilising selection, yet that individual heterogeneity in the types of resources individuals specialise on (Bolnick et al. 2007), act to maintain additive genetic variation underpinning these traits. Desirable resource accrual traits, and their optimum values, are specific to the environment in which individuals find themselves. For example, the traits expressed by high-predation guppies in high-predation environments are well-adapted to an environment where the limiting factor is predation and the primary cause of death is predation. In contrast, in the low-predation environments, guppies express traits that make them well-adapted to an environment where the primary cause of death is starvation and the population is food-limited.

In addition to optimising resource accrual traits, evolution also optimally energy utilisation to maximise fitness (Kooijman and Kooijman 2010). It does this by optimising the life history – age and size at sexual maturity, the number and size of offspring produced at each reproductive attempt, and life expectancy (Stearns 1976)– which is achieved via evolving an optimal energy budget which determines investment in maintenance, development, and reproduction, at each age and size (Hin and de Roos 2019).

I primarily focus on the guppies as they provide a well-characterised example of a general phenomenon: if the primary causes of death or failures to breed in a population are altered by a biotic or abiotic perturbation, so too is the limiting factor, the population dynamics (Schindler 1974, Sibly and Hone 2002, Rohr et al. 2003), selection, and the course of evolution (Walters

and Juanes 1993, Fishman and Willis 2008). Population size and selective regimes change rapidly in a focal species, and in interacting ones, and evolution selects for phenotypic traits and trait values that allow organisms to optimally detect, acquire, and utilize food given the primary causes of death and failures to breed in the environment in which species find themselves. These processes determine the transient dynamics between ecological and evolutionary (quasi)-equilibria.

In the remainder of this paper, I describe properties of ecosystems in ecological and evolutionary stochastic equilibria, before considering the biological conditions required for these equilibria to occur. While considering these equilibria I address the paradox of why so much genetic diversity is observed. I then address the paradox of stasis, before considering eco-evolutionary feedbacks as systems moves between ecological and evolutionary equilibria.

Characterising Populations at Ecological and Evolutionary Equilibria

I start by considering a single population. I define a population as being stationary and at a stochastic ecological and evolutionary equilibrium when both its size and genetic, phenotypic, sex, and age structure fluctuate within bounds but show no persistent temporal trends (Caswell et al. 2004). In formal demography, this equilibrium is a special case, as populations can achieve structural stationarity, yet can also change in size with time as the population grows at a constant stochastic rate (Tuljapurkar 1989). Because I require a stationary distribution of population sizes N_t, the special case I consider requires the long-run stochastic growth rate a to equal zero, where

$$a = \overline{\log(\lambda_t)} = \frac{1}{T}\sum_{t=1}^{T}\log(\lambda_t) \qquad (1)$$

with t being time (Tuljapurkar and Orzack 1980). The equation defines the long-run stochastic growth rate of the population as the arithmetic mean of the logged per-time step population

growth rates λ_t calculated across a time series of length T where $\lambda_t = \frac{N_{t+1}}{N_t}$. But how does this formulation relate to the ecological and evolutionary equilibria I describe above, where there is also no persistent temporal trend in allele and genotype frequencies, and phenotypic trait means and variances? Examining the determinants of λ_t helps answer this question.

I consider a population as consisting of individuals, each with a very large number of phenotypic trait and genotypic attributes. From these individuals, I can construct a multivariate distribution describing the number of individuals in each individual attribute (or structural) class at time t (Ellner et al. 2016). For example, in a very simple case where a population is structured by the individual attributes sex, age, weight, and genotype at a locus X, there may 23 individuals within the population at a particular point in time that are male, aged 35 years, weigh 82kg and express genotype *AA* at locus *X*, but only seven individuals that are female, aged 74, weigh 52kg with genotype *BB* at locus *X*. All other sex, age, weight and genotype classes will also contain a particular number of individuals (that could be zero). Over time, the numbers of individuals in each structural class can fluctuate (Ellner and Rees 2006), but as long as there are no persistent temporal trends in these time series of numbers, the population will be at a stationary equilibrium. It is possible to estimate the long-run stochastic growth rate for each structural class using equation (1) above; at ecological and equilibrium, these rates will all be zero (Tuljapurkar and Orzack 1980).

The per-time step growth rate of the entire population $\lambda_t = \frac{N_{t+1}}{N_t}$ can be expressed as $\lambda_t = S_t + R_t$ where S_t is the annual per capita survival rate, and R_t is the annual per capita recruitment rate (defined as the per capita production of offspring that are produced between times t and $t + 1$ that survive to enter the population at time $t + 1$ weighted by the relatedness of offspring to parents (Coulson et al. 2006)). If we ignore dispersal, change in population size over a time step is consequently caused by any difference in the numbers of individuals that enter the

population via birth, and the numbers that leave it via death. But what determines S_t and R_t at a particular time t? Both rates vary across structural classes (e.g. individual attributes), and with the environment (Leslie 1945, Caswell 2001). The values of S_t and R_t at any particular time t consequently depend upon the population's genetic, phenotypic trait, age and sex structure.

Survival, development, reproduction, mutation, recombination, mate choice, and genetic and non-genetic inheritance are all processes that can alter the population's structure between time t to $t + 1$ (Coulson et al. 2017). With the exception of genetic inheritance, all these processes can be influenced by aspects of the biotic or abiotic environment, and it is environmental variation that continually generates variation in population structure via impacting these processes (Figure 2). Structured demographic models based on Figure 2 can be constructed to capture the effects of the environment on each of these processes, and used to iterate distributions of population structure and size from one-time step to the next (Coulson et al. 2017).

Structured demographic models have been constructed for small numbers of individual attributes such as one or two genetic loci (Charlesworth 1994), one or two phenotypic traits (Easterling et al. 2000), age (Leslie 1945), or sex (Schindler et al. 2015). Despite a focus on only a small number of attributes, these models have provided significant ecological and evolutionary insight. Models consist of functions that capture the processes (Figure 2) that can alter distributions of individual attributes by moving individuals into and out of each structural class at a point in time (Ellner et al. 2016). For example, survival functions determine the proportion of individuals within a class that remain within a population, development functions determine the rates at which surviving individuals move between structural classes, reproductive functions determine the expected number of offspring produced by individuals within each structural class, while mutation, mate choice, and genetic and non-genetic

inheritance functions, determine the attributes of offspring and the structural classes in which they enter the population. I cumulatively refer to survival and reproductive functions as demographic functions, and mutation, mate choice, and genetic and non-genetic inheritance functions as inheritance functions. Any function, with the exception of those that describe genetic inheritance, can contain terms describing the influence of biotic and abiotic environmental drivers.

Structured demographic models do not need to include all levels of biological organization found within a population (Figure 2). For example, models have been constructed that structure populations by only age, genotype, or phenotypic trait, or by just two of these three levels of organization. When these simple models are constructed, they make assumptions about the processes that link levels of biological organization that are not explicitly incorporated into models (Traill et al. 2014). For example, models that include genotypes, but not phenotypes, assume that each genotype always develops with perfect fidelity into the same phenotype trait value, such that fitness can be directly predicted from the genotype without having to model phenotypic development (Charlesworth 1994). I primarily consider cases where populations are structured by alleles, genotypes and phenotypic traits (Coulson et al. 2011, Coulson et al. 2017).

As previously mentioned, each genotype (and consequently allele) will have a long run stochastic growth rate of zero at ecological and evolutionary equilibrium. There is another equivalence that individuals in particular structural classes will share: when genotypes are additive, genotypes within offspring cohorts are expected to have identical reproductive values (Sæther and Engen 2015). The reproductive value is the expected number of descendants of an individual in a particular structural class at time t, at some distant time point in the future (Fisher 1930, Caswell 2001). There are two ways reproductive value can be calculated for genotypes. First, by keeping track of the number of descendent copies of each allele within the

population with time (Barton and Etheridge 2011). Second, by recording the number and relatedness of descendants alive in future time steps of individuals that carried a particular allele at time t (Fisher 1930). Descendants are included in the calculation regardless of whether they carry alleles found in the original genotype themselves; genetic inheritance in sexually reproducing species means that descendants do not necessarily carry ancestral alleles. The two quantities are expected to be equivalent, although stochasticity in survival, reproduction and inheritance can result in an individual with a particular allele having very many descendants with none, or very few, carrying copies of it. Reproductive value can be calculated for any structural class – genotype, phenotype, age, sex. However, at evolutionary equilibria, reproductive values of offspring genotype or phenotypic trait classes are only equivalent when genotypes and phenotypes are additive functions of underlying alleles. This requires a little more explanation.

In structured models of sexually reproducing species, alleles do not form structural classes. Instead, these classes consist of genotypes or phenotypic traits (Charlesworth 1994, Childs et al. 2016, Coulson et al. 2017). The dynamics of alleles, and hence microevolution, can be determined from the dynamics of the number of individuals within genotypic classes. A genotype is considered additive, if its contribution to a phenotypic trait is determined solely by the sum of the contribution of each of its alleles to a phenotypic trait (Falconer 1960). If a phenotypic trait value is determined by an interaction between alleles at a locus (dominance) or by interactions between genotypes at different loci (epistasis), the assumption of additivity is violated. A consequence of this is that microevolution cannot be inferred from the dynamics of phenotypic trait values.

If all genotypes at all loci that contribute to a phenotypic trait are additive, then the dynamics of the phenotypic trait, the genotypes that contribute to the trait, and the alleles that constitute the genotypes, are asymptotically predicted by their reproductive values (Fisher 1930). Under

these circumstances, when different genotypes and phenotypic trait values expressed in offspring cohorts have different reproductive values, then microevolution will occur and allele frequencies will change. When they all have identical reproductive values, the population is at evolutionary equilibrium.

Reproductive value is a key concept in biology as it is the expected asymptotic fitness of an individual with particular attributes. The reproductive value of a structural class is determined by the life history of individuals with those attributes. A life history describes key events within life – age and size at sexual maturity, the timing of reproductive events, the size and number of offspring produced at each successful reproductive attempt, and the age and size at death (Stearns 1976). Life history strategies can consequently be characterized with size- and age-specific survivorship, development, fertility and inheritance schedules (Stearns 1976) – all of which can be calculated from the functions that constitute structured demographic models (Childs et al. 2004).

A life history strategy plays out on a per generation time scale, and can be described with per generation summary statistics such as generation length, mean lifetime reproductive success R_0, and life expectancy (Caswell 2001, Steiner et al. 2014, Tuljapurkar et al. 2009a). R_0 describes the rate of population growth per generation and is a per generation version of λ_t. In a deterministic population that exhibits no temporal trend in numbers $\log(R_0) = 0$.

R_0 can be calculated for individuals within each genotypic or phenotypic structural class (Tuljapurkar et al. 2009b). When additivity is assumed, individuals in all structural classes will have equal expected values of R_0 when the population is at ecological and evolutionary equilibria. When the assumption of additivity is violated, this will not necessarily be the case.

Biologists are often interested in the evolution of life histories, without focusing on evolution of the resource accrual traits that influence energy acquisition and the optimal life history

(Stearns 1976). To do this, life history strategies are assumed to be clonally and near perfectly inherited, rather than as arising as a consequence of underlying resource accrual traits (Childs et al. 2004). Under this assumption, the reproductive value of a life history will be associated with its long-run stochastic growth rate when measured in the presence of competing, clonally inherited, life histories. R_0 can usually (but not always) also predict which clonally inherited life history will grow to dominate all others (Metz et al. 1992, Metz et al. 1995, Ripa and Dieckmann 2013). Adaptive dynamics and game theory consequently rely on the assumption of clonal inheritance. The approach is useful as invasion approaches can be used to identify the evolutionarily stable life history strategy, and in particular the optimal value of life history trade-offs such as those between offspring size and offspring number. However, genetic architecture significantly influences ecological and evolutionary dynamics (Schreiber, Patel, and terHorst 2018), except in very specific cases (Geritz and Kisdi 2000, Metz and de Kovel 2013), and I consequently focus on cases where inheritance is not assumed to be clonal.

The conditions for a stochastic ecological and evolutionary equilibrium within a population – a long-run stochastic growth rate of zero for each structural class – are relatively straightforward, but they impose constraints on the values of reproductive value and the life history when additivity is assumed. Structured demographic models of populations at stochastic ecological and evolutionary equilibrium can be constructed from demographic, development, and inheritance functions that describe the rates of movement of individuals between structural classes from time t and $t + 1$. From these models, it is then possible to calculate long-run stochastic growth rates, reproductive values, temporal dynamics of the number of individuals, and descriptors of the life history for each class (Coulson et al. 2011, Coulson et al. 2017).

Structured demographic models provide a remarkably powerful tool to study the dynamics of populations, allele and genotype frequencies, and phenotypic trait distributions. The properties

of models at ecological and evolutionary equilibria are also well understood. However, for these equilibria to be achieved, particular conditions are necessary.

Conditions Required for Ecological and Evolutionary Stationarity

A long-run stochastic growth rate of $a = 0$ in a single species population requires density-dependence: a pattern that describes a decline in the per time step population growth rate λ_t as population size increases (Engen and Sæther 1998). Density-dependence occurs when a direct species interaction, such as predation, herbivory, or rarity of a resource species, limits a population's growth rate (Hassell 1975). Populations are consequently limited by aspects of the environment that prevent organisms detecting, acquiring and utilizing sufficient resources to survive and reproduce (Murray 1982). Limiting factors determine key causes of mortality or failures to breed within a population (Stearns 1976, Gaillard et al. 2000). For example, prey species that are predator-limited are limited by their ability to accrue resources while avoiding predation.

Ecologists have long been interested in how species that rely upon the same resources or limiting factor can coexist (Gause 1932). The general solution to this problem is that coexistence of competing species occurs when individuals within a species compete more strongly for a resource than individuals between species. In contrast, if interspecific competition is stronger than intraspecific competition, then the better competitor species will drive the other extinct (MacArthur and Levins 1967).

Four different mechanisms can contribute to the relative strengths of intra- (density dependence) and inter-specific competition for a resource or limiting factor. They act by either increasing the strength of intraspecific competition or by reducing the strength of interspecific competition (Chesson 2000b). The first mechanism, termed density-fitness covariance, does the former. It describes any mechanism that acts to increase the strength of intraspecific

competition relative to interspecific competition, such that each population increases in density when its numbers drop (Chesson 2000a). An example of this is when competing species utilise the same resource, but are segregated in space, such that they tend to compete with conspecifics rather than with hetero-specifics. The second set of mechanisms is termed "stabilising" and work by decreasing the strength of interspecific competition by ensuring each species has a refuge that protects it from extinction (MacArthur and Levins 1967). An example of a stabilising mechanism is two species that do not have completely overlapping niches, but instead partition some resources or limiting factors between themselves. The third coexistence mechanism is termed the storage effect, which occurs when different species respond to environmental variation in space or time in contrasting ways, with different species being more competitive in some types of environment than others (Warner and Chesson 1985). For example, one species may be a better competitor in winter, while the other may gain an advantage in summer. The final mechanism is termed relative non-linearity where different species benefit in different ways from fluctuations in the abundance of the limiting resource via non-linear effects of environmental variation on their population growth rates (Chesson 1994). These last two mechanisms can contribute to coexistence when they act to increase the strength of intraspecific competition to a greater extent than they increase the strength of interspecific competition.

To incorporate these ecological coexistence mechanisms into demographic models it is necessary to construct a model for each interacting species, and to couple them (Adler et al. 2010, Bassar et al. 2017). This can be achieved by making the demographic, development, or inheritance functions of each species a function of the size or structure of both the focal species and of the competitor species. Such models capture the indirect effects of two species competing for a resource or other limiting factor; the resource or shared predator are not explicitly included in models. Direct effects can be incorporated into models by formulating

demographic, development, and inheritance functions of focal species to be functions of the size and structure of interacting resource or consumer species on neighbouring trophic levels (Lachish et al. in press).

Ecological coexistence of multiple species requires direct interactions to limit each population such that its long-run stochastic growth rate is zero. This might sound like a big ask, but most species only interact strongly with a relatively small number of others, and when this happens, interacting species often coexist by limiting one another (Allesina and Tang 2012). Consider, for example, the case of the lynx and snowshoe hare, where both species cycle, with the predator dynamics lagging a quarter of a cycle behind that of the prey (Keith and Windberg 1978). The predatory lynx is limited by availability of the snowshoe hare prey, particularly in periods following high lynx abundances. In contrast, the hare is limited by lynx predation, particularly when lynx are abundant. The strength of these limiting factors fluctuate (reasonably) predictably with time, and the two populations cycle. Their long-run stochastic growth rates are both zero, but the numbers of both species cycle, in an endless entwined pattern, where each species limits the other, at least some of the time (Krebs et al. 1986). Because many limiting factors are biotic, it appears that ecosystem stability may be the norm, particularly when limitation of each population operates primarily via a small number of strongly interacting species.

The case of the lynx and snowshoe hare is a special one, and few systems are this simple. However, different species that share a resource or limiting factor are able to coexist via one or more of the mechanisms described above because they have adaptations that allow them to do so. In particular, different species may have adaptations that increase their fitness by making them specialists in particular environments (e.g. the storage effect) or by allowing them to utilise a unique resource that is unavailable to individuals of competitor species (e.g. a stabilising mechanism) (MacArthur and Levins 1967, Warner and Chesson 1985). Successful

species are often those that have been able to innovate in a way that allows them to utilise a previously unobtainable or under-utilised resource.

Rotifers feeding on algae provide a particularly interesting example of how phenotypic variation that allows adaptation to specific environments permits coexistence. The coupled dynamics of lynx and snowshoe hare provide an example of Lotka-Volterra predator-prey dynamics. Algae-rotifer dynamics deviate from such classic predator-prey expectations, with the predatory rotifer population lagged a half cycle, rather than the expected quarter cycle, behind that of their prey (Yoshida et al. 2003). The reason for this is that the algae come in two different phenotypic forms – clumpers and soloists. The two forms are clonal, and rarely reproduce sexually. They consequently act like two different species, even though they are in fact two genetically distinct clones of the same species. Individuals of the soloist clones have high fitness when the predators are rare. They can grow quickly, efficiently utilising abundant resources, and they outcompete the clumper clone. Survival is high, as rotifers are rare, and the population of soloists increases rapidly. The fitness of the soloist individuals starts to decline as predator numbers increase, and their population becomes predator limited. Rotifer numbers increase because the soloists make easy prey. However, the decline of soloists is simultaneous with an increase in the fortunes of the clumpers. Individuals of this clone band together into groups that are too large to be easily predated. They are not as efficient at turning resources into new clones as the soloists are, but when soloists are largely absence, such inefficiency is not an issue. As the clumpers dominate, the predatory rotifer population starts to decline as accessible prey abundance declines, and the time of the soloist dominance comes around once again. The two clones are able to coexist because the clumper has an adaptation that favours them in the high predation environment, while the soloists dominate in a low predation environment (Hiltunen et al. 2014). Population limitation of the two clones via resource limitation and predation allow coexistence of different phenotypes: the two clones coexist via

the storage effect which is facilitated by the adaptive ability to clump or not. Mechanisms such as this must be abundant in nature give so many species coexist.

The algae-rotifer system provides a link between coexistence of two species that share a predator but cannot reproduce, and the maintenance of genetic variation in sexually reproducing diploid species. The observation is particularly useful, as it reveals that the mechanisms that allow ecological coexistence of species in communities at equilibrium, may also contribute to evolutionary equilibria – another problem that needs solving if we are to understand stationary ecosystems.

Trivial evolutionary equilibria occur when all genetic variation is eroded such that all individuals are genetically identical (Wright 1969, Crow and Kimura 1970). However, such equilibria are not informative when considering the types of evolutionary transients observed in Trinidadian freshwater streams when predators are removed and the community moves between stationary states quite rapidly. More interesting equilibria maintain additive genetic variance. For this to happen, either stabilising selection and mutation-selection balance, a particular form of phenotypic plasticity, or frequency-dependent selection, must be in operation (Gillespie 1994). But how are these related to the coexistence mechanisms that ecologists focus on when considering species coexistence?

The strength of selection is determined by the association between phenotypic trait values and survival and reproduction (Fisher 1930, Price 1970). It is a within generation process, most easily measured over a time step using viability and fertility differentials (Lynch and Walsh 1998). How selection translates to the underlying genotypes and alleles is determined by the genotype-phenotype map that determines how phenotypic traits develop. Directional selection requires increasing or decreasing functions between phenotypic trait values and survival and reproduction, while stabilising selection requires humped-shaped associations, where the highest survival or reproductive rates are observed at intermediate phenotypic trait values

(Barton and Partridge 2000). Many evolutionary models assume simple additive genotype-phenotype maps described in the previous section that allow microevolution to be inferred directly from the dynamics of the phenotypic trait. This assumption is known as the phenotypic gambit (Lynch and Walsh 1998).

If the phenotypic gambit is assumed (and frequency-dependence is not operating), evolutionary equilibria require stabilising selection. Yet stabilising selection (as well as directional selection) erodes additive genetic variance unless some other process replaces it. When selection is weak (i.e. the hump of the association between the phenotype and fitness is quite flat), mutations can generate novel additive genetic variance at a rate that counters losses due to selection in a process termed selection-mutation balance (Bürger and Lande 1994).

Phenotypic plasticity occurs when the same genotype can generate different phenotypes in different environments (Pigliucci et al. 2006). If multiple genotypes can generate the optimal phenotypic trait value, each genotype will have maximal fitness and will be able to coexist.

The third process that can maintain additive genetic variance is frequency-dependent selection (Ayala and Campbell 1974). This occurs when a phenotypic trait value, and the underlying genotypes and alleles, experience higher survival and reproductive rates the rarer they become, such that they increase in frequency when rare. There are a number of processes that can generate frequency-dependent selection including heterozygote advantage, disassortative mate choice, spatial variation in the optimum phenotypic trait value, and heritable individual specialisation in resource use or limiting factor (Hartl et al. 1997). This last process occurs when the strength of competition increases with phenotypic similarity between competing individuals, with coexistence of individual variation being facilitated by the four coexistence mechanisms that operate at the species level (Bassar et al. 2016). For example, fitness-density covariation can occur when individuals with different phenotypic trait values feed on the same resources but in different locations – i.e. there is small-scale genetic variation underpinning

phenotypic variation. Stabilising mechanisms occur when populations consist of individual specialists that exhibit different foraging phenotypes and feed on different resources. In the Cocos Island finch, some individuals exclusively forage on seeds and invertebrates found on the ground, while others forage solely on arboreal insects, rarely venturing onto the ground (Werner and Sherry 1987). When survival, reproductive, or development rates of individuals with different phenotypic trait values are impacted by environmental variation in different ways, then the storage effect can occur, and depending upon the way that this environmental variation impacts demographic, development or inheritance functions, relative non-linearity can also arise (Warner and Chesson 1985, Chesson 1994, 2000a).

The same processes can consequently maintain genetic diversity within a population, and species diversity within a community. And when these processes are operating, ecological and evolutionary equilibria can be achieved. Each species, and each structural class in each population has a long-run stochastic growth rate of zero. At these equilibria, a number of other properties of stationarity may be observed, included equivalence of reproductive values of genotypes in the structural classes of offspring, and equivalent mean lifetime reproductive successes of individuals regardless of their phenotypic trait values. But such patterns are not always observed, and this conveniently leads me to the paradox of stasis.

A solution to the paradox of stasis

When the phenotypic gambit is assumed, phenotypic variation between individuals can be partitioned into a contribution attributable to additive genetic variation (Falconer 1960, Lynch and Walsh 1998). This can be estimated by statistically modelling phenotypic variation as a function of relatedness between individuals (Kruuk 2004). The ratio of the additive genetic variance of a phenotypic trait, to the variance of the trait itself, is the narrow sense heritability, h^2. The closer h^2 is to one, the larger the proportion of phenotypic variance that is attributable to additive genetic differences between individuals. When $h^2 = 0$, then none of the phenotypic

variation is attributable to additive genetic differences between individuals. The phenotypic variance that is not attributable to the additive genetic variance can be partitioned into various other contributions, but the one I focus on is the environmental variance. I assume that an individual's phenotypic trait Z_i is equal to the sum of an additive genetic contribution A_i (termed its breeding value) and an environmental component E_i such that $Z_i = A_i + E_i$ (Lynch and Walsh 1998).

In populations at evolutionary stasis, distributions of phenotypic traits are stationary and show no persistent temporal trends in their means or variances (Lande 2009). If additivity is assumed, and they are heritable (e.g. $h^2 > 0$), this means they should not be subject to persistent directional selection (Merilä et al. 2001, Estes and Arnold 2007, Haller and Hendry 2014, Rollinson and Rowe 2015, Bonamour et al. 2017). Paradoxically, many size-related traits, such as body mass in fish (O'Sullivan et al. 2019), and horn length and antler size in ungulates (Kruuk et al. 2002, Traill et al. 2014, Coulson et al. 2018), are heritable, under directional selection, but do not evolve as predicted (Merilä et al. 2001). Individuals with larger trait values have higher reproductive values, and greater values of R_0, but they have long-run stochastic growth rates of $a = 0$. Structured demographic models that do not explicitly incorporate evolution, capture these dynamics well (Traill et al. 2014). These models predict no change in mean body size with time, even though the trait has an estimated non-zero heritability from both observation and from model predictions (Coulson et al. 2010). Put another way, evolution should occur, but the size-related traits are in fact at evolutionary equilibria. Why does this happen? In short, the assumptions of additivity and the phenotypic gambit may be violated, the demographic functions that determine phenotypic selection may be incorrectly characterised, or the non-zero heritabilities may be an illusion. I argue here that, for size-related traits exhibiting stasis, the assumption of the phenotypic gambit is violated. However, to understand

why, it is useful to address a question that is yet to be satisfactorily answered: why are organisms the size that they are (Smith and Lyons 2013, Bhat et al. 2020)?

Body size is a fundamental component of life history. Within a species, individuals that are able to grow to large sizes are typically able to invest proportionally more energy in reproduction than those that grow to smaller sizes. Such within-species hyper-allometric scaling of reproductive investment is widespread, and may be universal (Barneche et al. 2018). Achieving large size is consequently desirable because it results in a fitness return via an increase in reproductive output. But if this is the case, why are not all species large? There is a risk to individuals of growing to large sizes before starting reproduction: development takes time, and delaying reproduction to older ages increases the risk of death before sexual maturity is reached (Blanckenhorn 2000). There is consequently a time to maturity-reproductive output trade-off that is determined by the associations of body size with survival, reproductive output, and development rate throughout the life course (Childs et al. 2004, Bhat et al. 2020). At some point on this trade-off, fitness will be maximised, and that determines size and age at sexual maturity. The optimal age and size at sexual maturity, and adult body size, is consequently determined by the shape of age- and size-specific fitness and transition functions (Kentie et al. in press). Given this, the evolution of body size can be predicted by integrating across the entire life cycle assuming trade-offs are appropriately identified (Childs et al. 2004). Reproductive output can be divided into two other aspects of the life history strategy: offspring number and offspring size (Fleming and Gross 1990). These two quantities also trade-off against one another, with there being optimal values for both litter size and mean offspring size.

Rates of development are largely determined by the ability of individuals to acquire resources from the environment (Reznick et al. 2000). Individuals partition the energy they obtain into maintenance (staying alive), acquiring more resources, development, and reproduction (De Roos et al. 2003, Kooijman and Kooijman 2010, Smallegange et al. 2017). The way that

resources are partitioned varies with age and size. The optimum body size and life history strategy are achieved by adopting a specific energy budget that partitions energy into each component of the life history at each age and size (Bhat et al. 2020). There is consequently a very close association between energy budgets and life history; this has led some authors to redefine fitness in terms of energy (Brown et al. 1993). Although at one level such an approach is appealing, it is inconsistent with standard evolutionary theory where selection, and fitness, are strictly defined in terms of numbers of descendants produced (Fisher 1930). Energy accrual needs to be linked to survival, development, reproduction, and inheritance to understand body size evolution (Bhat et al. 2020).

Individuals within populations compete for energy in the presence of limiting factors determined by the primary causes of death and failures to breed (Berryman 2004). For example, if prey (food) availability limits a predator population, individual predators compete over prey. In order to be competitive at predation, individuals need to express phenotypic traits that aid successful prey capture and consumption. Such traits could include camouflaged pelage, fast running speeds, weaponry associated with killing prey, and an ability to consume prey quickly. Selection is consequently expected to operate most strongly on phenotypic traits associated with prey capture and consumption as prey availability limits the population. In contrast, prey living in a predator-limited population are selected to acquire food resources without being predated. They experience selection for the accrual of enemy-free energy. In general, selection is expected to operate most strongly on traits associated with the accrual of energy given a population's limiting factors and the primary causes of death and failures to breed.

Those individuals with phenotypic trait values that are well-matched to the environment in which they find themselves are better able to accrue resources than those with less optimal phenotypic trait values (Charlesworth 1989). They consequently grow faster, to larger age-specific sizes, have lower age-specific mortality rates, and higher rates of age-specific

reproductive output. Those individuals that accrue most resources consequently perform well at all aspects of life compared to those that accrue fewer resources, and this heterogeneity in resource accrual between individuals can mask life-history trade-offs (Van Noordwijk and de Jong 1986, Metcalf 2016). A focus on resource accrual traits is consequently likely key to understanding how individuals obtain utilise energy in as an optimal way as possible to optimise life history and energy budgets, and maximise fitness (Bhat et al. 2020).

We can break down the accrual of resources into two separate processes: detection and acquisition. The senses, and the ability to process the information they reveal, are associated with the detection of resources, while many behaviors and some aspects of morphology are associated with their acquisition. The optimal set of phenotypic traits, and their values, associated with the detection and acquisition of resources will vary as a function of the population's limiting factor and the primary causes of death and failures to breed.

Once resources are accrued, they need to be utilised. To do this, at each age and size, individuals need to allocate the resources they have accrued to maintenance, acquiring more resources, development, and reproduction (Kooijman and Kooijman 2010), in a manner that is expected to maximise their reproductive value via optimising the life history (Goodman 1982, Bhat et al. 2020). This is a hard-to-solve state-dependent decision-making problem that is constrained (McNamara and Houston 1996). Life history constraints mean that the total amount of energy an individual can allocate to a particular activity remains within bounds. For example, a long-lived iteroparous species with low reproductive effort, cannot suddenly switch strategies and invest all its energy into a single reproduction event, sacrificing its own survival. Energy budgets are plastic, but within limits that are set by past fluctuations in energy availability that populations have adapted to (DeWitt et al. 1998). One of the most pernicious effects of environmental change occurs when it alters resource availability outside the historical

bounds that organisms can cope with via plasticity, and does so sufficiently quickly that species cannot adapt quickly enough to avoid extinction.

Phenotypic traits associated with resource detection, acquisition and utilisation are likely subject to stabilising selection. This is because a trait value below a particular threshold will likely carry survival or reproductive costs as it makes it challenging to accrue resources, while an over-engineered trait carries a cost. For example, consider eye sight in Mexican cavefish. Vision can be critical for detecting predators, mates, and energy. Invest too little in developing vision, and the risk is an early death or a failure to find a mate. However, vision is expensive, commanding up to 15% of an individual's energy budget (Moran et al. 2015). Visual acuity beyond being able to observe a mate, a predator, or food, is over-engineered and carries an energetic cost, and this is why the loss of cave fish vision in predator-free environments is adaptive. There is consequently a sweet spot, where vision is good enough to thrive, but not too good to be too expensive. Individuals with trait values at the sweet spot will acquire most resources and get the most out of them given the limiting environment, are expected to develop at a faster rate, and will have highest survival and reproductive rates, while those with smaller or larger values will achieve smaller sizes and have lower expected fitness (Figure 3).

If the resource accrual traits are heritable (and random mating is assumed), individuals with non-optimal resource accrual trait values and small body sizes will be expected to produce offspring that also have non-optimal trait values and small body sizes. In contrast, those individuals with resource accrual traits at the optimal value will be more likely to produce offspring that resemble them in these traits. Body size will appear to be heritable and subject to directional selection (Figure 3), but will not evolve to large values as the mean of the resource accrual trait will be at the optimal value when the population achieves evolutionary equilibrium. In addition, life history trade-offs will be hard to detect, because individuals with more optimal resource accrual traits and energy budgets acquire more energy and utilise it more

effectively in development and reproduction than those with less optimal trait values (Van Noordwijk and de Jong 1986).

For the arguments above to hold, genetic variation needs to be maintained in the resource accrual trait. These traits may be determined by many loci of small effect, which means additive genetic variation is lost relatively slowly (Lande 1982). Selection-mutation balance could theoretically contribute to the maintenance of genetic variation for resource accrual traits in such a scenario.

Frequency-dependent selection, operating via individual heterogeneity in resource use (Svanbäck and Bolnick 2006), could also maintain genetic and phenotypic variation via fitness-density covariance, stabilising mechanisms, the storage effect, or relative non-linearity (Bolnick et al. 2011). For example, if a new mutation generates a phenotypic innovation that allows an individual to utilise an under-utilised, or new, resource, that individual will accrue more resources, grow quickly, have high survival, and produce many offspring. If some of this individual's descendants are also equipped to utilise the resource, the frequency of the new innovation will increase, but the novel resource being utilized will decline in abundance. Eventually the frequency of the new innovation will achieve an equilibrium point where it, and the resource, are in equilibrium. Random fluctuations in the biotic and abiotic environment can generate fluctuations in the numbers of genotypes and phenotypic traits, and this could generate frequency-dependent selection in resource accrual traits, contributing to maintain additive genetic variation.

It is possible that frequency-dependent and stabilising selection can operate simultaneously on resource accrual traits. If stabilising mechanisms contribute to the maintenance of genetic and phenotypic diversity, different phenotypic optima may exist among individuals that specialise on different resources. This would manifest as a flat-humped fitness function for the resource accrual trait when averaged across multiple time steps.

In this section I have argued that body size is determined by an interaction between breeding values A_i and the environmental component of the phenotype E_i such that body size $Z_i \neq A_i + E_i$ but rather $Z_i = A_i + E_i|A_i$ (Coulson et al. 2017). I propose that this is plausible, because A_i is in fact a breeding value for a resource accrual trait subject to stabilising selection that impacts body size by determining the quantities of resources accrued by each individual. In general, when a phenotypic appears heritable, is subject to directional selection, but does not evolve, it seems most likely that the assumption of additivity is violated. In some cases, the amount of resources accrued may be determined by body size. How might this affect evolution?

Body size as a resource accrual trait

In some instances, individuals with large body size are able to access more resources than those that are smaller. For example, large lions can prevent smaller members of the pack feeding on a kill, while large individuals of many species may be able to dominate smaller individuals in competition for a territory. In these cases it may be aggression that is the resource accrual trait, and body size is a consequent of how aggressive individuals are, but it does seem plausible that body size plays a role in resource accrual in some species. It certainly has the potential to play a key role as a resource accrual trait in seasonal environments where resource availability varies within a year.

The long run stochastic growth rate can be approximated as

$$a \sim \log(\bar{\lambda}_t) - V_{E,t}$$

where the first term is the log of the mean of the per time-step population growth rates, and the second term, $V_{E,t}$, is a function of the logged variance in the per time-step population growth rates (Lande et al. 2003). When $a = 0$, then obviously $\log(\bar{\lambda}_t) = V_{E,t}$. Mean fitness can consequently be increased when evolution operates on traits that either increase $\log(\bar{\lambda}_t)$ or decrease $V_{E,t}$ (Lande et al. 2017). Body size, hibernation, and migration are all traits that can

evolve to decrease $V_{E,t}$ in seasonal environments. For example, individuals of large size of warm-blooded species have a higher body mass to volume ratio than their smaller counterparts and consequently use relatively less energy to keep warm in cold environments (Coulson et al. 2001). A consequence of this is they may be able to survive winters more easily at higher latitudes than smaller individuals. Bigger individuals can also store larger fat reserves than smaller individuals to utilise during winter when energy is scarce. Large body size may consequently allow non-hibernating species to exist in areas where smaller competitor species cannot survive, thus accessing resources that are only available to them. However, the flip side to this, is that large size also requires more energy for maintenance (Brown et al. 1993, West et al. 1997), so resources must be sufficiently abundant during the summer months for individuals to accrue sufficient resources to lay down enough fat to survive the winter. It is possible that productivity in the growing season, and the harshness of the winter season, may both select for larger size within species as distance to the poles decreases, a phenomenon termed Bergmann's rule. It is also possible that climate change resulting in shorter and warmer winters size may allow smaller individuals to survive, leading to a reduction in body size within populations (Ozgul et al. 2009).

In cases where body size is itself a resource accrual trait, it may be additive, and may evolve as predated by evolution. Evidence for this comes from the observation that when body size is selected for in artificial settings it can evolve as predicted using methods from quantitative genetics. This insight might help explain why quantitative genetics so often works well in artificial environments but fails to do so in natural ones (Merilä et al. 2001).

In artificial environments, energy is easy to detect and to acquire *ad libitum*. Selection is consequently largely relaxed on resource accrual traits, but is instead targeted at phenotypic traits we consider desirable. Only those individuals with desirable trait values are permitted to breed. This targeting selects for individuals that budget the largest proportions of the energy

they accrue to the traits we desire. Artificial selection consequently selects for particular energy budgets that result in the traits we wish to evolve.

In the above sections I argue that populations and communities achieve ecological and evolutionary quasi-equilibria for protracted periods of time over which species composition remains constant. I then explain the set of conditions required for these equilibria to be attained. Next, I address the issue of the paradox of stasis, whereby traits that are at evolutionary equilibrium apparently should not be. How can we construct models of the phenomena I have covered?

Population models of ecological and evolutionary stasis

In the section "**Characterising Populations at Ecological and Evolutionary Equilibrium**" I briefly explain that models can be structured to track the dynamics of distributions of individual attributes based on functions that describe associations of these attributes with survival, reproduction, development, and inheritance. I now expand on these earlier comments.

Structured demographic models can be constructed in discrete or continuous time. Discrete- and continuous-time modelling has proceeded largely independently, but has arrived at remarkably similar conclusions. Both approaches combine demographic, development, and inheritance functions to track the dynamics of distributions of genotypes and phenotypic traits (Figure 4). Models can be structured by structured class or individual-based (e.g. Dunlop, Heino and Dieckmann 2009, Romero-Mujalli, Jeltsch and Tiedemann 2018).

Discrete time models called integral projection models (IPMs) of phenotypic trait distributions were initially developed by Easterling et al. (2000). Since then, models have been extended to incorporate explicit genotype-phenotype maps (Coulson et al. 2011, Childs et al. 2016, Coulson et al. 2017, Rees and Ellner 2019), frequency-dependence (Schindler et al. 2015), density-dependence (Rees et al. 2014), abiotic variation (Ellner and Rees 2006), and species

interactions (Adler et al. 2010, Bassar et al. 2017, Lachish et al. in press). These models have been used to study the dynamics of populations and distributions of phenotypic traits, breeding values and additive genotypes, non-additive genotypes, and life history strategies. The work has identified circumstances when eco-evolutionary feedbacks occur (Coulson et al. 2011). In these models, fitness, population dynamics and evolution are all emergent properties of the demographic, development and inheritance functions used to construct the models.

Continuous time models that track distributions of individual attributes have started to receive significant attention more recently. For example, DeLong and Gibert (2016) introduced Gillespie eco-evolutionary models that are a form of continuous time individual-based model, and Doebeli et al. (2017) argue that evolutionary models developed from birth and death rate functions to track distributions of heritable phenotypic traits are useful because fitness is an emergent property that does not need to be defined. Along similar lines, Lowe et al. (2017) argue that demography and population genetics need explicitly combining to understand eco-evolutionary dynamics.

Because the two separate literatures have arrived at the same conclusions, it suggests that models based on demographic, development and inheritance functions offer great promise in providing novel ecological, evolutionary, and eco-evolutionary insight. I now focus on discrete time models that track distributions of alleles, genotypes, breeding values, and phenotypes for three reasons. First, the theory is more developed than for continuous time models, second, the approach has gained more traction amongst empiricists, and third, I am more familiar with this approach than with continuous time equivalents. However, the conclusions will extend to continuous time models.

IPMs are of the general canonical form:

$$N_{t+1}(\mathbf{Z}') = \int [D_t(\mathbf{Z},\mathbf{\Theta})S_t(\mathbf{Z},\mathbf{\Theta}) + H_t(\mathbf{Z},\mathbf{\Theta})R_t(\mathbf{Z},\mathbf{\Theta})]N_t(\mathbf{Z})d\mathbf{Z}$$

where $\mathbf{Z}$ is the set of individual attributes being iterated forwards, $N_t(\mathbf{Z})$ is the distribution of these attributes, the functions $S_t(\mathbf{Z}, \mathbf{\Theta})$ and $R_t(\mathbf{Z}, \mathbf{\Theta})$ are demographic functions describing how the individual attributes and the environment $\mathbf{\Theta}$ at time t influence the rates of survival and reproduction respectively, and the functions $D_t(\mathbf{Z}, \mathbf{\Theta})$ and $H_t(\mathbf{Z}, \mathbf{\Theta})$ are transition functions describing development and inheritance of the individual attributes. These functions are probability density functions such that they can move individuals between individual attribute classes but they do not alter the size (or volume) of the distribution. The transition functions can become quite complicated when different attributes included in Z have different development and inheritance rules (Schindler et al. 2013, Childs et al. 2016, Coulson et al. 2017). Feedbacks occur when properties of $N_t(\mathbf{Z})$ contribute to the environment $\mathbf{\Theta}$ either directly or indirectly via interactions with other species.

How can models be constructed that achieve ecological and evolutionary equilibrium? First, these models need to iterate forward the dynamics of genotypes and phenotypic trait distributions. Demographic functions describe the growth rate of each part of the distribution being iterated but do not move individuals between categories; transition functions – e.g. development and inheritance functions – describe these movements (Coulson 2012). Second, models need to include ecological feedbacks such as species interactions, and stabilizing or frequency-dependent selection operating on genetic variation.

Demographic and transition functions are consequently central to constructing structured models of ecological and evolutionary dynamics and feedbacks. A key challenge in constructing models for multivariate distributions is that different types of individual attributes, or structural classes, have different development and inheritance properties, and consequently require different functional forms for their transition functions (Childs et al. 2016, Coulson et al. 2017) (Figure 4). Genotypes and breeding values, for example, remain fixed throughout life such that development functions simply keep individuals in the same class throughout life

(Charlesworth 1994). For models containing these attributes to achieve a non-trivial evolutionary equilibrium, demographic functions need to capture a process such as frequency-dependent selection that maintains additive genetic variance, while simultaneously preventing directional evolution occurring indefinitely. Transition functions are also required to capture genetic inheritance, and the formation of offspring genotypes and breeding values as a function of parental values and patterns of mate choice (Figures 4(A-D)).

If I assume that resource accrual traits are additive and heritable and retain a fixed shape throughout life, but scale with body size, demographic and genetic inheritance functions that are similar to those for genotypes and breeding values are required, but so too is a development function that specifies how the size of the trait changes across the lifespan via changes to the environmental component of the phenotype (Figures 4(E-H)). These development functions keep the breeding values or genotypes associated with the resource accrual traits constant throughout life, while allowing the trait to develop with age, via change in the value of the environmental component of the phenotype.

Traits that exhibit the paradox of stasis such as size-related traits at equilibrium, need to develop with age, may show directional selection, but are not specified with an additive genotype-phenotype map (Coulson et al. 2010). Large parents may produce large offspring, and traits may statistically appear to be heritable but do not evolve (Figures 4(L)). Traits such as this require demographic, development, and inheritance functions, but the inheritance functions do not need to explicitly include rules for genetic inheritance for the trait itself because these traits are emergent consequences of an individual's resource accrual trait value and the environment. Similarly, development functions can be specified to be determined by the value of resource accrual traits and the quantity of resources accrued (Lachish et al. in press).

The final trait type is life history traits such as size and age at sexual maturity. These traits are often referred to as latent traits, and they are only expressed once during an individual's life (Childs et al. 2016). If these traits are under genetic control, the underlying genotypes need to be tracked throughout life, with the trait only expressed at one point in time, determining when reproduction occurs for the first time. The genetic architecture underpinning the trait can be subject to selection when the trait is not expressed if the trait genetically covaries with phenotypic traits that are expressed and are subject to selection.

IPMs have been developed to track the dynamics of each trait type, but all trait types are yet to be combined into a single model. One way to do this would be construct a model of i) a resource accrual trait that is determined by a breeding value and an environmental component of the phenotype, ii) body size, where the development function is determined by the value of the resource accrual trait and the amount of resources accrued, and iii) age and size at sexual maturity is determined by a breeding value and an environmental component of the phenotype. An initial model might focus on a resource species and a consumer species. The resource accrual trait in the resource species would define the ability to escape consumption, while the resource accrual trait in the consumer species would define success at consuming resources.

In such a model where the initial conditions are away from the evolutionary and ecological equilibrium, the breeding values for the resource accrual traits will change each time step in a way determined by the covariance between breeding value and annual survival and reproductive rates at each age (Coulson et al. 2017). The dynamics of these traits will be accurately predicted by their per time-step selection differentials. Body sizes will change with time as the distribution of the resource accrual traits and the numbers of resources and consumers change. Body size dynamics will not necessarily be well-predicted by their per-time selection differentials. Neither will be the dynamics of age- and size at sexual maturity (Childs et al. 2011). In order to understand the dynamics of this trait it is necessary to understand how

evolution optimizes the trade-off between the risk of mortality prior to sexual maturity against any benefits of delaying reproduction to a later stage of development (Childs et al. 2004). The optimization of the trade-off maximizes reproductive value. A feedback now occurs: as reproductive value is maximized, age-specific survival and reproductive rates change, which means that the distribution of annual fitness changes, which alters the strength of selection on the resource accrual traits. However, eventually an ecological and evolutionary equilibrium will be achieved.

Transitions between equilibria

Sudden shifts in the environment $\boldsymbol{\Theta}$ be they biotic, such as the addition or removal of a species, or abiotic such as a volcanic eruption, can alter the causes of death or failures to breed in some species. These changes will alter predicted values of the demographic and transition functions. For example, the loss of a predator species may result in a shift from top-down to bottom-up regulation of a prey species (Figure 5(A)-(B)) reflected by a reduction in the influence of a predator population on survival, reproduction, development or inheritance of a focal species, coupled with an increase in the role of a resource species on these functions. Such a change in a limiting factor can result in rapid change in population size of affected species (Figure 1(A)), and alter selection pressures on phenotypic traits associated with resource accrual (Figure 5(a)-(B)) and utilization (Figure 5(C)). Novel selection on these traits can result in a shift in phenotypic trait means via plasticity, (Figure 1(B)), and a slower rate of evolution, altering the frequency of alleles associated with resource accrual traits. Evolution occurs at a slower rate to the initial change in population size, such that the long-run stochastic growth rate of the population rapidly returns to being close to zero following the initial environmental perturbation. The novel selective regime on resource accrual traits can alter the optimal form of associations between body size and survival, reproduction, development, and non-genetic inheritance, leading to evolution of the life history. Change in the life history may result in

additional novel selection pressures on resource accrual traits – a form of eco-evolutionary feedback.

If a change in limiting factor, population size, and selection pressures on resource accrual traits impacts the size of "keystone species" within the system, trophic cascades can occur where populations of other species within the ecosystem are impacted (Paine 1966, Bronstein *et al.* 2004, Georgelin, Kylafis and Loeuille 2015). In this case, the distances between the population structures of the species within the community at the initial and new equilibrium will be large (Johansson & Dieckmann 2009). In contrast, if the changes in one species do not have substantial effects on keystone species, then a major shift in ecological and evolutionary equilibrium may not be observed (Brown and Vincent 1992).

These transitions between equilibria can be captured with structured demographic models of interacting species that have achieved ecological and evolutionary stasis by setting the population of one species in the community to zero, by introducing a new species, or by changing the distribution of an abiotic driver. Any function that includes population size of the removed or added species, or the abiotic driver, will be directly impacted. Indirect effects will then cascade to other species whose demography might not be directly impacted by environmental perturbation, but might impacted by species that are directly impacted.

Back to the guppies, how to evolve an emu, and evolutionary innovation

The motivation for this paper was understanding the observations that i) communities often appear to be in equilibrium for protracted periods of time, yet ii) maintain additive genetic variance for many traits, allowing them iii) to evolve following an environmental perturbation, yet iv) many species exhibit traits, such as size, that do not evolve as predicted but instead exhibit stasis. When systems are perturbed from their equilibrium by the addition, or removal, of a species, they tend to a new ecological and evolutionary equilibrium (Bronstein *et al.* 2004,

Georgelin, Kylafis and Loeuille 2015. Well-adapted individuals in each of the equilibrium states, can express different resource accrual and life history traits, with selection on these traits determined by the limiting environment. I have focused on traits associated with the accrual of food, but similar arguments hold for traits associated with the acquisition of mates. In order to understand observed dynamics, I have focused on the properties of ecological and evolutionary equilibria, the conditions required for these properties to be observed, how systems are expected to move from one state to another, and how one could go about modelling these dynamics using existing, well-developed, approaches (see also Johansson & Dieckmann 2009). The focus on resource accrual and utilization traits allows me not only to explain observations from the guppy system, but also to provide a more general framework. However, can the logic be extended to other systems to explain patterns, and used to provide general insights?

As a demonstration, I focus on the evolution of the emu – a species close to my heart as my father-in-law once hand-raised an extremely cute one-day old orphaned chick named Emma-Steve to a hugely irascible "pet" (figure 6). Apart from reading about emus and using them as a hypothetical test case for my framework, I learned two other things about *Dromaius novaehollandiae*: they should not be given the run of the house given their fondness of storing keys in their gizzards, but they are easily reintroduced into the wild. Emma-Steve turned out to be Steve, and he has raised offspring once released back into the wild.

Flightless ratites evolved from flighted birds on multiple occasions, with their ancestors likely similar to tinamous – a group of New World flighted birds that superficially resemble partridges (Harshman et al. 2008). Tinamou are poor fliers, and rarely fly for more than 100m or so, but flight appears to be an adaptation to escape terrestrial predators. They have a generalist diet, much like emus, and feed on the ground (Pearson and Pearson 1955). The oldest fossilized ancestor of ratites, *Calciavis grandei*, was thought to be a competent flier, but was also likely a ground feeder (Nesbitt and Clarke 2016).

I hypothesize that flight in the flighted ancestor of the emu was a resource accrual trait that allowed birds to forage in the presence of predators. The need to fly to escape predation was likely lost during an era when predators were absent from the landscape, and this opened up the possibility for an increase in size. Increased size, and in particular the ability to take large strides and cover large distances quickly, are likely resource accrual traits that evolved following the loss of flight to allow emus to utilize spatially and temporally heterogenous resources, allowing them to thrive in unpredictable environments – in other words, size became a resource accrual trait. Modern day emus do have well-developed predation-avoidance traits. The claws on their feet can be used to fight off predators such as dingoes (*Canis dingo*), and they are vigilant with excellent vision. These adaptations possibly arose as predators increased in abundance in the unpredictable environments that emus had evolved to exploit. Although this is speculative, the loss of the ability to fly appears to have preceded an increase in body size in a number of bird species, including island specie such as the dodo (*Raphus cucullatus*).

I consequently hypothesize that potentially three significant environmental perturbations occurred during the evolution of the emu. First, a loss of predators in the environment led to relaxed selection on the ability to fly. Second, an increase in aridity, and in environmental predictability led to an increase in size that allowed emus to forage over large areas. Third, as predators started to become more abundant on the landscape, emus evolved a suite of anti-predator traits that allowed them to accrue resources in a more dangerous environment.

The environmental changes I describe in the guppies happen quickly when guppies invade new low predation environments: the escape from predation is instantaneous. In contrast, the changes that I have hypothesized that impacted emus may have occurred more gradually, and particularly the hypothesized change to a drier, less predictable environment. Particularly interesting biotic changes that can knock ecosystems to new ecological and evolutionary equilibria are new phenotypic innovations, such as the ability to fly, to migrate, or to hibernate,

that will have opened up resources in previously inaccessible environments. Such innovations provide the link between micro- and macroevolution.

The final observation I have made in the sections above is that some species removals or additions will not generate significant cascades throughout a system, but may instead influence a small number of species. Others will generate trophic cascades.

The most pronounced trophic cascades occur when the composition of the dominant producer species changes. For example, in Yellowstone, it is argued that the decline in elk numbers due to increased wolf predation has led to forests replacing grasslands (Fortin et al. 2005). The effect is currently localized to small areas as the two decades since wolves were reintroduced is not sufficient time for a forest to displace a grassland. However, if the effects observed on small spatial scales are eventually repeated on a larger scale, the reintroduction of wolves will be responsible for a pronounced trophic cascade as forests replace grasslands on the Northern range.

Less pronounced trophic cascades can occur when only a small part of a food web is affected, with impacts localized to a few species. For example, a decline in the density of a predatory bird may influence the dynamics of its passerine prey and the insects on which they feed, but effects on the species structure of the primary producers is likely to be minimal (Borer et al. 2005). Those species directly impacted may experience altered causes of death or failures to reproduce, and novel selection pressures, but community structure and ecosystem function is unlikely to be significantly impacted to a sufficient extent to generate a pronounced trophic cascade.

In the streams of Northern Trinidad, the wolf fish and pike cichlids are key predators that limit guppy numbers. Removing these species generates a trophic cascade because guppy numbers increase and they become the dominant consumer within the ecosystem. They are able to alter

the distribution and composition of producer species which cause further ripples throughout species within the ecosystem.

In this paper I have linked population limitation to community dynamics to evolution via species interactions and the accrual of resources. The ideas in present are consistent with many observations from a range of systems, but many of them are speculative. This manuscript should be seen as a perspective, rather than a comprehensive review. I hope that rather than being the last word, the paper generates discussion, tests of some of the hypotheses proposed, and acts to stimulate new models of the interplay between ecology and evolution.

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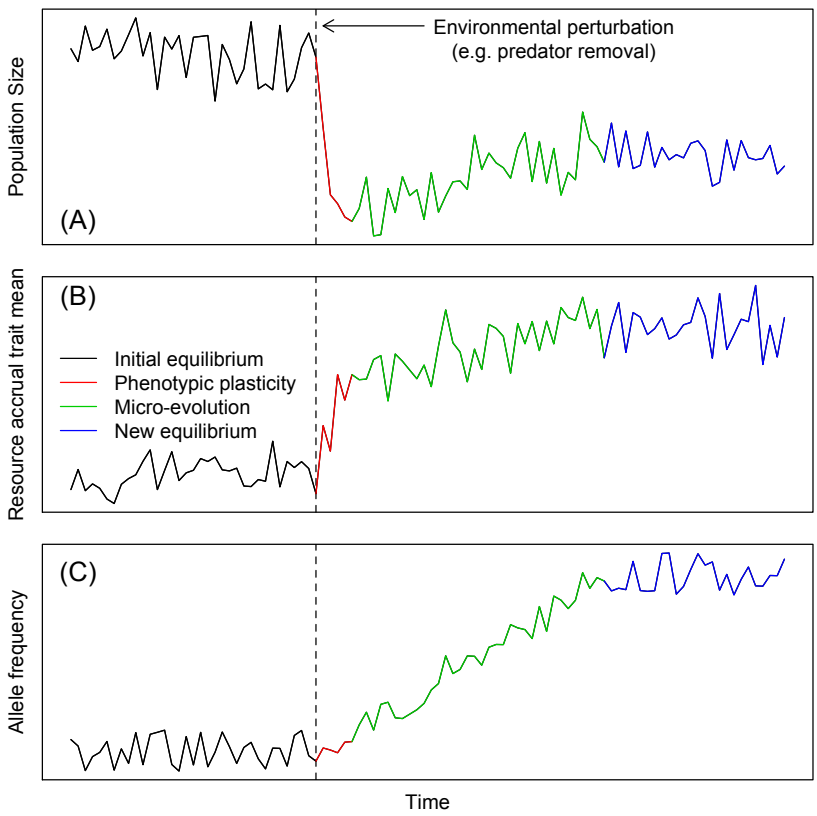

969

970 **Figure 1.** The (A) population, (B) phenotypic trait, and (C) micro-evolutionary dynamics of
971 populations as they move from one stationary state to another. At ecological and evolutionary
972 equilibrium, there are no temporal trends in population size, phenotypic trait distributions, or
973 allele frequencies (black lines). Following an environmental perturbation (dotted vertical line)
974 ecological and evolutionary change occurs (red and green lines) until a new stationary state is
975 achieved (blue lines). In this example, population size changes quickly following the
976 perturbation, while phenotypic and evolutionary changes occur more slowly. There will be a
977 period when phenotypic plasticity is likely stronger than microevolution, which is reflected in
978 quite rapid phenotypic change (B). Evolution occurs more slowly, resulting in gradual change
979 in population size, the mean of phenotypic traits, and allele frequencies. I have given an
980 example of ecological and evolutionary change in a single population, but similar patterns will
981 be observed in other species within the community.

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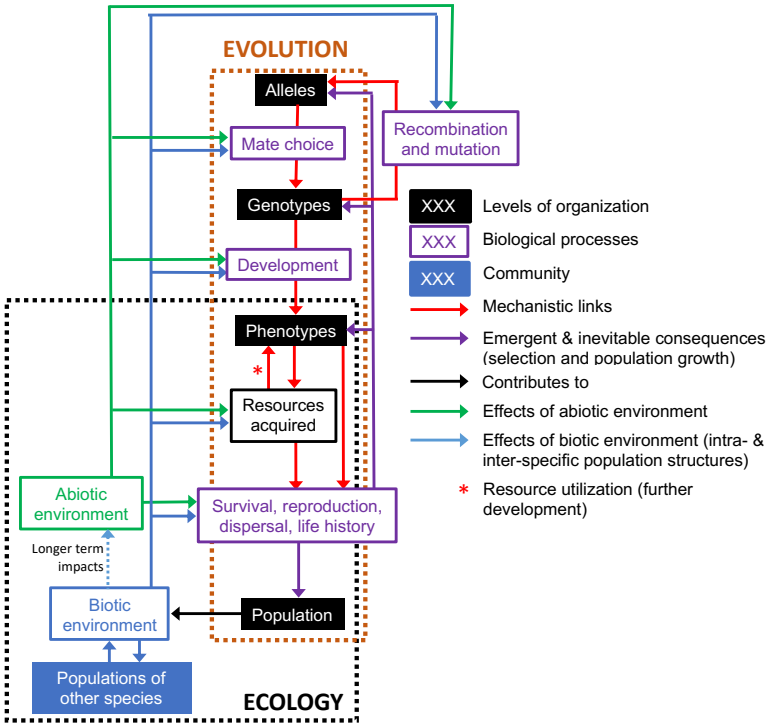

Figure 2. Complex eco-evolutionary feedbacks can arise from the dynamics of distributions of alleles, genotypes and phenotypes (levels of biological organization). These levels are mechanistically linked by key biological processes. Mate choice determines how alleles form genotypes in offspring, with development determining how phenotypes develop from genotypes. Phenotypes impact which resources individuals acquire and can influence survival, reproduction, dispersal and life history (demography). Acquired resources, such as a territory, can also influence demography directly, while also feeding back to impact further phenotypic development (including state-dependent behaviors). Selection and population dynamics are emergent consequences of which phenotypes survive and reproduce. The size and structure of the focal species and those species with which it interacts, constitute the biotic environment. The biotic environment, along with the abiotic environment, can directly influence the distribution of resources, but also biological processes in both the focal species and other species within the community. Recombination and mutation generate genetic variation and can be influenced by the environment.

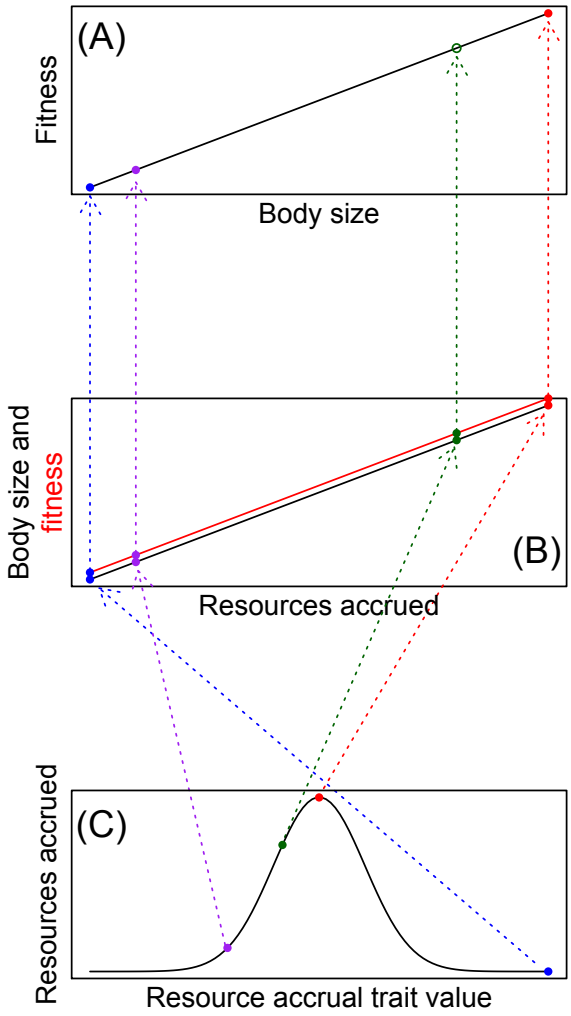

Figure 3. (A) A positive association between body size and fitness arises as (B) individuals that accrue most resources are larger and have higher fitness, which (C) is due to an n-shaped association between resource accrual and the resource accrual trait values. The dotted lines help visualize the map across functions.

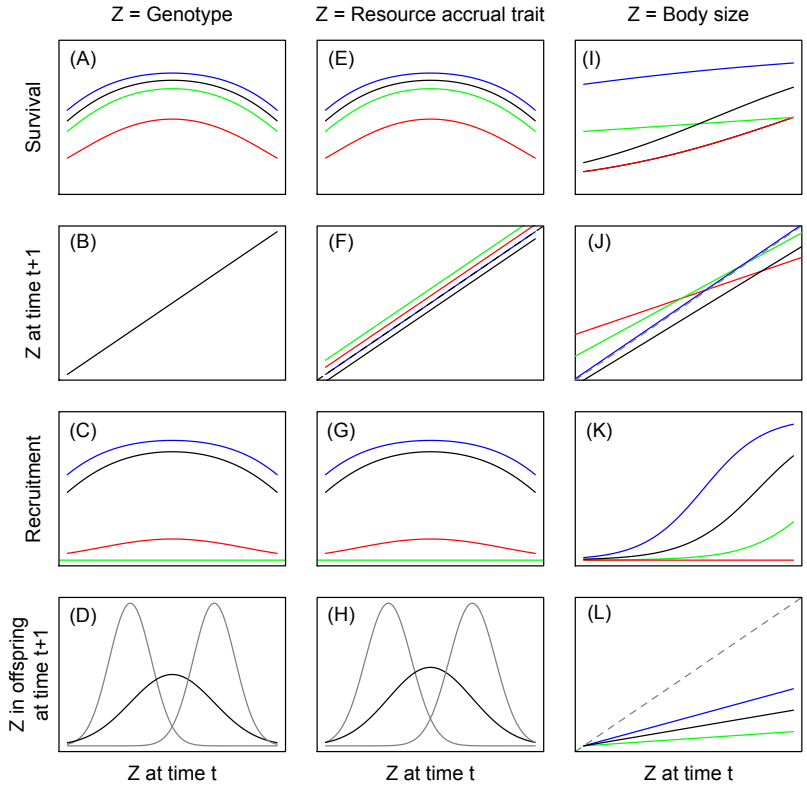

Figure 4. The form of survival (A, E, I), development (B, F, J), reproduction (C, G, K) and inheritance (D, H, L) functions for different individual attribute types. (A-D) form of functions for a breeding value or genotype that is subject to stabilizing viability (A) and fertility (C) selection, that does not develop throughout life (B), and exhibits genetic inheritance (D). The two narrower grey distributions in (D) represent breeding values or genotypes in parents, while the flatter black distribution represents the distribution in offspring following genetic inheritance. Similar dynamics are observed for a resource accrual trait that maintains its shape throughout life but increases in size with age as the environmental component of the phenotype develops (F). The trait is genetically inherited (H). Body size (I-L) is subject to directional viability (I) and fertility (K) selection, develops with age, and appears heritable (L) with parents and offspring have more similar values than non-related individuals. Different colored lines represent different ages, showing how functions can vary with age. In (B), (D) and (H) the same functions are observed at each age.

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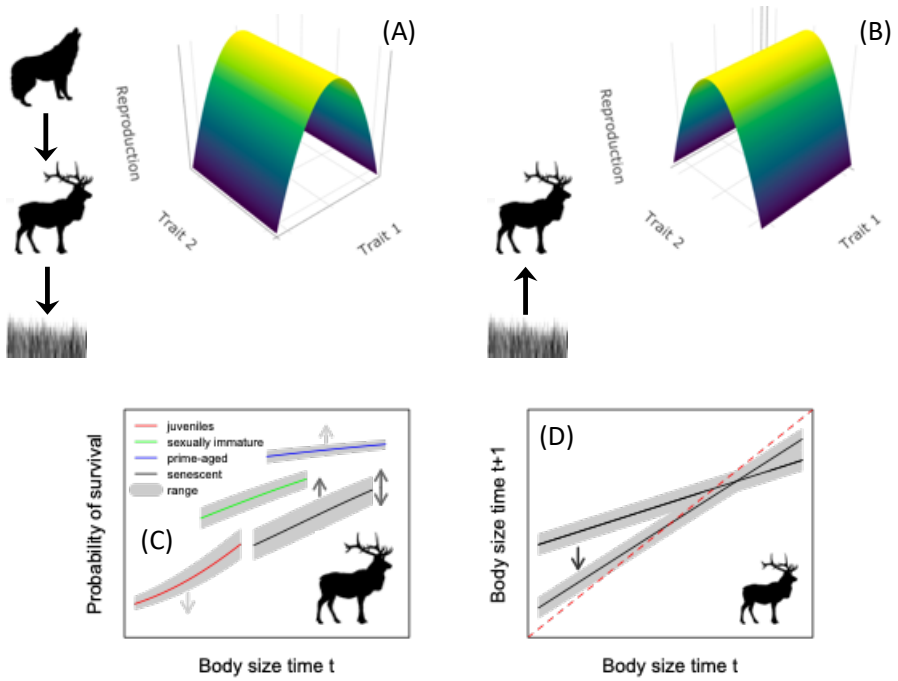

1020

1021 **Figure 5.** An environmental perturbation, such as the loss of a predator, can result in a
1022 period of transience between ecological and evolutionary equilibria. The removal of a
1023 predator can result in a change in limiting factor and a switch from top down (A) to bottom
1024 up (B) regulation. The change in the primary cause of death and failure to reproduce can
1025 relax selection on phenotypic traits associated with the original limiting factor and impose
1026 selection on traits associated with the new one (3D surfaces in A and B). These changes can
1027 alter demographic (C – survival as an example) and transition (D – development as an
1028 example) functions for size-related traits. In this example, a switch in limiting factor an
1029 increase in prime adult survival occurs with a simultaneous decrease in juvenile survival (C,
1030 gray arrows), an increase in the mean and variance in senescent survival (C black arrows),
1031 and a slowing in development rates (D, black arrow). In the original and novel equilibrium
1032 these functions take values that result a long stochastic growth rate of zero, although the
1033 mean and variance in population size may have changed (Figure 1(A)).

1034

Figure 6

Figure 6. Emma-Steve, the irascible emu.

References

Abrams, P. A., and X. Chen. 2002. The evolution of traits affecting resource acquisition and predator vulnerability: character displacement under real and apparent competition. The American Naturalist **160**:692-704.

Adler, P. B., S. P. Ellner, and J. M. Levine. 2010. Coexistence of perennial plants: an embarrassment of niches. Ecology Letters **13**:1019-1029.

Allesina, S., and S. Tang. 2012. Stability criteria for complex ecosystems. Nature **483**:205.

Ayala, F. J., and C. A. Campbell. 1974. Frequency-dependent selection. Annual Review of Ecology and Systematics **5**:115-138.

Barneche, D. R., D. R. Robertson, C. R. White, and D. J. Marshall. 2018. Fish reproductive-energy output increases disproportionately with body size. Science **360**:642-645.

Barton, N., and L. Partridge. 2000. Limits to natural selection. BioEssays **22**:1075-1084.

Barton, N. H., and A. M. Etheridge. 2011. The relation between reproductive value and genetic contribution. Genetics **188**:953-973.

Bassar, R. D., D. Z. Childs, M. Rees, S. Tuljapurkar, D. N. Reznick, and T. Coulson. 2016. The effects of asymmetric competition on the life history of Trinidadian guppies. Ecology Letters **19**:268-278.

Bassar, R. D., J. Travis, and T. Coulson. 2017. Predicting coexistence in species with continuous ontogenetic niche shifts and competitive asymmetry. Ecology **98**:2823-2836.

Berryman, A. A. 2004. Limiting factors and population regulation. Oikos **105**:667-670.

Bhat, U., C. P. Kempes, and J. D. Yeakel. 2020. Scaling the risk landscape drives optimal life-history strategies and the evolution of grazing. Proceedings of the National Academy of Sciences **117**:1580-1586.

Blanckenhorn, W. U. 2000. The evolution of body size: what keeps organisms small? The Quarterly Review of Biology **75**:385-407.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution **26**:183-192.

Bolnick, D. I., R. Svanbäck, M. S. Araújo, and L. Persson. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. Proceedings of the National Academy of Sciences **104**:10075-10079.

Bonamour, S., C. Teplitsky, A. Charmantier, P. A. Crochet, and L. M. Chevin. 2017. Selection on skewed characters and the paradox of stasis. Evolution **71**:2703-2713.

Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? Ecology **86**:528-537.

Bronstein, J.L., U. Dieckmann, and R. Ferrière. 2004. Coevolutionary dynamics and the conservation of mutualisms. Pp. 305–32 in Evolutionary Conservation Biology, eds. Ferrière R, U. Dieckmann & D. Couvet Cambridge University Press, Cambridge

Brown J. S. & T. L. Vincent. 1992. Organization of predator-prey communities as an evolutionary game. Evolution **46**:1269-1283

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**:1771-1789.

Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. The American Naturalist **142**:573-584.

Bürger, R., and R. Lande. 1994. On the distribution of the mean and variance of a quantitative trait under mutation-selection-drift balance. Genetics **138**:901-912.

Caswell, H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer, Sunderland, MA.

Caswell, H., T. Takada, and C. M. Hunter. 2004. Sensitivity analysis of equilibrium in density-dependent matrix population models. Ecology Letters **7**:380-387.

Charlesworth, B. 1994. Evolution in age-structured populations. Cambridge University Press, Cambridge, UK.

Charlesworth, D. 1989. Evolution of low female fertility in plants: pollen limitation, resource allocation and genetic load. Trends in Ecology & Evolution **4**:289-292.

Chesson, P. 1994. Multispecies competition in variable environments. Theoretical Population Biology **45**:227-276.

Chesson, P. 2000a. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology **58**:211-237.

Chesson, P. 2000b. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics **31**:343-366.

Chesson, P. L. 1986. Environmental variation and the coexistence of species. In Community Ecology edited by J. Diamond and T. Case. Pp 240-256.

Childs, D., T. Coulson, J. Pemberton, T. Clutton-Brock, and M. Rees. 2011. Predicting trait values and measuring selection in complex life histories: reproductive allocation decisions in Soay sheep. Ecology Letters **14**:985-992.

Childs, D. Z., M. Rees, K. E. Rose, P. J. Grubb, and S. P. Ellner. 2004. Evolution of size–dependent flowering in a variable environment: construction and analysis of a stochastic integral projection model. Proceedings of the Royal Society of London B: Biological Sciences **271**:425-434.

Childs, D. Z., B. C. Sheldon, and M. Rees. 2016. The evolution of labile traits in sex-and age-structured populations. Journal of Animal Ecology **85**:329-342.

Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in ecology. Oikos **121**:1337-1350.

Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall, and J.-M. Gaillard. 2006. Estimating individual contributions to population growth: evolutionary fitness in ecological time. Proceedings of the Royal Society B: Biological Sciences **273**:547-555.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science **292**:1528-1531.

Coulson, T., B. E. Kendall, J. Barthold, F. Plard, S. Schindler, A. Ozgul, and J.-M. Gaillard. 2017. Modeling adaptive and nonadaptive responses of populations to environmental change. The American Naturalist **190**:313-336.

Coulson, T., D. R. MacNulty, D. R. Stahler, R. K. Wayne, and D. W. Smith. 2011. Modeling effects of environmental change on wolf population dynamics, trait evolution, and life history. Science **334**:1275-1278.

Coulson, T., S. Schindler, L. Traill, and B. E. Kendall. 2018. Predicting the evolutionary consequences of trophy hunting on a quantitative trait. The Journal of Wildlife Management **82**:46-56.

Coulson, T., S. Tuljapurkar, and D. Z. Childs. 2010. Using evolutionary demography to link life history theory, quantitative genetics and population ecology. Journal of Animal Ecology **79**:1226-1240.

Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Harper and Row, New York.

De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters **6**:473-487.

DeLong, J. P., and J. P. Gibert. 2016. Gillespie eco-evolutionary models (GEMs) reveal the role of heritable trait variation in eco-evolutionary dynamics. Ecology and Evolution **6**:935-945.

DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution **13**:77-81.

Doebeli, M., Y. Ispolatov, and B. Simon. 2017. Point of view: Towards a mechanistic foundation of evolutionary theory. ELife **6**:e23804.

Dunlop E.S., M. Heino & U. Dieckmann 2009. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications **19**:1815–1834

Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. Ecology **81**:694-708.

Ellner, S. P., D. Z. Childs, and M. Rees. 2016. Data-driven modelling of structured populations: A Practical Guide to the Integral Projection Model. Springer, NY.

Ellner, S. P., and M. Rees. 2006. Integral projection models for species with complex demography. The American Naturalist **167**:410-428.

Engen, S., and B.-E. Sæther. 1998. Stochastic population models: some concepts, definitions and results. Oikos: **83**:345-352.

Estes, S., and S. J. Arnold. 2007. Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales. The American Naturalist **169**:227-244.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. Oliver And Boyd, Edinburgh.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon, Oxford.

Fishman, L., and J. H. Willis. 2008. Pollen limitation and natural selection on floral characters in the yellow monkeyflower, *Mimulus guttatus*. New Phytologist **177**:802-810.

Fleming, I. A., and M. R. Gross. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology **71**:1-11.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320-1330.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367-393.

Gause, G. F. 1932. Experimental studies on the struggle for existence: I. Mixed population of two species of yeast. Journal of Experimental Biology **9**:389-402.

Georgelin, E., G. Kylafis and N Loeuille 2015 Eco-Evolutionary Dynamics of Plant–Insect Communities Facing Disturbances: Implications for Community Maintenance and Agricultural Management. Advances in Ecological Research **52**:91-114.

Geritz, S. A., & É. Kisdi. 2000. Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. Proceedings of the Royal Society of London. Series B: Biological Sciences. **267**:1671-1678.

Gillespie, J. H. 1994. The causes of molecular evolution. Oxford University Press, Oxford UK.

Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. The American Naturalist **119**:803-823.

Haller, B. C., and A. P. Hendry. 2014. Solving the paradox of stasis: squashed stabilizing selection and the limits of detection. Evolution **68**:483-500.

Harshman, J., E. L. Braun, M. J. Braun, C. J. Huddleston, R. C. Bowie, J. L. Chojnowski, S. J. Hackett, K.-L. Han, R. T. Kimball, and B. D. Marks. 2008. Phylogenomic evidence for multiple losses of flight in ratite birds. Proceedings of the National Academy of Sciences **105**:13462-13467.

Hartl, D. L., A. G. Clark, and A. G. Clark. 1997. Principles of population genetics. Sinauer associates, Sunderland, MA.

Hassell, M. 1975. Density-dependence in single-species populations. The Journal of Animal Ecology:283-295.

Hastings, A. 2004. Transients: the key to long-term ecological understanding? Trends in Ecology & Evolution **19**:39-45.

Hiltunen, T., N. G. Hairston Jr, G. Hooker, L. E. Jones, and S. P. Ellner. 2014. A newly discovered role of evolution in previously published consumer–resource dynamics. Ecology Letters **17**:915-923.

Hin, V., and A. M. de Roos. 2019. Evolution of size-dependent intraspecific competition predicts body size scaling of metabolic rate. Functional Ecology **33**:479-490.

Johansson, J., & U. Dieckmann. 2009. Evolutionary responses of communities to extinctions. Evolutionary Ecology Research **11**:561–588.

Keith, L. B., and L. A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildlife Monographs **58**:3-70.

Kentie, R., S. M. Clegg, S. Tuljapurkar, J.-M. Gaillard, and T. Coulson. in press. Life history strategy varies with the strength of competition in a food-limited ungulate population. Ecology Letters.

Kooijman, B., and S. A. L. M. Kooijman. 2010. Dynamic energy budget theory for metabolic organisation. Cambridge University Press, Cambridge.

Krebs, C. J., B. Gilbert, S. Boutin, A. R. Sinclair, and J. N. Smith. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976-84. The Journal of Animal Ecology **55**:963-982.

Kruuk, L. E., T. H. Clutton-Brock, J. Slate, J. M. Pemberton, S. Brotherstone, and F. E. Guinness. 2000. Heritability of fitness in a wild mammal population. Proceedings of the National Academy of Sciences **97**:698-703.

Kruuk, L. E., J. Slate, J. M. Pemberton, S. Brotherstone, F. Guinness, and T. Clutton-Brock. 2002. Antler size in red deer: heritability and selection but no evolution. Evolution **56**:1683-1695.

Kruuk, L. E. B. 2004. Estimating genetic parameters in natural populations using the ‘animal model&#x2019. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences **359**:873-890.

Lachish, S., E. Brandell, M. Craft, A. Dobson, P. Hudson, D. MacNulty, and T.Coulson in press. Investigating the dynamics of elk population size and body mass in a seasonal environment using a mechanistic integral projection model. The American Naturalist.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology **63**:607-615.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. Journal of Evolutionary Biology **22**:1435-1446.

Lande, R., S. Engen, and B.-E. Saether. 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford UK.

Lande, R., S. Engen, and B.-E. Sæther. 2017. Evolution of stochastic demography with life history tradeoffs in density-dependent age-structured populations. Proceedings of the National Academy of Sciences **114:**11582-11590.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika **33**:183-212.

Lewontin, R. C. 1969. The meaning of stability. Brookhaven Symposia in Biology **22**:13-24.

Lowe, W. H., R. P. Kovach, and F. W. Allendorf. 2017. Population genetics and demography unite ecology and evolution. Trends in Ecology & Evolution **32**:141-152.

Lundberg, P., E. Ranta, and V. Kaitala. 2000. Species loss leads to community closure. Ecology Letters **3**:465-468.

Lynch, M., and B. Walsh. 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates, Sunderland, MA.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist **101**:377-385.

McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. Nature **380**:215-221.

Merilä, J., B. Sheldon, and L. Kruuk. 2001. Explaining stasis: microevolutionary studies in natural populations. Genetica **112**:199-222.

Metcalf, C. J. E. 2016. Invisible trade-offs: Van Noordwijk and de Jong and life-history evolution. The American Naturalist **187**:iii-v.

Metz J. A. J. and C. G. F. de Kovel. 2013. The canonical equation of adaptive dynamics for Mendelian diploids and haplo-diploids. Interface Focus **3**:20130025

Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. Van Heerwaarden. 1995. Adaptive Dynamics: a Geometrical Study of the Consequences of Nearly Faithful Reproduction. *in* S. J. van Strien and S. M. Lunel, editors. Stochastic and Spatial Structures of Dynamical Systems. International Institute for Applied Systems Analysis, Amsterdam.

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define 'fitness' for general ecological scenarios? Trends in Ecology & Evolution **7**:198-202.

Moran, D., R. Softley, and E. J. Warrant. 2015. The energetic cost of vision and the evolution of eyeless Mexican cavefish. Science Advances **1**:e1500363.

Murray, B. G. 1982. On the meaning of density dependence. Oecologia **53**:370-373.

Nesbitt, S. J., and J. A. Clarke. 2016. The anatomy and taxonomy of the exquisitely preserved Green River formation (early Eocene) Lithornithids (Aves) and the relationships of Lithornithidae. Bulletin of the American Museum of Natural History **2016**:1-91.

O'Sullivan, R. J., T. Aykanat, S. E. Johnston, A. Kane, R. Poole, G. Rogan, P. A. Prodöhl, C. R. Primmer, P. McGinnity, and T. E. Reed. 2019. Evolutionary stasis of a heritable morphological trait in a wild fish population despite apparent directional selection. Ecology and Evolution **9**:7096–7111.

Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. Science **325**:464-467.

Paine, R. 1966. Food web complexity and species diversity. The American Naturalist **100**:65-75.

Pearson, A. K., and O. P. Pearson. 1955. Natural history and breeding behavior of the tinamou, *Nothoprocta ornata*. The Auk **72**:113-127.

Pigliucci, M., C. J. Murren, and C. D. Schlichting. 2006. Phenotypic plasticity and evolution by genetic assimilation. Journal of Experimental Biology **209**:2362-2367.

Price, G. R. 1970. Selection and covariance. Nature **227**:520-521.

Rees, M., D. Z. Childs, and S. P. Ellner. 2014. Building integral projection models: a user's guide. Journal of Animal Ecology **83**:528-545.

Rees, M., and S. P. Ellner. 2019. Why so variable: can genetic variance in flowering thresholds be maintained by fluctuating selection? The American Naturalist **194**:E13-E29.

Reznick, D., M. J. Butler IV, and H. Rodd. 2001. Life-history evolution in guppies. VII. The comparative ecology of high-and low-predation environments. The American Naturalist **157**:126-140.

Reznick, D., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution **36**:160-177.

Reznick, D., L. Nunney, and A. Tessier. 2000. Big houses, big cars, superfleas and the costs of reproduction. Trends in Ecology & Evolution **15**:421-425.

Reznick, D., and A. P. Yang. 1993. The influence of fluctuating resources on life history: patterns of allocation and plasticity in female guppies. Ecology **74**:2011-2019.

Reznick, D. N., and H. Bryga. 1987. Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. Evolution **41**:1370-1385.

Ripa, J., and U. Dieckmann. 2013. Mutant invasions and adaptive dynamics in variable environments. Evolution, **67**:1279–1290.

Rohr, J. R., A. A. Elskus, B. S. Shepherd, P. H. Crowley, T. M. McCarthy, J. H. Niedzwiecki, T. Sager, A. Sih, and B. D. Palmer. 2003. Lethal and sublethal effects of atrazine, carbaryl, endosulfan, and octylphenol on the streamside salamander (*Ambystoma barbouri*). Environmental Toxicology and Chemistry: **22**:2385-2392.

Rollinson, N., and L. Rowe. 2015. Persistent directional selection on body size and a resolution to the paradox of stasis. Evolution **69**:2441-2451.

Romero-Mujalli, D., F. Jeltsch and R. Tiedemann. 2018. Individual-based modeling of eco-evolutionary dynamics: state of the art and future directions. Regional Environmental Change **1**:1-12.

Sæther, B.-E., and S. Engen. 2015. The concept of fitness in fluctuating environments. Trends in Ecology & Evolution **30**:273-281.

Schindler, D. W. 1974. Eutrophication and recovery in experimental lakes: implications for lake management. Science **184**:897-899.

Schindler, S., J. M. Gaillard, A. Grüning, P. Neuhaus, L. W. Traill, S. Tuljapurkar, and T. Coulson. 2015. Sex-specific demography and generalization of the Trivers–Willard theory. Nature **526**:249.

Schindler, S., P. Neuhaus, J.-M. Gaillard, and T. Coulson. 2013. The influence of nonrandom mating on population growth. The American Naturalist **182**:28-41.

Schreiber, S. J., S. Patel, and C. terHorst. 2018 Evolution as a coexistence mechanism: Does genetic architecture matter? The American Naturalist **191**: 407-420.

Sibly, R. M., and J. Hone. 2002. Population growth rate and its determinants: an overview. Philosophical Transactions of the Royal Society of London B: Biological Sciences **357**:1153-1170.

Smallegange, I. M., H. Caswell, M. E. M. Toorians, and A. M. Roos. 2017. Mechanistic description of population dynamics using dynamic energy budget theory incorporated into integral projection models. Methods in Ecology and Evolution **8**:146-154.

Smith, F. A., and S. K. Lyons. 2013. Animal body size: linking pattern and process across space, time, and taxonomic group. University of Chicago Press, Chicago, US.

Stearns, S. C. 1976. Life-history tactics: a review of the ideas. The Quarterly Review of Biology **51**:3-47.

Steiner, U. K., S. Tuljapurkar, and T. Coulson. 2014. Generation time, net reproductive rate, and growth in stage-age-structured populations. The American Naturalist **183**:771-783.

Svanbäck, R., and D. I. Bolnick. 2006. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B: Biological Sciences **274**:839-844.

Traill, L. W., S. Schindler, and T. Coulson. 2014. Demography, not inheritance, drives phenotypic change in hunted bighorn sheep. Proceedings of the National Academy of Sciences **111**:13223-13228.

Travis, J., D. Reznick, R. D. Bassar, A. López-Sepulcre, R. Ferriere, and T. Coulson. 2014. Do eco-evo feedbacks help us understand nature? Answers from studies of the Trinidadian guppy. Advances in Ecological Research **50**:1-40.

Tuljapurkar, S. 1989. An uncertain life: demography in random environments. Theoretical Population Biology **35**:227-294.

Tuljapurkar, S., J.-M. Gaillard, and T. Coulson. 2009a. From stochastic environments to life histories and back. Philosophical Transactions of the Royal Society of London B: Biological Sciences **364**:1499-1509.

Tuljapurkar, S., and S. H. Orzack. 1980. Population dynamics in variable environments I. Long-run growth rates and extinction. Theoretical Population Biology **18**:314-342.

Tuljapurkar, S., U. K. Steiner, and S. H. Orzack. 2009b. Dynamic heterogeneity in life histories. Ecology Letters **12**:93-106.

Van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. The American Naturalist **128**:137-142.

Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences **50**:2058-2070.

Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. The American Naturalist **125**:769-787.

Werner, T. K., and T. W. Sherry. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin's finch" of Cocos Island, Costa Rica. Proceedings of the National Academy of Sciences **84**:5506-5510.

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science **276**:122-126.

Wright, J. S. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia **130**:1-14.

Wright, S. 1969. Evolution and the Genetics of Populations: Vol. 2. The Theory of Gene Frequencies. University of Chicago Press, Chicago, US.

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston Jr. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. Nature **424**:303.