PEDRO BOLANHO MENDES

ECO-EVOLUTIONARY DYNAMICS IN PREDATOR-PREY INTERACTIONS:

A QUANTITATIVE GENETIC APPROACH TO

PREDATOR-INDUCED ADAPTATIONS

LAVRAS – MG

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> Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e monitoramento de ecossistemas sob interferência antrópica, para a obtenção do título de Mestre.

Prof. DSc. Lucas Del Bianco Faria

Orientador

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DINÂMICA ECO-EVOLUTIVA DE INTERAÇÕES PRESA-PREDADOR: UMA ABORDAGEM DE GENÉTICA QUANTITATIVE SOBRE ADAPTAÇÕES INDUZIDAS PELA PREDAÇÃO

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LAVRAS – MG
2019

Aos meus pais e irmãs.

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... If you're going to try, go all the way.
There is no other feeling like that.
You will be alone with the gods, and the nights will flame with fire.
You will ride life straight to perfect laughter.
It's the only good fight there is.
(Charles Bukowski)

RESUMO

Diversos estudos teóricos e empíricos indicam que a evolução pode ser rápida o suficiente para afetar a dinâmica ecológica. Entender e monitorar os mecanismos por trás da reciprocidade entre os efeitos das dinâmicas ecológicas e evolutivas é o objetivo central da área da dinâmica eco-evolutiva. Apesar das evidências sobre a importância da reciprocidade na natureza, existem vários processos ecológicos que podem mimetizar os efeitos da evolução na ecologia, obscurecendo sua relevância. Uma alternativa é o desenvolvimento de modelos matemáticos mecanísticos para elucidar quando e como a evolução não é trivial. Neste estudo, nós usamos modelos matemáticos para explorar a interação entre diferentes teorias em ecologia e biologia evolutiva. Nós analisamos um conjunto de equações diferenciais que descrevem a dinâmica eco-evolutiva de interações presa-predador. No primeiro capítulo, nós focamos em entender como a teoria r/K interage com a dinâmica eco-evolutiva. No segundo capítulo, nós focamos em entender como a saciedade do predador afeta as predições da hipótese da predação estágio-dependente. Nossos resultados gerais são: 1) o resultado da interação difere entre contextos r- e K-seletivos; 2) a preferência do predador pode gerar um continuum rápido-lento de história de vida quando é assumido a estrutura da população. Nós discutimos como a teoria r/K requer a suposição de estrutura de estágio para refletir a evolução da história de vida e como a interseção entre hipóteses pode afetar as predições ecológicas.

Palavras-chave: Ecologia evolutiva, dinâmica runaway, link ecogenético, demografia, crescimento populacional, traços anti-predação.

ABSTRACT

Several theoretical and empirical studies indicate that evolution may be rapid enough to affect ecological dynamics. Tracking and understanding the mechanisms underlying reciprocity between the effects of ecological and evolutionary dynamics is the central goal of the field of eco-evolutionary dynamics. Despite the evidences suggesting the importance of reciprocity in nature, there are many ecological processes that may mimicry the effects of evolution in ecology, obscuring its relevance. One alternative is to develop mechanistic mathematical models to clarify when and how evolution will not be trivial. In this work, we use mathematical models to explore the interplay among different theories in ecology and evolutionary biology. We analysed a set of differential equations describing the eco-evolutionary dynamics of predator-prey interactions. In the first chapter, we focused in how r/K theory interplays with eco-evolutionary dynamics. In the second chapter, we focused in how predator satiation affects the predictions of the stage-dependent predation hypothesis. Our general results are: 1) the outcome of interaction differs between r- and K-selective contexts; 2) predator preference can generate a fast-slow life-history continuum when stage structure is assumed. We discuss how r/K theory requires the assumption of stage structure to reflect life-history evolution and how the intersection of hypothesis may affect ecological predictions.

Keywords: Evolutionary ecology, runaway dynamics, ecogenetic link, demography, population growth, anti-predator traits.

SUMÁRIO

Part I

1   Introduction

The increased rate of the contemporary environmental change suggests that rapid adaptation may be a key mechanism to reverse populations decline (GONZALEZ et al., 2012; FERRIERE; LEGENDRE, 2013). However, several ecological processes may mimicry the effects of rapid evolution (LUO; KOELLE, 2013), making it difficult to predict when evolutionary dynamics are not trivial (SCHOENER, 2011). Part of this difficulty results from the complex net effect among traits, genes and the ecological contexts underlying the evolutionary trajectories in nature (DELONG, 2017). One way to enhance predictability is to develop proper mechanistic mathematical theories to understand when and how trait dynamics may interact with demography to produce different outcomes. Because individuals are the unit of selection (SUBER, 2000), such theories must be based on individual traits rather then in population properties (RUEFFLER; EGAS; METZ, 2006; KOKKO; LÓPEZ-SEPULCRE, 2007).

The major objective of this study is to explore the predictions that emerge from the interplay among different theories in ecology and evolutionary biology. Our aim was to investigate how eco-evolutionary dynamics link with the r/K theory (MACARTHUR; WILSON, 1967), and how this link can be used to explore life-history evolution. We tracked the selection gradients of predator-prey system to investigate how demographic parameters affect system dynamics in different selective contexts. The models used here are differential equations describing how prey vulnerability to predation changes with predators and preys densities.

Because of the inherent complexity around this theme, we start this work with a brief and comprehensive overview of the major concepts of the field. We cover the basic historical and developmental background to clarify the mechanisms underlying the interplay between ecology and evolution. Concepts like selection gradients, reciprocity and genetic architecture are presented and contextualized below. We finish this part with a brief overview on the major findings and interpretations of the overall results in this dissertation.

In the second part of this document we present two chapters. In the first chapter, we explore the relationship between the r/K theory and eco-evolutionary dynamics. We show how to track the r- and K-selection gradients, and how the continuum between these two opposite selections is affected by predators and preys parameters. We assume unstructured populations

and discuss how the outcome of predator-prey interactions varies between r- and K-selective contexts.

In the second chapter, we investigate how the intersection of r/K theory and eco-evolutionary dynamics can be used to study life-history evolution. We show a simple way to incorporate stage structure in the eco-evolutionary model. In this chapter we focused on how predator preference for each stage can generate a fast-slow life-history continuum. Specifically, we ask whether predator satiation hypothesis can affect the predictions of the stage-dependent predation hypothesis, from life-history theory. We discuss the implications of our findings for the interpretation of empirical data and for the theory for predator-prey interaction.

2 Theoretical Framework

2.1 When Ecology Affects Evolution

Although the word *ecology* can not be found in the book "On the Origin of Species" Charles Darwin assumed an intrinsic relationship between ecology and evolution (DARWIN, 1859). Such relationship is evident in his third chapter, *Struggle for Existence*, when Darwin notes:

> "Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life.- (DARWIN, 1859): page 64.

Darwin's *Struggle for Existence* describes what we nowadays consider the core of ecological theory (SCHEINER; WILLIG, 2008). Several studies have shown that, indeed, ecology shapes evolution (JOHNSON; ROMERO, 2004; SIMON et al., 2016; KOTRSCHAL et al., 2017). In a sense, the theoretical foundation for such ecology-to-evolution (eco-to-evo) effects is the same mechanism which allows adaptation, namely natural selection. Natural selection is the key concept that enables the interplay between ecology and evolution (SCHOENER, 2011). Because selection acts over individual fitness, which in turn is an ecological quantity (MCPEEK, 2017), it is logical to expect that selection strongly depends on the ecological context.

Despite the fact that Darwin did not expressed a profound knowledge in the field of mathematics, the theory of evolution is fundamentally a mathematical theory (PEARSON, 1903; PAGE; NOWAK, 2002). Fortunately, after Darwin, many theoreticians have put a great effort into developing a mathematical theory on the mechanisms involved in evolutionary biology. Such effort resulted in some of the most beautiful and elegant set of equations in biology

(QUELLER, 2017). These theoretical frameworks describe how species traits that affect individual fitness change over time. For the moment, the most fundamental theorem of evolution is the Price equation (PRICE, 1970; PRICE, 1972; QUELLER, 2017; LUQUE, 2017). Coined by George Price in 1970 (PRICE, 1970), this equation was shown to be useful in a variety of contexts with a trait or allele ϕ of individual or type i. The Price equation can be written as:

$$\Delta\overline{\phi} = \frac{1}{\overline{W}}(\mathrm{Cov}(W_i, \phi_i) + \mathrm{E}(W_i\delta_i)). \tag{1}$$

Equation 1 tell us that the change in the average trait value is proportional to the covariance between individual fitness, W_i, and trait value ϕ_i. Function $\mathrm{E}(W_i\delta_i)$ describes the bias in trait value due to factors other than genetics (such as epigenetics, plasticity or parental effects), where δ is the change in trait value during the individual life time (see Queller 2017, for a comprehensive explanation). The status of fundamental theorem comes from the fact that many other relevant theorems of evolution can be derived from Price's equation. Note that, although not explicit, the Price equation is intrinsically related to ecology through the fitness value W. Fitness is an ecological quantity because it describes the individual performance at current moment, which is a function of all the ecological variables that interact with an organism during its life. In this sense, ecology is, indeed, one of the corner stones in evolutionary biology.

2.1.1 Density-Dependent Selection

One way to explicitly incorporate ecological effects into evolutionary dynamics is to assume density-dependent selection (hereafter DDS). DDS happens when either the shape, direction or/and strength of natural selection vary with population density (MUELLER, 1997). The logic explanation for such interaction is that individual organisms perceive all the components of its surrounding as environmental factors, including their conspecifics. In this sense, altering population density also affects the environment, consequently affecting the selective context experienced. One of the earliest experiment on how density affects selection was made by Charles Birch (BIRCH, 1955). Using an experiment with *Drosophila pseudoobscura* populations, Birch was able to observe that the set of genes selected in crowded populations were different from those selected when population was low in density. David Pimentel (PIMENTEL, 1961) also discussed how population regulation feed-back to genetic composition, changing the properties of natural selection. The arguments supporting DDS are mostly based on popula-

tion regulation mechanisms such as competition for resources. A simple way to describe the complex mechanism of population regulation is to assume the logistic population growth. The logistic equation is composed by an exponential growth rate r, and by a term describing the sensitivity to depressant effects of density, l. The logistic equation in its most simple format is

$$\frac{dN}{dt} = N[r - Nl]. \tag{2}$$

The simplicity and the realism of the logistic equation make it one of the most used mathematical equations in theoretical ecology (ROSS, 2009). Among ecologists, equation 2 is probably most known in its carrying capacity format:

$$\frac{dN}{dt} = Nr\left(1 - \frac{N}{K}\right) \tag{3}$$

where K stands for the carrying capacity and equals r/l. Equations 2 and 3 tell us that the rate of growth in N will decrease as the current N gets close to its carrying capacity. In this sense, if a trait affects both r and K antagonistically, a trade-off between the optimum trait value for r and for K will emerge. The properties of natural selection (strength, direction and shape) acting on trait value will vary with population density. Therefore, selection will be density-dependent (TRAVIS; LEIPS; RODD, 2013).

One of the first theories in DDS is the r- and K-selection theory (r/K theory). In 1962, Robert MacArthur showed how Fisher's theorem of natural selection behaves when individual fitness is assumed to vary with population density. Assuming the logistic population growth, MacArthur showed that the carrying capacity, K, always replaces the intrinsic growth rate, r, as a measure of fitness when population is crowded. Using such argument, MacArthur and Wilson (MACARTHUR; WILSON, 1967) coined the term r- and K-selection to explain the variation in selective pressures that shapes populations in under- versus over-crowded states (REZNICK; BRYANT; BASHEY, 2002). Later, the theory of r/K selection was used to explain the variation among the different patterns of life-history in nature (PIANKA, 1970). However, it is worth to remember that the r/K theory was build under the theory of density-dependent selection, which is not an explanatory theory for life-history variation (BOYCE, 1984).

One of the main differences between r- and K-selective environments is the cause of mortality (PIANKA, 1970; REZNICK; BRYANT; BASHEY, 2002; DAŃKO et al., 2018). When the source of mortality does not depend on population density, selection will favour

phenotypes with greater reproductive rate. In this scenario, fitness is absolute because it does not depends on population density (although (BERTRAM; MASEL, 2017) showed that relative density-independent fitness accurately describes fitness when selection is strong), and we expect to see a predominant *r*-selection (REZNICK; BRYANT; BASHEY, 2002). On the other hand, because population crowding may increase mortality by competition among individuals, we expect a *K*-selection in high densities. In this case, relative fitness is a reasonable measure of individual fitness (LANDE, 1976) because selection favours the quality rather than the number of offspring (PROMISLOW; HARVEY, 1990). Additionally, the effects of mortality may also depend on how population regulation emerges from population parameters (REZNICK; Butler IV; RODD, 2001; REZNICK; BRYANT; BASHEY, 2002).

2.1.2 The Genetic Architecture

The genetic mechanisms of trait inheritance are various in nature. Such variation comes from the number of genes controlling the trait expression and from the interaction among those genes. This genetic configuration is known as genetic architecture (HANSEN; WAGNER, 2001; HANSEN, 2006; KOKKO et al., 2017). In some cases, genetic architecture may be simple enough to be described by the population genetics framework, which is based on the Mendelian mode of inheritance. For such situations, the change in an allele frequency, p, can be described by the Wright's formula:

$$\Delta p = \frac{p(1-p)}{2\overline{W}} \frac{\partial \overline{W}}{\partial p} \tag{4}$$

Equation 4 can only be used for traits that are controlled by few genes, with known interactions among them. However, the genetic basis of ecological traits are often controlled by multiple genes with many pleiotropic effects (RIDENHOUR; NUISMER, 2014). Quantitative genetics is the field that treats such complex situations. In a theoretical perspective, one of the most used frameworks that incorporates quantitative genetics was published by Russel Lande (LANDE, 1976). With the assumption of unknown genes, Lande shows that the rate of change in a mean phenotype $\bar{z}$ equals:

$$\Delta\bar{z}(t) = \frac{h^2\sigma^2}{\overline{W}} \frac{\partial \overline{W}}{\partial \bar{z}(t)} \tag{5a}$$

$$= h^2\sigma^2 \frac{\partial \ln\overline{W}}{\partial \bar{z}(t)} \tag{5b}$$

where h^2 and σ^2 stands for heritability and variance of z. Note the similarity between the partial derivative terms in equations 5 and 4. This term represents the gradient of selection. The gradient of selection stands for how the individual fitness varies due to the evolving character. The other part of the right-hand-side of equations 5 and 4 describes the genetic architecture of the respective traits/allele. Because these models assume that evolution happens in a time scale much slower than ecological dynamics, fitness is assumed to be constant over time. In this sense, the properties of genetic architecture do not directly affect individual fitness function, and therefore evolution does not directly affects ecology.

2.2   When Evolution Affects Ecology

Recently, several empirical and theoretical studies suggested that evolution can happen fast enough to affect ecological dynamics (TURCOTTE; REZNICK; HARE, 2013; FARKAS; MONTEJO-KOVACEVICH, 2014; KLEMENT, 2016; VETSIGIAN, 2017). Such temporal convergence between evolutionary and ecological dynamics (HAIRSTON et al., 2005) allows for reciprocity between the effects. In other words, ecology affects evolution, evolution affects ecology. If there is reciprocity, individual fitness changes with time. In such situation, the gradients of selection in equations 4 and 5 would also depend on the genetic architecture. The field that studies the routes of reciprocity between ecology and evolution is known as eco-evolutionary dynamics (PELLETIER; GARANT; HENDRY, 2009; SCHOENER, 2011).

Several experimental and field studies suggest that eco-evolutionary dynamics govern species interactions and ecosystem functions (TURCOTTE; REZNICK; HARE, 2013; AGRAWAL et al., 2013; DELONG; LUHRING, 2018; WITTMANN; FUKAMI, 2018). Eco-evolution may also be found in contemporary human populations. In a study (PELLETIER et al., 2017), the authors found that 6.1% of the variation found in the women age at first reproduction is due to genetics, which in turn shows an evolutionary change during the last 108 years. The authors argue that such change may affect human population growth, closing the eco-evolutionary feedback loop. Another relevant application of eco-evolutionary dynamics is in cancer biology. Because tumoral cells present fast ecological dynamics and relatively high mutational rates, evolutionary shifts in cancer cells population may affect and be affected by ecological dynamics (ALFAROUK et al., 2013; KLEMENT, 2016; GATENBY; BROWN, 2017). Eco-evolution is also relevant in conservation biology. Prey recognition of novel predators is predicted to depend on the eco-evolutionary experience of preys (CARTHEY; BLUMSTEIN, 2018; DAVIS et

al., 2019). In fact, theoretical studies are increasingly showing that predator-prey interaction is driven by eco-evolutionary dynamics (YOSHIDA et al., 2003; ELLNER; BECKS, 2011; VELZEN; GAEDKE, 2017). This is because predators exert a strong selection over prey species, and if there is enough genetic variation, preys may evolve fast (CORTEZ, 2016). The rapid evolution of prey in response to predators have been observed in both experimental (PALMER, 1990; MEYER et al., 2006) and field studies (RODD et al., 1991).

The major challenge in eco-evolutionary theory is to access whether its occurrence is trivial or not. The idea of triviality comes from empirical data suggesting the lack of correlation between trait dynamics and population cycles (SCHOENER, 2011). However, some studies suggest that such lack of feedback may occur when the evolving trait is related to many ecological functions (DELONG, 2017). This creates trade-offs between optimum trait values for each ecological function affected. Depending on the context, these trade-offs generate multiple opposite pressures that cancel out, suppressing the effect of trait dynamics on demography (DELONG, 2017). One way to overcome this barrier is to search for reciprocity among other ecological variables in the environment. In many situations, reciprocity may be found in indirect ecological interactions (ESTES; BRASHARES; POWER, 2013). The logic is that eco-evolutionary feedback loops happen when trait dynamics affect environment, and, in turn, environment affects selection (LION, 2017). Therefore, reciprocity may be found in a specific environmental measure that is affected by that trait. In this sense, eco-evolutionary dynamics need a proper mathematical theory to help to unravel when reciprocity is relevant, and could be used to predict evolution (LUO; KOELLE, 2013).

3   Concluding Remarks

Our results suggest that population regulation plays an important role in shaping ecological and evolutionary dynamics. Because density can produce different selective contexts, the regulatory mechanisms will affect how many other environmental factors affect individual fitness and selection. As we show in chapter one, all system parameters can affect the r/K continuum. Changing predators parameters on the direction of increasing the risk of predation will always produce a predominant K-selection. On the other hand, when parameters are changed in order to decrease predation risk, predominant r-selection is always achieved. Such outcome is only possible by assuming that preys face density-dependent selection even in abscence of predators (trait ζ affects both r and l). If this is not assumed, the direction of selection would not

change with density because K grows linearly with r ($K = r/l$). In this sense, the assumption of density-dependent selection elucidates how the r/K theory interplays with eco-evolutionary dynamics.

Since the famous work of Pianka (PIANKA, 1970), the r/K theory has been used to study life-history evolution. Indeed, empirical data supports the match between population regulation processes and life-histories in nature (GADGIL; SOLBRIG, 1972; FRANCO et al., 1996; OLI, 2004; BIELBY et al., 2007; AKTIPIS et al., 2013). However, as we show, r/K theory does not require the assumption that trait selection must affect life-history. Instead, it only requires the assumption that selection is density-dependent. In this sense, r/K theory only describes how selection on traits is affected by density. The life-history of an organism is not a trait, but rather a pattern of reproduction, somatic maintenance and senescence (VITT; CALDWELL, 2013). Because these processes happen at different moments during individual lifetime, different traits play different roles in life-history at each moment. The fast-slow life-history continuum is related on how fast reproduction and maturation happens during organisms life. As we show in the second chapter, maturation rate does not directly influences the overall population density, and therefore it cannot be tracked unless stage structure is assumed. In this sense, the applications of the r/K theory seem to be beyond life-history adaptation. In fact, the fast-slow life-history seems to be a special case of the r/K continuum.

3.1 Future Directions

Many interesting questions could be evaluated from our results. One question that stands is how the shape of density-dependence affects the results of our study. The answer could be elucidated by using the θ-logistic function (ROSS, 2009; ABRAMS, 2009), and evaluating how the value of θ changes the outcome, or by assuming a dynamical prey resource. Another relevant point is the fact that all models tested here are based on the idea that nature is stationary. Even when seasonality, stochasticity and/or cycles are achieved, the long term run of the dynamics is always a predictable, recurrent dynamic (CHESSON, 2017). However, nature is far from stationary, specially in cases of gradual environmental change, as we face nowadays. To overcome such challenge, theory may benefit from the assumption of an asymptotic environmentally determined trajectory (AEDT) (CHESSON, 2017). AEDT assumes a continuous, non-recursive environmental change. In this sense, the equilibrium points are always changing, depending on the trajectory. It would be interesting to evaluate how the outcome of interac-

tion is affected when, for example, handling time and sensitivity to density is affected by these asymptotic trajectories. We believe that, integrating such framework into eco-evolutionary dynamics may enhance our ability to predict ecological and evolutionary dynamics, and maybe increase the applicability of biological theories.

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Part II - Articles

The eco-evolutionary dynamics of a predator-prey model under r- and K-selective environments

The American Naturalist

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Abstract

The context dependence of selective pressures suggests that the outcome of ecological interactions may vary with the environmental context. Several empirical and theoretical studies indicate that the role of predator in prey adaptation is dependent on how density regulation emerges in prey populations. In this sense, it is expected that the outcome of predator-prey interactions that happen in different density regulation contexts may differ. Here, we investigate a system of differential equations describing the eco-evolutionary dynamics of predator-prey populations. We partition the gradient of selection into its r- and K-selection components and evaluate how population parameters affect systems dynamics under different selective contexts. We found that r-selective contexts tended to present more unstable dynamics than K-selective contexts. Alternately, interactions happening in K-selective contexts tended to be more stable. We discuss the implications of our findings for the theory of density-dependent selection and eco-evolutionary dynamics.

Introduction

Fitness-related traits can affect many biological functions (Abrams & Matsuda 1997, DeLong 2017) and the outcome of evolution depends on the net effect of selective pressures acting on that trait (DeLong 2017, McPeek 2017). In this sense, fitness is context-dependent (Travis et al. 2013). The context may influence fitness by changing either the genetic expression (Jaenisch & Bird 2003), the relevance of that trait to ecological interactions (McPeek 2017), or both (Jarvis et al. 1998). In the case where ecological interactions change the relative importance of a trait, adaptation may also change the nature of interaction (Gangur et al. 2017, TerHorst et al. 2018). If adaptation is fast enough to alter ongoing ecological interactions and this alteration also changes the ongoing adaptive processes, eco-evolutionary dynamics theory may help to explain the mechanisms of evolution (Hairston et al. 2005, Pelletier et al. 2009).

The eco-evolutionary theory is based on the idea of reciprocity between ecology and evolution (Reznick 2013). There is, ecology alters evolution, and evolution alters ecology, forming a feedback loop (eco-evo feedback). This reciprocity happens when there is temporal convergence between ecology and evolution (Hairston et al. 2005). The most common route of reciprocity is density-dependent selection (DDS) (Kokko & López-Sepulcre 2007, Travis et al. 2013). DDS happens when some property of natural selection (strength, direction or shape) changes due to shifts in population density (Clarke 1972, Mueller 1997). Therefore, DDS suggests that the ecological context of natural selection depends on population density.

One of the earliest proposed mechanisms to explain how density alters selection is in the work of MacArthur (1962). In such paper, Robert MacArthur gives a mathematical formulation on how the population carrying capacity replaces the intrinsic growth rate as a measure of fitness when population is crowded. This mechanism was used to formulate the theory of r- and K-selection (hereafter r/K theory) in MacArthur & Wilson (1967). The r/K theory is based on the parameters r and K, from the logistic growth equation. Later, this theory was used to predict how life-history traits evolve in response to population density (Pianka 1970). Because a simple

r/K axis is not likely to be enough to explain the variety of life-history traits, this idea generated an extensive discussion on the applicability of the r/K theory (Reznick et al. 2002). However, the r/K theory in its original formulation is simply a mechanism for DDS (Boyce 1984, MacArthur 1962, Roughgarden 1971).

Incorporating ecological scenarios in evolutionary dynamics is one way to enhance the predictability of evolutionary biology theory (Lässig et al. 2017). This is because ecological interactions change the context of natural selection, altering the dynamics of evolutionary processes. In a *in vitro* experiment, Nakamura et al. (2006) found differences on the microevolution of cells cultivated under r-selection *versus* in K-selection environments. Many other studies found results that corroborate to the prediction that the outcome of evolution is different for r- and K-selection environments (Aleksic et al. 1993, Becks & Agrawal 2013, Engen & Sæther 2016, Engen & Saether 2017, Mueller & Ayala 1981). However, less attention was given for the role of r- and K-selection on inter-specific interactions, such as predation (Reznick et al. 2002).

The idea of context-dependent fitness implies that we should expect different outcomes depending on the structure of inter-specific interaction. Studies suggest that the risk of predation alters the eco-evolutionary outcome of preys (DeLong & Luhring 2018, Khater et al. 2016, Reznick & Endler 1982), and this effect depends on how density regulation emerges in prey populations (Farkas & Montejo-Kovacevich 2014, Jeschke & Tollrian 2000, Reznick et al. 2001). These studies imply that the predictability of eco-evolutionary dynamics in natural populations may be a function of both the inter and intra-specific ecological interactions of evolving populations.

Because of the increasing evidence that predator-prey dynamics are strongly affected by eco-evolutionary dynamics (Cortez 2015, Friman et al. 2014, Hairston et al. 2005, Hiltunen & Becks 2014, Jones & Ellner 2007, Yoshida et al. 2003) we find relevant to discuss the implications of different selective contexts to eco-evolutionary dynamics of predator-prey systems. Here, our goal was to explore the relationship between the r/K theory and the eco-evolutionary dynamics of a predator-prey system. We focused on two questions: 1) How does system stability behaves over an r/K continuum axis?; and 2) How do predator parameters affects stability when natural

selection on prey is predominant *r*- or predominant *K*-selection? We show how DDS bridges r/K theory and eco-evolutionary theory, and how the nature of selective regimes alters the stability of predator-prey systems.

Methods

General Approach

We use a simple model of ordinary differential equations to describe the eco-evolutionary dynamics of a predator-prey system. We use the quantitative genetics framework from Lande (1976) and Abrams, Matsuda & Harada (1993). Here, letters P and N represent the densities of predator and prey population, respectively. In our model, prey vulnerability to predation is represented by a quantitative trait ζ. We assume genetic variability in ζ which allows the average vulnerability, $\overline{\zeta}$, to evolve in response to selection. The evolution of $\overline{\zeta}$ happens fast enough to affect and be affected by ecological dynamics (population densities), forming an eco-evolutionary feedback loop (Schoener 2011). Because quantitative traits usually affect many biological functions through pleiotropy (Cheverud 1996), we assume that vulnerability also affects prey growth rate. In this sense, natural selection over trait will be composed by the selective pressures generated by the influence of trait value in the biological functions.

Ecological Dynamics

We assume that the growth rate of prey population depends on both N and P, and on the average trait value $\overline{\zeta}$. The equation describing prey population dynamics is:

$$\frac{dN}{dt} = g(N, \overline{\zeta}) - f(N, P, \overline{\zeta}) \tag{1a}$$

where the function $g(N, \overline{\zeta})$ describes the interactions among prey individuals as a function of their phenotypes and population density. The function $f(N, P, \overline{\zeta})$ is the predator functional response on prey population.

Because ζ alters predator fitness by either affecting their numerical response and/or their functional response, predator population growth will also depend on all three variables (N, P and $\bar{\zeta}$). The equation that defines the population growth of P is:

$$\frac{dP}{dt} = b(P, N, \bar{\zeta}) \tag{1b}$$

The function $b(P, N, \bar{\zeta})$ in equation 1b describes how energy acquired from consuming N is converted into new predators, and how much it is used on the maintenance of other fitness-related activities (e.g. thermoregulation, immunological responses).

Evolutionary Dynamics

Evolution is defined as the temporal change in the frequency of genotypes in a given population (see McPeek 2017). This change can be tracked either by direct measures of alleles frequency, or by the change in the average trait value of a population (Lion 2017). In this paper, we assume that evolutionary change is the change in the average trait value. The rate of change in $\bar{\zeta}$ is proportional to the additive genetic variance (heritability, H^2, multiplied by the phenotypic variance σ^2) of that trait and to the gradient of selection (Abrams, Matsuda & Harada 1993, Lande 1976). The later is calculated by taking the partial derivative of the mean fitness in respect to individual trait value averaged over the trait distribution. If we assume that trait distribution is constant and relatively narrow around the mean, theory predicts that the selection gradient can be approximated by the partial derivative of individual fitness with respect to individual trait and evaluated where $\zeta = \bar{\zeta}$ (Abrams 2014, Abrams & Matsuda 1997, Abrams, Matsuda & Harada 1993, Abrams, Harada & Matsuda 1993, Lande 1976, Matsuda & Abrams 1994, McPeek 2017). Thus, the rate of change in $\bar{\zeta}$ is given by:

$$\frac{d\bar{\zeta}}{dt} = v(\bar{\zeta}) \left. \frac{\partial}{\partial \zeta} \left[\frac{dN}{Ndt} \right] \right|_{\zeta = \bar{\zeta}} \tag{1c}$$

Where $v(\bar{\zeta})$ is the function describing the additive genetic variance. Together, equations 1a, 1b and 1c describe the general eco-evolutionary dynamics of a predator-prey system.

Tracking r- and K-Selection

r/K theory is a DDS model based on the logistic equation (Boyce 1984, Reznick et al. 2002). Because of this, we must assume that the function g in equation 1a is a logistic equation, therefore:

$$g(N,\overline{\zeta}) = N[r(\overline{\zeta}) - l(\overline{\zeta})N] \tag{2a}$$

where r is the intrinsic growth rate and l is the sensitivity to depressant effects of density (Travis et al. 2013). Equation 2a can be also written in the carrying capacity format:

$$g(N,\overline{\zeta}) = Nr(\overline{\zeta}) \left(1 - \frac{N}{K(\overline{\zeta})}\right) \tag{2b}$$

where K is the carrying capacity and equals to $r(\overline{\zeta})/l(\overline{\zeta})$ (see Ross (2009) for details on this transformation).

Now, the gradient of selection in equation 1c can be also written as:

$$\frac{\partial}{\partial \zeta}\left[\frac{dN}{Ndt}\right]\bigg|_{\zeta=\overline{\zeta}} = \frac{\partial}{\partial \zeta}\left[\frac{g(N,\overline{\zeta})}{N}\right]\bigg|_{\zeta=\overline{\zeta}} - \frac{\partial}{\partial \zeta}\left[\frac{f(N,P,\overline{\zeta})}{N}\right]\bigg|_{\zeta=\overline{\zeta}}. \tag{3}$$

Using the format of equation 2b, we can rewrite function $g(N,\overline{\zeta})$ as $g(N,r(\overline{\zeta}),K(\overline{\zeta}))$. Therefore, the first term in the right hand side of equation 3 will be, by the chain rule from Calculus:

$$\frac{\partial}{\partial \zeta}\left[\frac{g}{N}\right]\bigg|_{\zeta=\overline{\zeta}} = \left[\frac{\partial(g/N)}{\partial r}\frac{dr}{d\zeta} + \frac{\partial(g/N)}{\partial K}\frac{dK}{d\zeta}\right] \tag{4a}$$

Where the first and the second term inside the brackets in the right hand side of equation 4a describe how selection acts over ζ through $r(\zeta)$ and $K(\zeta)$, respectively. Despite the fact that $K = r/l$, the first term inside the brackets in equation 4a must be derived considering only $r(\zeta)$ that is evident in equation 2b because it is where we assume r-selection is acting. The first term in the right hand side of the gradient selection (equation 3) becomes:

$$\frac{\partial}{\partial \zeta}\left[\frac{g}{N}\right]\bigg|_{\zeta=\overline{\zeta}} = \left[\left(1 - \frac{N}{K}\right)r'\right] + \left[\left(\frac{rN}{K^2}\frac{r'l - rl'}{l^2}\right)\right] \tag{4b}$$

Now, replacing K for r/l leads to

$$\frac{\partial}{\partial \zeta}\left[\frac{g}{N}\right]\bigg|_{\zeta=\overline{\zeta}} = \underbrace{\left[r'\left(1 - \frac{lN}{r}\right)\right]}_{r\text{-selection}} + \underbrace{\left[N\left(\frac{r'l}{r} - l'\right)\right]}_{K\text{-selection}} \tag{4c}$$

Where the first and the second term inside the brackets in equation 4c are the *r*- and *K*-selection terms (r_{sel} and K_{sel}), respectively. These terms are based on individual trait value which is the central unit of evolutionary biology (Suber 2000). The carrying is not a trait. Instead, it emerges from the current population density and phenotipic distribution (Kokko & López-Sepulcre 2007, Rueffler et al. 2006). In this sense, our model allows to capture *K*-selection based on individual traits.

Note that increasing density also increases the quantity $r'lN/r$ in equation 4c. This quantity describes how population density shifts the overall selection from *r*- to *K*-selection. Thus, equation 4c predicts that increasing population density decreases *r*-selection and increases *K*-selection. If we simplify equation 4c we get $r' - Nl'$, which is the gradient selection derived from logistic equation in the original format (equation 2a). Thus, the quantity $r'lN/r$ does not affect trait evolution, but allows us to track how shifts in density change the selective milieu experienced by prey.

Specific Model and Stability Analysis

We analysed a specific case of system 1. We assume that the function *g* in equation 1a is identical to equation 2a. Therefore, both the intrinsic growth function, *r*, and the sensitivity to depressant effects of density, *l*, are increasing functions of trait. The interpretation of equation 2a is that increasing values of ζ increases the rate of successful reproduction but also increases the negative effects of population crowding. We assume that predators exert a Holling type II functional response (Holling 1959) with handling time *h*. The quantitative trait ζ represents prey vulnerability to predation. Predators only attack vulnerable preys, thus the attack rate is defined by ζ. In this sense, decreasing vulnerability to predation affects both *r* and *l* through ecological pleiotropy (DeLong 2017). Predators are assumed to be specialists and have a linear numerical response.

The ecological subsystem of this system is described by the following equations:

$$\frac{dN}{dt} = N\left[a + b\bar{\zeta} - N(k_0 + k_1\bar{\zeta}) - \frac{\bar{\zeta}P}{1 + h\bar{\zeta}N}\right] \tag{5a}$$

$$\frac{dP}{dt} = P\left[e\frac{\bar{\zeta}N}{1 + h\bar{\zeta}N} - d\right] \tag{5b}$$

Where a and b in 5a represent the innate growth rate and the trait-dependent growth rate, respectively. k_0 and k_1 represent the innate sensitivity to density and the trait-dependent sensitivity to density, respectively. e and d in equation 5b are the predators conversion rate and death rate, respectively. This ecological subsystem is analogous to the Rosenzweig-MacArthur predator-prey model.

Prey individual fitness, dN/Ndt, is evaluated at the individual trait value, ζ. However, because predator satiation is a function of the average vulnerability value, prey fitness is dependent of both individual trait ζ and the average value $\bar{\zeta}$ (Abrams & Matsuda 1997). The equation describing prey fitness is:

$$\frac{dN}{Ndt} = a + b\zeta - N(k_0 + k_1\zeta) - \frac{\zeta P}{1 + h\bar{\zeta}N}.$$

We assume a constant and narrow distribution for prey phenotypes. Thus, we kept both heritability and phenotype variance as constants: $H^2\sigma^2 = V$. Where V is the additive genetic variance. Under our assumptions, the rate of change in the average trait value is

$$\frac{d\bar{\zeta}}{dt} = V\chi(\bar{\zeta})\left[b - k_1N - \frac{P}{1 + h\bar{\zeta}N}\right] \tag{5c}$$

where the function $\chi(\bar{\zeta})$ is a boundary function that precludes trait value from trespass biologically reasonable values. We assume only a bottom limit to trait, thus $\chi(\bar{\zeta}) = exp(-s/\bar{\zeta} - s)$, where s is the bottom limit for trait values. This function is the same used in Abrams & Matsuda (1997). If $k_1 = 0$ system 5 goes back to exactly the same model analysed in Abrams & Matsuda (1997).

The equilibrium densities and equilibrium trait value for system 5 for preys, predators and

trait value are:

$$N_e = \frac{a}{k_0} \tag{6a}$$

$$P_e = \frac{eb}{e - dh} \left(1 - \frac{ak_1}{bk_0} \right) \tag{6b}$$

$$\overline{\zeta_e} = \frac{dk_0}{(e - dh)a} \tag{6c}$$

Where subscript e in the left hand side of equations 6a, 6b and 6c indicates equilibrium density or equilibrium trait value. The equilibrium points for the case where $k_1 = 0$ are discussed in Abrams & Matsuda (1997). Note that assuming $k_1 > 0$ does not change prey equilibrium nor trait equilibrium. However, it reduces predator equilibrium density. Predator equilibrium increases with bk_0 and decreases with ak_1. When this two quantities are equal, predator can no longer persist in the environment. The Jacobian Matrix and the Routh-Hurwitz conditions for stability can be found in section "Stability Analysis" of Appendix A.

r- and K-Selection Terms

The r- and K-selection terms (r_{sel} and K_{sel}, respectively) are omitted in equation 5c for simplicity, but their quantities are

$$r_{sel} = b \left(1 - \frac{(k_0 + k_1\zeta)N}{a + b\zeta} \right) \tag{7a}$$

and

$$K_{sel} = N \left(\frac{b(k_0 + k_1\zeta)}{a + b\zeta} - k_1 \right) \tag{7b}$$

respectively. Stability between r_{sel} and K_{sel} implies that $r_{sel} + K_{sel} = 0$. Which leads to

$$\frac{r_{sel}}{K_{sel}} = -1 \tag{8a}$$

When this happens, r- and K-selection terms cancel out and the quantity $\partial(g/N)/\partial\zeta$ becomes 0. In this case, trait adaptation is guided solely by predation pressure. Thus, trait value will

decrease until $\overline{\zeta} = s$. If s is too small, the attack rate of predators becomes so low that predators will be brought to extinction. In our case, quantity 8a is

$$bk_0 = ak_1 \tag{8b}$$

Solving this quantity for any prey parameter will give us the prey parameter value that precludes predators from persist.

For coexistence to be possible, r- and K-selection terms must not cancel out. This happens, for example, when

$$\frac{r_{sel}}{K_{sel}} = 1 \tag{9a}$$

which in our case translates into the following balance between predator and prey parameters:

$$\frac{e}{d} - h = \left(\frac{bk_0}{a} - k_1 \right) \left(\frac{bk_0}{a(bk_0 - ak_1)} \right) \tag{9b}$$

Equality 9b tell us that all prey and predators parameters affect the equality between r- and K-selection terms. Solving this equation for any parameter will give us the predator or prey parameter that allow for coexistence in a environment where r- and K-selection terms are equal.

Simulations

To evaluate the behaviour of r- and K-selection gradients for a range of parameters we calculated the mean value between the maximum and minimum values of the long term dynamics of the r_{sel} and K_{sel} terms. All the bifurcation diagrams were performed for a 0.01 parameter interval. To skip the transient dynamics, we used the last 2000 values from simulated time series of 10000 time-steps. We performed all our numerical analysis in R (R Development Core Team 2011). The R codes for the models and figures of this paper are deposited at https://github.com/pbolanhom/CI.

To generate the continuum between predominant r- and K-selection we performed bifurcation diagrams for a range of parameters that increases the quantity $r'Nl/r$ when densities and trait

value are at equilibrium. To evaluate how predators parameters affect system dynamics in r- and K-selective environment, we performed bifurcation diagrams for a range of predators parameters in two situations: when the parameter that generates the continuum is at its value that generates r- and K-selection.

We show a table with parameters interpretations in the Appendix A.

Results

The Effect of Prey Innate Growth Rate on System Stability

As we can see in equations 6a, 6b and 6c, prey growth rate, a, influences the interior equilibrium points of all three variables. Increasing a increases prey equilibrium density and decreases both equilibrium value of predator density and trait value. An interpretation of this is that the larger the innate growth rate smaller is the advantage of ζ to prey because prey reaches the carrying capacity in a faster pace. Once the carrying capacity is reached, trait becomes disadvantageous to prey. This is because at the carrying capacity selection gives advantage to phenotypes that are less sensible to depressant effects of population growth (low $l(\zeta)$).

In the context of r/K theory, the quantity $Nr'l/r$ from equation 4c translates into the following

$$ba \left(\frac{a(e-dh) + k_1 d}{a^2(e-dh) + bdk_0} \right). \tag{10}$$

Quantity 10 obviously increases with a, which means that increasing the innate growth rate decreases r-selection (r_{sel}) and increases the K-selection term (K_{sel}). In this sense, a continuum between an r- and K-selection is generated for a range of a values. Figure 1 shows the properties of this continuum. When a is between the interval $0 < a < 0.294$ system produces a runaway evolution of increasing $\bar{\zeta}$. This type of dynamics are unstable because it increases indefinitely the trait value, leading population dynamics to cycles that increases in amplitude at each time-step. For the interval $0.295 < a < 1.37$ system produces a stable state that increases as a gets larger. Limit cycles happen within the interval $1.38 < a < 1.59$. Increasing a within such interval

increases the period between this cycles. When a is equal or larger than 1.6, predators cannot persist because the carrying capacity is reached so fast that selection leads trait value to its minimum value ($\overline{\zeta} = s$). The time series and phase space for these dynamics are in the "Time Series" section of the Appendix A.

Solving equation 9b for a (this algebraic treatment is on the "Parameter Values" section of Appendix A) gives us the point where the innate growth rate allows for equality between r_{sel} and K_{sel} ($a = 0.64$). This value is shown as a vertical black line in figure 1. For our set of parameters, stability happens for a larger range of predominant K-selection than for predominant r-selection. In fact, the runaway dynamic turns into a stable state at the same point where r-selection starts to decrease and K-selection starts to increase (figure 1d). When a is exactly bk_0/k_1, $K_{sel} = 0$. When a is larger than this value, K_{sel} decreases exponentially to negative values. From this point forward K_{sel} is negative, but its magnitude is much larger than r_{sel}.
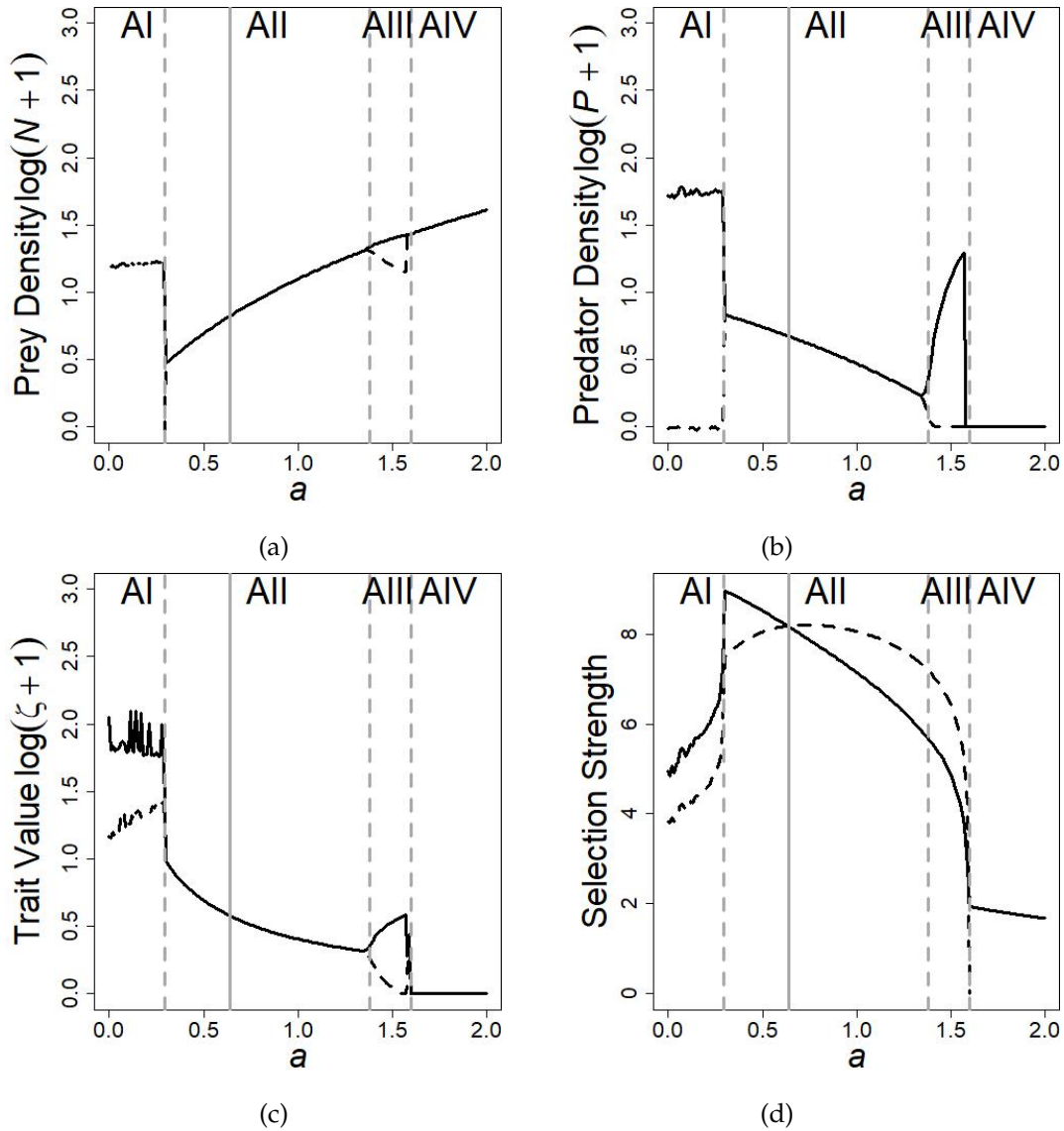
Figure 1: System 5 stability for a range of a values. Panel a), b) and c) are the maximum (solid black lines) and minimum (dashed black lines) for prey density, predator density and trait value, respectively. Panel d) illustrates how r_{sel} (solid black line) and K_{sel} (dashed black line) behave for the range of a values. Solid grey line separates the plot area where r-selection is predominant ($a < 0.64$) and the area where K-selection is predominant ($a > 0.64$). The type of system behaviour is denoted by A, separated by the dashed grey lines: AI is the runaway evolution; AII is the steady state; AIII is the limit cycles; and AIV is the predator extinction. Parameters are: $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$. Initial conditions are: $N = 0.5$, $P = 0.5$, $\overline{\zeta} = 1$.

The Effects of Predator Parameters in Predominant r- and in Predominant K-Selection

a values that are greater than the *a* value that allows equality 9b generate a predominant *K*-selection, while smaller values generate predominant *r*-selection. In this sense, symmetrical values such as $a = 0.34$ and $a = 0.94$ generate predominant *r*- and *K*-selection environments. An illustration of these environments is on the section "The *r*- and *K*-Selective Environments" in Appendix A. Because *a* affects all equilibrium values, we predict that the outcome of a predator-prey interaction may be different when it happens in a predominant *r*-selective environment *versus* in a predominant *K*-selective environment.

Figures 2, 3 and 4 show how theses differences emerge. In *r*-selective environments, runaway dynamics happened for small values of conversion efficiency ($0.5 < e < 0.89$) and large values of both handling time and death rate ($1.16 < h < 2$ and $0.56 < d < 1$, respectively). In all the cases, the outcome of interaction in *K*-selective environment presented a reduced range of parameter that generated runaway evolution ($0.5 < e < 0.56$, $1.84 < h < 2$ and $0.91 < d < 0.1$).

Limit cycles happened for small values of death rate in both *r*- and *K*-selective environments ($d < 0.08$ and $d < 0.33$, respectively) and for large values of conversion efficiency in *K*-selective environments ($e > 2.2$). In the case of death rate, the amplitude of cycles was greater in the *K*-selective environment than in *r*-selective environment. In all the cases, cycles amplitude was greater for predator density, followed by trait values and then prey density.

For handling time and death rate, steady states happened for a larger range of parameters in *K*-selective environment ($0 < h < 1.83$ and $0.34 < d < 0.9$) and compared to *r*-selective environment ($0 < h < 1.15$ and $0.09 < d < 0.55$). On the other hand, the range of conversion efficiency for which system produced a stable state was greater in the *r*-selective environment than for *K*-selective environment ($e > 0.9$ and $0.57 < e < 2.1.$, respectively).

In the section "The Effects of Predator Parameters on the r/K Continuum" of the appendix A we show how r_{sel} and K_{sel} are affected by predators parameters. It is important to note that

these parameters change the relative contribution of each selective force for the overall natural selection. In this sense, although our analyses were based on the selective environment generated by prey innate growth rate value, this environment changes for the range of each predator parameter. We discuss more about this dynamic in the Appendix A.
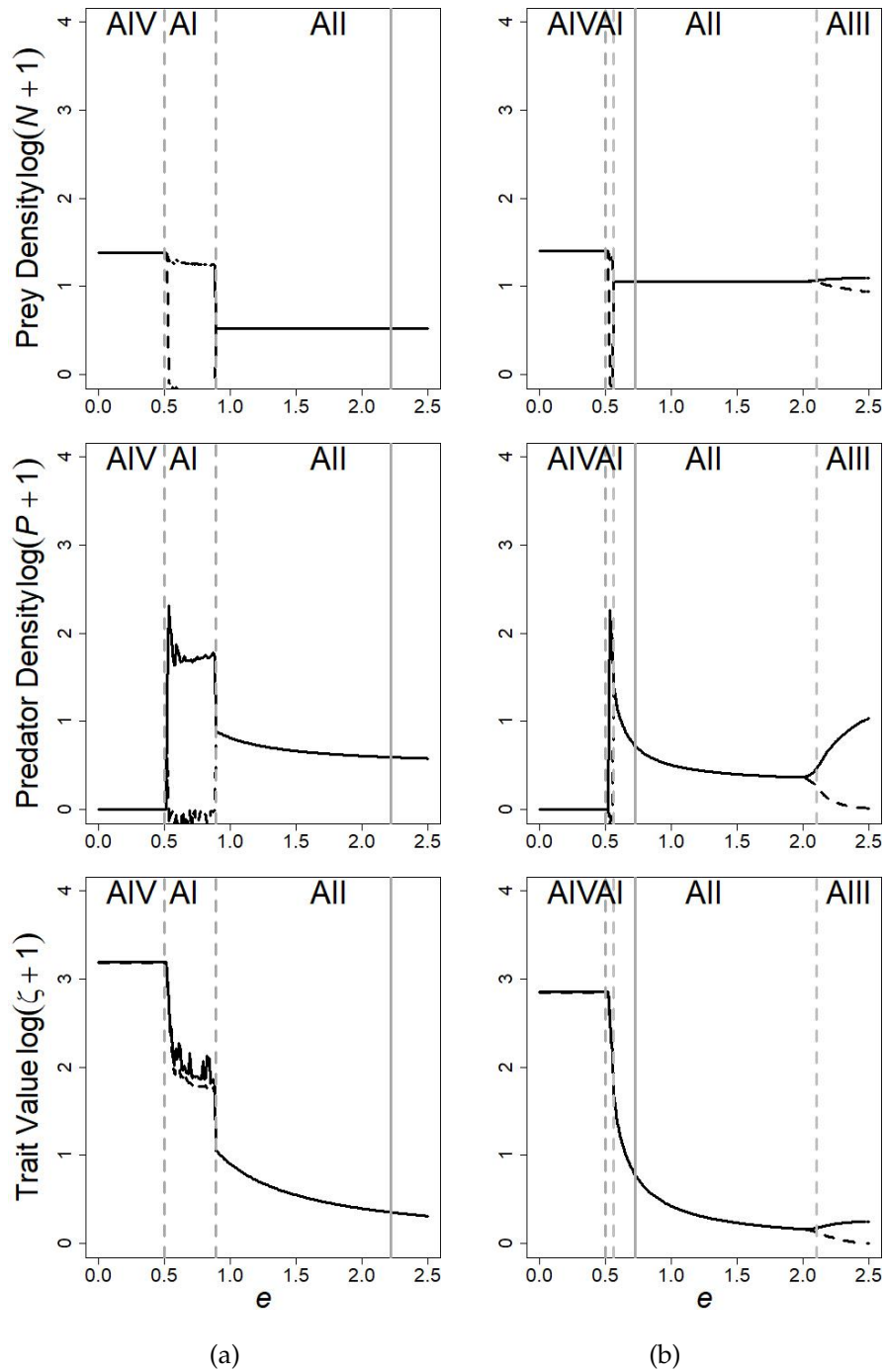
Figure 2: Maximum (solid black lines) and minimum (dashed black lines) values of prey density (top row), predator density (middle row) and trait value (bottom row) for a range of conversion efficiency values in: a) Predominant r-selection ($a = 0.34$); and b) Predominant K-selection ($a = 0.94$). Solid grey line separates the plot area where r-selection is predominant and the area where K-selection is predominant. The type of system behaviour is denoted by A, separated by the dashed grey lines: AI is the runaway evolution; AII is the steady state; AIII is the limit cycles; and AIV is the predator extinction. Parameters: $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$; Initial conditions: $N = 0.5$, $P = 0.5$, $\overline{\zeta} = 1$
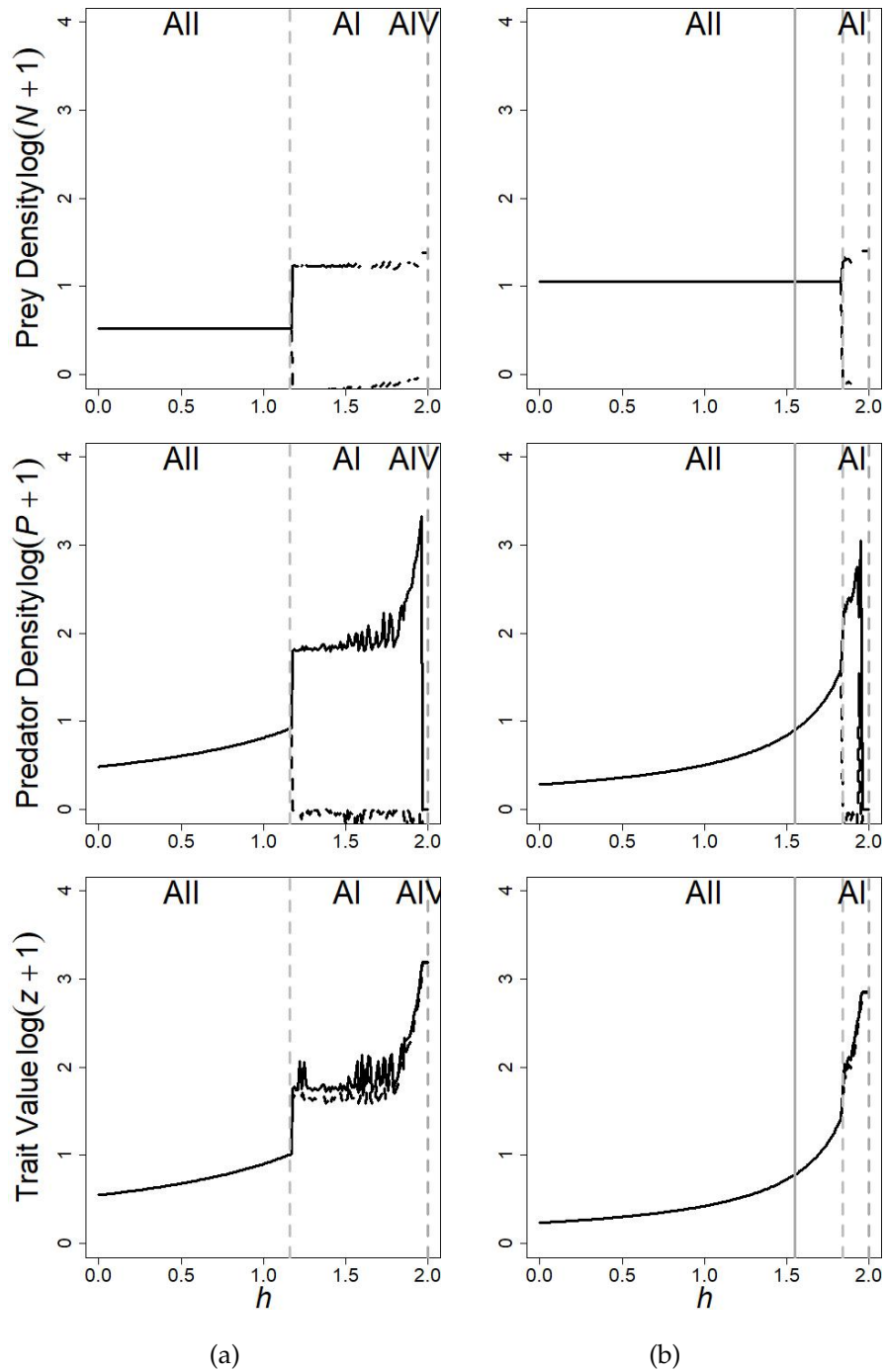
Figure 3: Maximum (solid black lines) and minimum (dashed black lines) values of prey density (top row), predator density (middle row) and trait value (bottom row) for a range of handling time values in: a) Predominant r-selection ($a = 0.34$); and b) Predominant K-selection ($a = 0.94$). Solid grey line separates the plot area where r-selection is predominant and the area where K-selection is predominant. The type of system behaviour is denoted by A, separated by the dashed grey lines: AI is the runaway evolution; AII is the steady state; and AIV is the predator extinction. Parameters: $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$; Initial conditions: $N = 0.5$, $P = 0.5$, $\bar{\zeta} = 1$
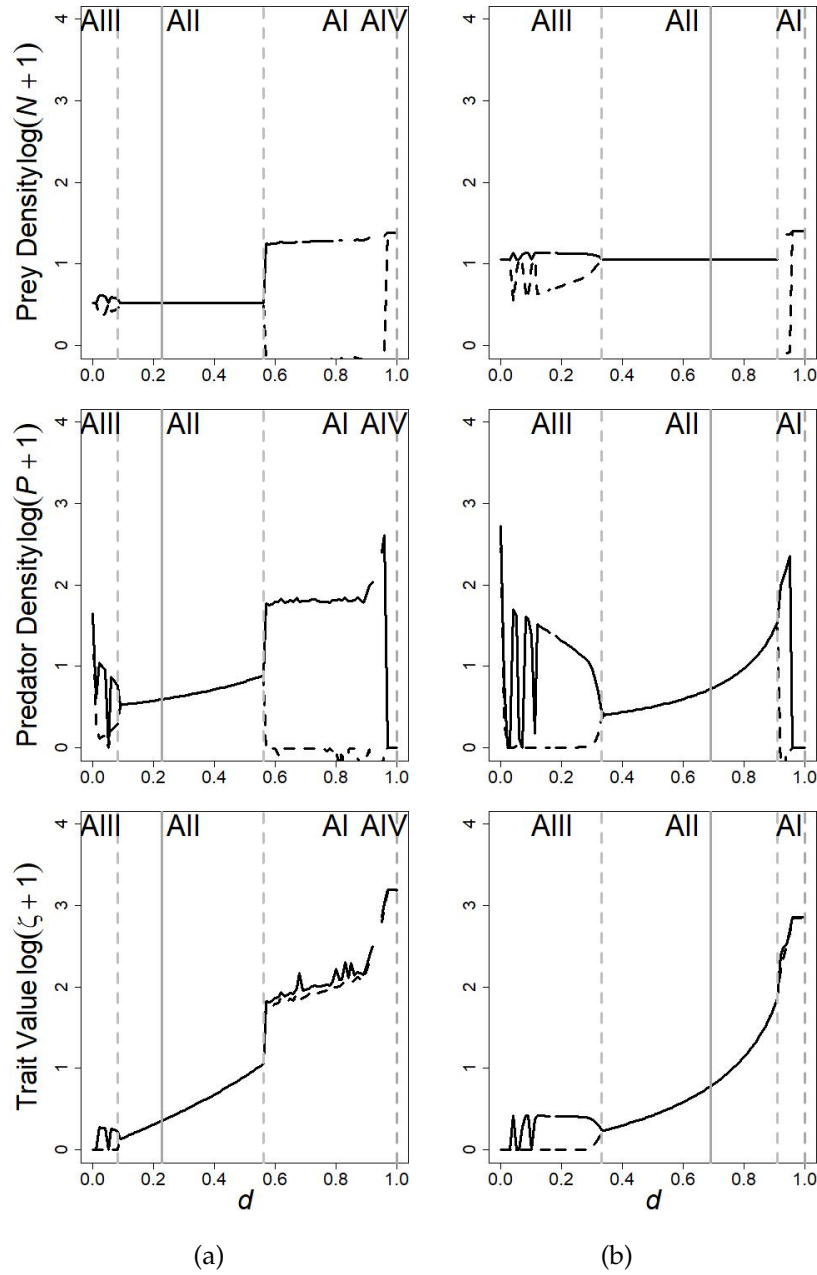
Figure 4: Maximum (solid black lines) and minimum (dashed black lines) values of prey density (top row), predator density (middle row) and trait value (bottom row) for a range of death rate values in: a) Predominant r-selection ($a = 0.34$); and b) Predominant K-selection ($a = 0.94$). Solid grey line separates the plot area where r-selection is predominant and the area where K-selection is predominant. The type of system behaviour is denoted by A, separated by the dashed grey lines: AI is the runaway evolution; AII is the steady state; AIII is the limit cycles; and AIV is the predator extinction. Solid grey line denotes the are in the panel where Parameters: $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$; Initial conditions: $N = 0.5$, $P = 0.5$, $\bar{\zeta} = 1$

Discussion

The effects of predation on prey in environments with different selective milieu are expected to produce different outcomes (Farkas & Montejo-Kovacevich 2014, Reznick et al. 2001). However, this effect on *r*- and *K*-selective environments were poorly explored. In this paper, we used a simple system of ordinary differential equations to explore how r/K theory relates to the eco-evolutionary dynamics of predator-prey interactions.

In this paper, we shown how density-dependent selection can be used to bridge r/K theory and eco-evolutionary dynamics. By assuming that trait adaptation affects the logistic growth of a population dynamics, the *r*- and *K*-selection dynamics can be tracked from eco-evolutionary dynamics. Our derivation of *r*- and *K*-selection terms is similar to the one used in some other studies. In Tanaka (1996) the author used a similar decomposition of the overall natural selection, but he assumed genetic variability in the carrying capacity. The problem with this assumption is that the carrying capacity is an emergent property of populations, rather than a real trait (Kokko & López-Sepulcre 2007, Rueffler et al. 2006). This assumption is likely valid if we derive the carrying capacity from the first principles of population dynamics. Engen et al. (2013) also derived the *r*- and *K*-selection terms in a stochastic model. Although both derivations are useful, neither considered temporal convergence between ecological and evolutionary processes. Also, most of the theoretical papers on r/K theory focused on single population dynamics, with not much attention in inter-specific interactions.

As noted by Pianka (1970), no species will be purely *r*- or *K*-selected, but will be found in a position along the r/K continuum. Indeed, our results suggest that, to our system, both extremities of the continuum produce unstable dynamics. However, instability for each extremity was generated by different processes. For strong *r*-selection, instability comes in the form of runaway dynamics. Runaway evolution consists of a continuous change in trait value (Matsuda & Abrams 1994) on the direction of increasing fitness. As pointed out by Abrams & Matsuda (1997) this behaviour happens when the interior equilibrium is locally unstable and population

dynamics produce cycles. Runaway processes are usually thought to happen in the context of sexual selection (McLeod & Day 2017) and for epigenetic processes such as maternal effects (Mousseau & Fox 1998). On the other extremity of the continuum, a strong K-selection precludes predator from persisting. In our model this happens because the innate growth rate is so high that population reaches the carrying capacity rapidly and with no great contribution of trait value. This translates into selective disadvantage of vulnerable phenotypes, and selection gives advantage for less vulnerable phenotypes, decreasing trait value until its minimum value.

Our results show that K-selection increases the stable state of the system for a range of predator handling time and death rate, while r-selection increases the stable state for a range of predator conversion efficiency. This means that, in r-selection environments, we expect to find stable interactions for a larger variety of predator conversion efficiency. On the other hand, we expect to find a stable interaction for a larger range of both handling time and death rate of predators in K-selection environments. Perhaps, because in r-selective environments prey species tend to be less controlled by its own density, predators are able to persist with high rates of conversion efficiency. On the other hand, the pressure of population crowding in K-selective environments is the dominant selective pressure, and prey population faces a greater mortality from this pressure. In this sense, even when the handling time and the death rate of predators is large, prey population density is not able to increase much more, precluding the processes that generate runaway evolution. Because the intrinsic mortality of populations in r-selective environments are usually density-independent (Pianka 1970, Reznick et al. 2002), predator parameters reduce trait equilibrium value (such as e) and can keep the outcome of interaction stable. But predators parameters that increase trait equilibrium value (such as h and d) can destabilize the system because prey is already experiencing density-dependent mortality in K-selective environments.

The simplicity of our model precludes us from giving more realistic predictions. In the ecological context, increasing the number of species in the food-web may enhance biological realism. This can be done either by adding species to existing trophic levels (such as competitors of either preys or predators) or to new trophic levels (such as apex predators or prey resource). Ecological

systems in continuous time with at least three species are known for their ability to generate a broad range of patterns found in nature (oscillations, chaos, stable states) (Hastings & Powell 1991). Complexity can be also enhanced by assuming some kind of population structure (e.g. age, sex), or by explicitly assuming a spatial structure to the environment. In the evolutionary context, pleiotropic effects are unlikely to be simple linear functions. A quadratic or a hyperbolic function will probably enhance biological realism (Abrams & Matsuda 1997). The shape of pleiotropic function plays an important role in shaping the conditions for species coexistence (Schreiber et al. 2016). Furthermore, we assume that prey vulnerability to predation is an unimodal trait. However, this unimodality is not always true. Indeed, for traits like speed, unimodality is probable true (prey must always run faster than predators, otherwise they will always get caught) (Abrams 2000). On the other hand, traits like body size are likely bimodal, there is, prey can escape from predators by either becoming bigger or smaller (Palmer 1990).

We believe that the confusion around r/K theory comes from two major reasons. First is the fact that r/K theory is based on parameters that describe population properties. Indeed, evolution is observed at the population level (McPeek 2017). However, natural selection acts at the individual level (Suber 2000). In order to interpret the intrinsic growth rate and the carrying capacity at the individual level, we must assume that the processes driving population dynamics can be derived from the individual phenotypes that compose that population (Rueffler et al. 2006). The second reason is the fact that r/K theory is essentially a DDS model, and interpreting it as a theory of life-history evolution narrows its applicability (Boyce 1984). Life-history traits are too complex to be described by a single axis of r/K continuum. Furthermore, the idea of a continuum between r- and K-selection suggests that the applicability of r/K theory is restricted to traits that evolve differently under different density regimes. This counteracts with the idea that r-selection is a density-independent selection and K-selection is density-dependent selection (Parry 1981). In fact, our derivation (equations 4a, 4a and 4c) suggests that when the performance of a trait value is sensible to population density, r-selection is the behaviour of selection under low population density, and K-selection is the behaviour of selection under high population density.

Therefore, r-selection must be also interpreted in the context of DDS. In this sense, we suggest that r/K theory can be used to explain adaptation when the performance of a given phenotype under natural selection is sensible to shifts in density.

Appendix A

Stability Analysis

In the main text, we analysed the following eco-evolutionary predator-prey system:

$$\frac{dN}{dt} = N\left[a + b\bar{\zeta} - N(k_0 + k_1\bar{\zeta}) - \frac{\bar{\zeta}P}{1 + h\bar{\zeta}N}\right] \tag{A1a}$$

$$\frac{dP}{dt} = P\left[e\frac{\bar{\zeta}N}{1 + h\bar{\zeta}N} - d\right] \tag{A1b}$$

$$\frac{d\bar{\zeta}}{dt} = V\chi(\bar{\zeta})\left[b - k_1N - \frac{P}{1 + h\bar{\zeta}N}\right] \tag{A1c}$$

This system is exactly the system 5 in the main text. The description parameters are in table 1 in the section "Parameter Values". Since the function $\chi(\bar{\zeta})$ does not affect local stability (Abrams, Matsuda & Harada 1993), the Jacobian matrix (J) for the local stability of system A1 is:

$$J = \begin{bmatrix} \frac{\partial \dot{P}}{\partial P} & \frac{\partial \dot{P}}{\partial N} & \frac{\partial \dot{P}}{\partial \bar{\zeta}} \\ \frac{\partial \dot{N}}{\partial P} & \frac{\partial \dot{N}}{\partial N} & \frac{\partial \dot{N}}{\partial \bar{\zeta}} \\ \frac{\partial \dot{\bar{\zeta}}}{\partial P} & \frac{\partial \dot{\bar{\zeta}}}{\partial N} & \frac{\partial \dot{\bar{\zeta}}}{\partial \bar{\zeta}} \end{bmatrix} = \begin{bmatrix} \frac{e\bar{\zeta}N}{1+h\bar{\zeta}N} - d & \frac{e\bar{\zeta}P}{(1+h\bar{\zeta}N)^2} & \frac{eNP}{(1+h\bar{\zeta}N)^2} \\ -\frac{N\bar{\zeta}}{1+h\bar{\zeta}N} & r - 2lN - \frac{\bar{\zeta}P}{(1+h\bar{\zeta}N)^2} & N\left[r' - l'N - \frac{P}{(1+h\bar{\zeta}N)^2}\right] \\ -\frac{V}{1+h\bar{\zeta}N} & V\left[\frac{P\bar{\zeta}h}{(1+h\bar{\zeta}N)^2} - l'\right] & V\left[r'' - Nl'' + \frac{PNh}{(1+h\bar{\zeta}N)^2}\right] \end{bmatrix}$$

Where dots above each variable represent the time derivatives. The coefficients of the determinant of matrix J are used to calculate the Routh-Hurwitz criteria for stability. Stability will happen if all the coefficients are positive. Therefore, the Routh-Hurwitz criteria for stability of system A1 are

$$C_1 = a\left[\frac{Vh(e-dh)}{ek_0}\left(\frac{ak_1}{k_0} - b\right) + 1\right] - \frac{d^2h}{e(e-dh)}\left[2k_1 + \frac{bk_0}{a}\right] > 0 \tag{A2a}$$

$$C_2 = \frac{Vab}{k_0}\left(1 - \frac{ak_1}{bk_0}\right)\left[\left(\frac{d^2h^2}{e^2}\left(\frac{bk_0}{a} - k_1 - \frac{k_1e}{dh}\right) - \frac{ah(e-dh)}{e}\right)\right.$$

$$\left. - \left(1 - \frac{e-dh}{e}\right)\left(\frac{bdk_0h}{ae} - k_1\left(\frac{dh}{e} - 1\right)\right) + \frac{(e-dh)^2}{e}\right] + \frac{d^2}{e}\left(\frac{k_0b}{a} - k_1\right) > 0 \tag{A2b}$$

$$C_3 = \frac{V(e-dh)^2a}{ek_0}\left(b - \frac{ak_1}{k_0}\right)\left[a + \frac{2k_1d}{(e-dh)a}\right] > 0 \tag{A2c}$$

$$C_1C_2 > C_3 \tag{A2d}$$

Condition C_1 will be violated if a values are too small or if V, k_1, k_0 or b are too large. Also, this first condition will be violated if the quantity $e - dh$ is small. C_2 is violated if either a, k_1 or V are too large. In addition, C_2 is violated if b is too low. Condition C_3 will be violated when a is large and for small values of b and k_0. k_1 can maintain C_3 only between a small interval of negative and positive values.

Parameters

Whenever the parameter value is not the one under analysis, the values used are show in table 1.

Parameter	Interpretation	Value
a	Prey innate growth rate	0.34; 0.64; 0.94
b	Prey trait-dependent growth rate	0.8
k_0	Prey innate sensitivity to density	0.5
k_1	Prey trait-dependent sensitivity to density	0.25
e	Predator conversion efficiency	1
h	Predator handling time	1
d	Predator death rate	0.5
V	Trait additive genetic variance	0.05
s	Trait minimum value	0.0001

Table A1: Table with parameter and their interpretation on system 5

Predator will not be able to persist whenever prey parameter satisfies the quantity

$$bk_0 = ak_1 \tag{A3}$$

Which for our set of parameters will lead to $a = 1.6$.

Solving the equation below for any parameter will give us the parameter value that allows

for equality between r_{sel} and K_{sel} (in the main text).

$$\frac{e}{d} - h = \left(\frac{bk_0}{a} - k_1\right)\left(\frac{bk_0}{a(bk_0 - ak_1)}\right) \tag{A4}$$

We solved this equation for a values, which leads to the following cubic polynomial equation:

$$a^3 k_1(dh - e) - a^2 dbk_0(k_1 - h) + (a - 1)db^2k_0^2 = 0 \tag{A5a}$$

Substituting all the parameters (except a) for the values in table 1 leads to:

$$-0.125a^3 + 0.15a^2 + 0.08(a - 1) = 0 \tag{A5b}$$

Which give us the a value that allows equality $r_{sel}/K_{sel} = 1$, $a \approx 0.64108$.

Figure A1 shows the isoclines of prey and predator and the terms of r- and K-selection for the cases where a allows for $r_{sel}/K_{sel} = -1$ and for a values that allow for $r_{sel}/K_{sel} = 1$. When $a = bk_0/k_1$ ($a = 1.6$), predators can no longer persist and go extinct. This happens because larger a leads to the carrying capacity fast. Once population is in the carrying capacity, increasing density tolerance may be more advantageous then increasing growth rate (Bertram & Masel 2017, Promislow & Harvey 1990).
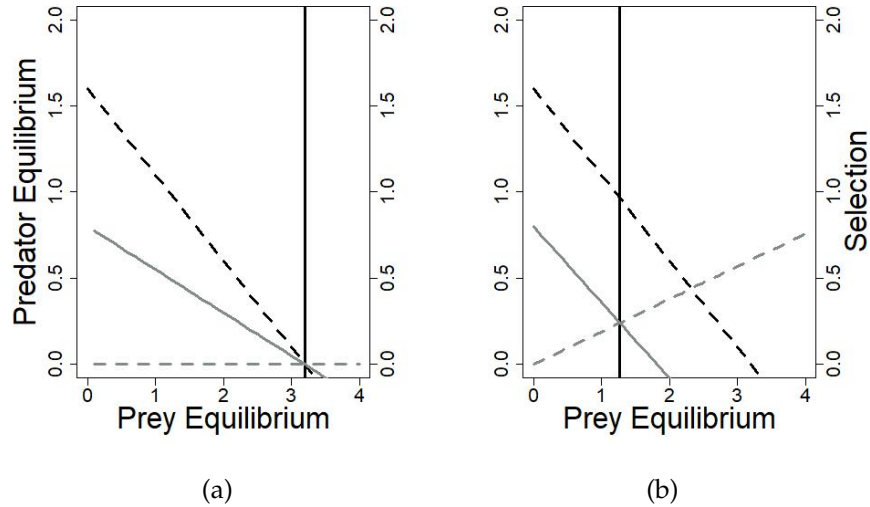
Figure A1: Populations isoclines and r- and K-selections. Solid black line is the predator isocline; Dashed black line is the prey isocline; Solid grey line is the r_{sel}; Dashed grey line is the K_{sel}. a) The case where $r_{sel}/K_{sel} = -1$ ($a = 1.6$). b) The case where $r_{sel}/K_{sel} = 1$ ($a = 0.64$). Common parameters are: $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$.

Time Series

To give an example of the system behaviours generated for a range of a values, we plotted the time series and phase spaces of four dynamical behaviours. In figure A2 we show an example of the runaway evolution when $a = 0.25$. The runaway begins after a long transient dynamics for this a value. Figure A3 shows the stable state when $a = 0.64$. Figure A4 gives an example of limit cycles generated when $a = 1.41$. The cycles are larger for predators density, followed by trait value and prey density. Finally, when $a \geq 1.6$, predators cannot persist. These dynamics are shown in figure A5.
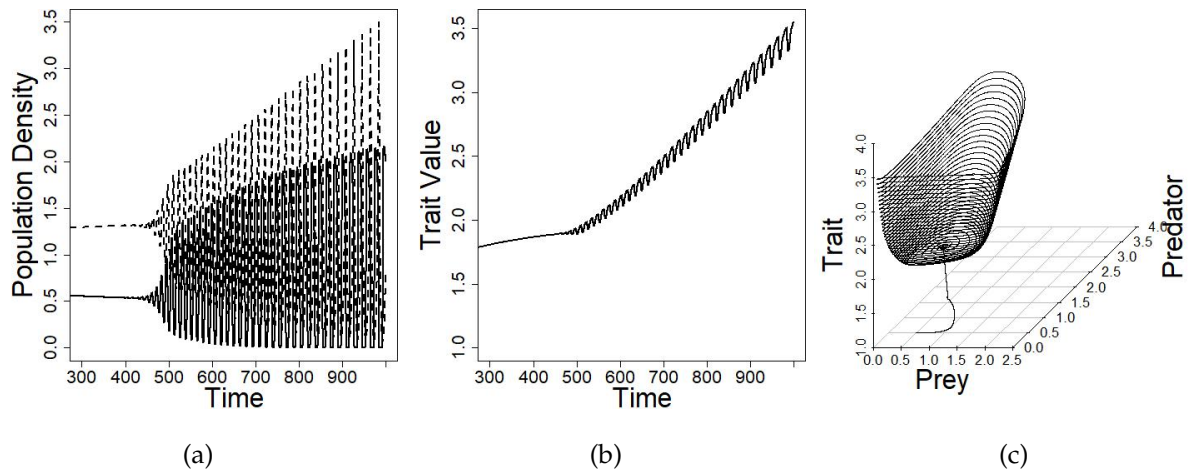
(a) (b) (c)

Figure A2: Runaway evolution. a) Population densities of prey (solid black line) and predators (dashed black line); b) trait dynamics; and c) Phase space with prey and predator densities and trait value. Parameters are: $a = 0.25$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$. Initial conditions are: $N = 0.5$, $P = 0.5$, $\overline{\zeta} = 1$.
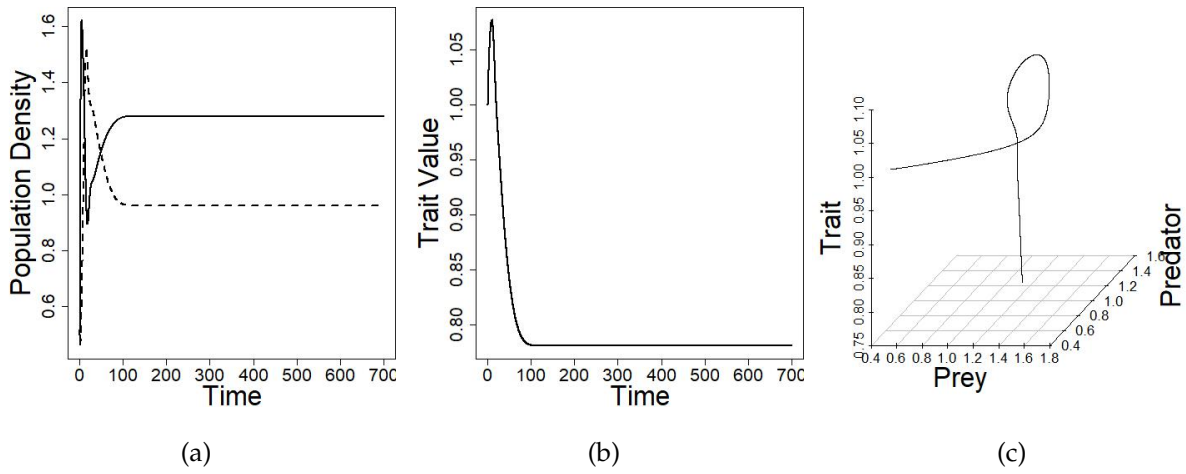
Stable state

(a) (b) (c)

Figure A3: Stable state. a) Population densities of prey (solid black line) and predators (dashed black line); b) trait dynamics; and c) Phase space with prey and predator densities and trait value. Parameters are: $a = 0.64$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$. Initial conditions are: $N = 0.5$, $P = 0.5$, $\bar{\zeta} = 1$.
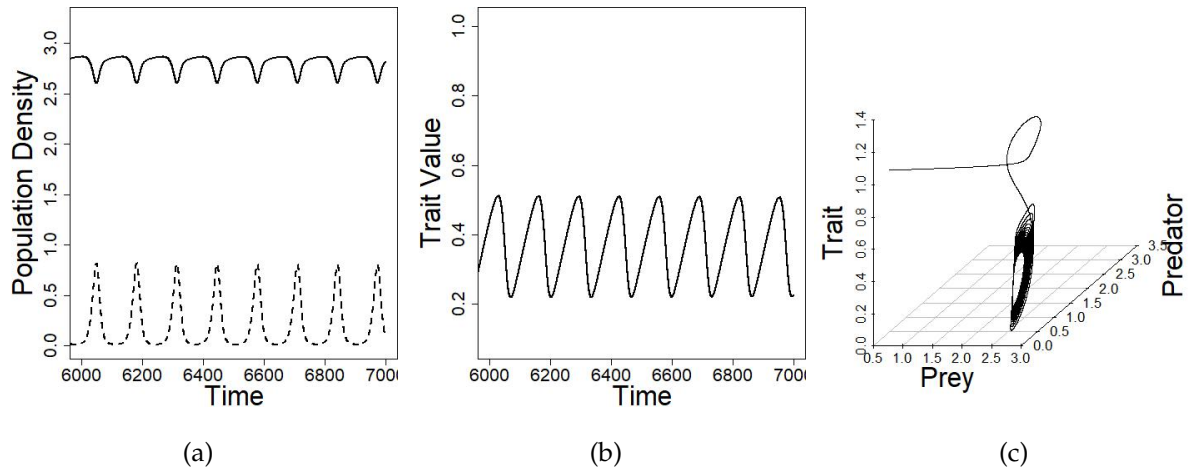
Cycles

Figure A4: Limit cycles. a) Population densities of prey (solid black line) and predators (dashed black line); b) trait dynamics; and c) Phase space with prey and predator densities and trait value. Parameters are: $a = 1.4$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$. Initial conditions are: $N = 0.5$, $P = 0.5$, $\bar{\zeta} = 1$.

Predator extinction
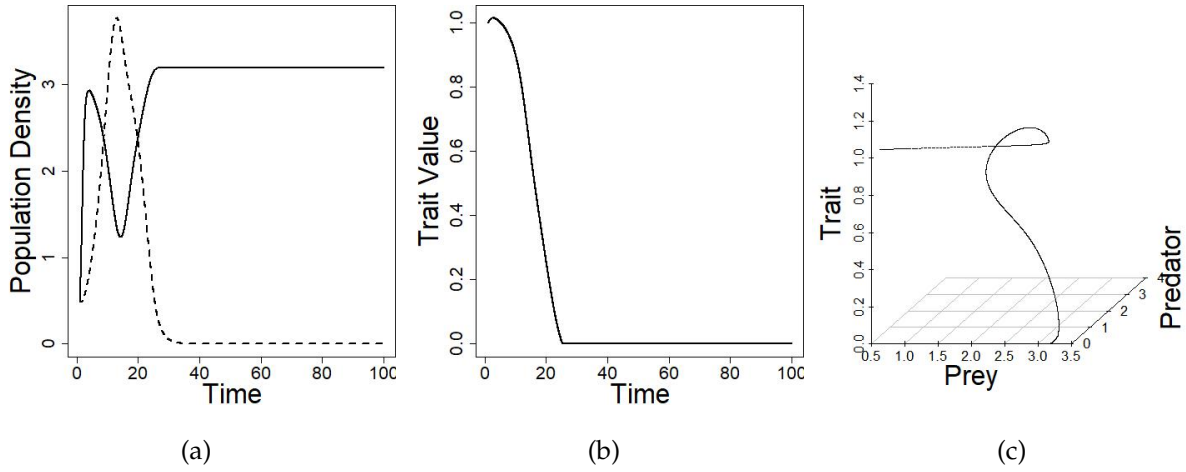

(a)　　　　　　　　　(b)　　　　　　　　　(c)

Figure A5: Predator extinction. a) Population densities of prey (solid black line) and predators (dashed black line); b) trait dynamics; and c) Phase space with prey and predator densities and trait value. Parameters are: $a = 1.6$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$. Initial conditions are: $N = 0.5$, $P = 0.5$, $\bar{\zeta} = 1$.

The r- and K-Selective Environments

To give an illustration of the *r-* and *K*-selective environments, we plotted the densities isoclines and the r_{sel} and K_{sel} term A6. This environments were generated by calculating symmetric points greater and smaller than $a = 0.64$. Therefore, $a = 0.34$ and $a = 0.94$ generates *r-* and *K*-selective environments, respectively. Figure A6 shows that these values can produce stable dynamics for both predominant selections.
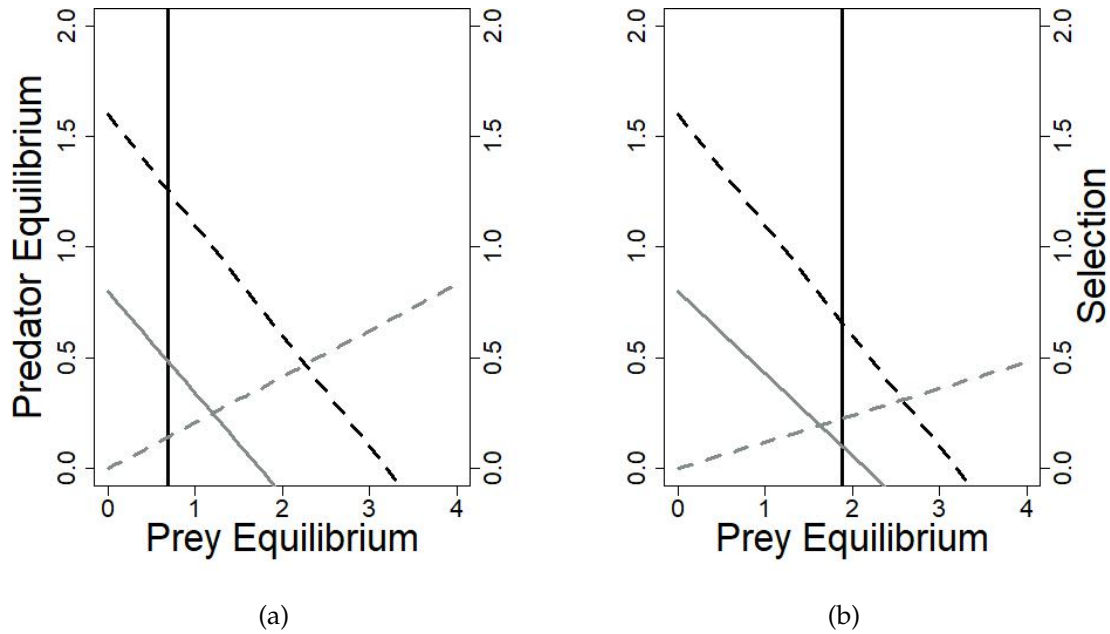
Figure A6: Populations isoclines and r- and K-selections. Solid black line is the predator isocline; Dashed black line is the prey isocline; Solid grey line is the r-selection term; Dashed grey line is the K-selection term. a) Predominant r-selection ($a = 0.34$). b) Predominant K-selection ($a = 0.94$). Common parameters are: $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $h = 1$, $e = 1$, $d = 0.5$, $V = 0.05$, $s = 0.0001$.

Effects on r- and K-Selection Dynamics

As we note in the main text, all parameters may affect the r/K continuum. This is shown in the figure A7. This figure shows how e, h and d affects the dynamics of r- and K-selection.
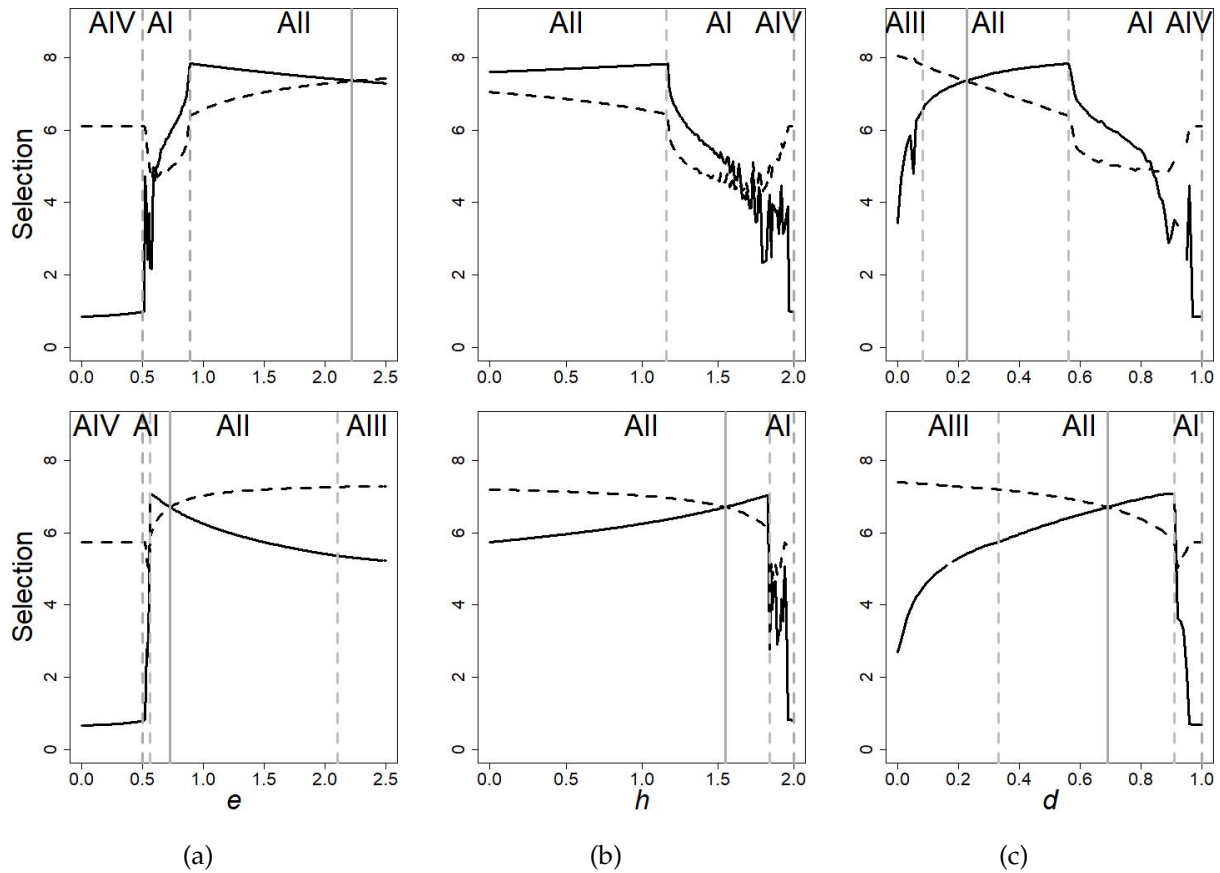
Figure A7: The behaviour of r- (solid line) and K- (dashed line) selection strength for a range of predators parameters for $a = 0.34$ (top row) and $a = 0.94$ (bottom row). a) Conversion efficiency e; b) Handling time h; and c) Death rate d. Solid grey line separates the plot area where r-selection is predominant and the area where K-selection is predominant. The type of system behaviour is denoted by A and separated by the dashed grey lines: AI is the runaway evolution; AII is the steady state; AIII is the limit cycles; and AIV is the predator extinction. Parameters are: $a = 0.63$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $V = 0.05$, $s = 0.0001$. Initial conditions are: $N = 0.5$, $P = 0.5$, $\overline{\zeta} = 1$.

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The interplay between predator satiation and foraging effort shapes prey life-history

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Abstract

The stage-dependent predation hypothesis suggests that increasing predation over adult stages may give advantage to phenotypes with earlier maturation and increased reproductive effort (fast life-history). On the other hand, the advantageous phenotypes when predation is major-illy over juveniles are those that maturate later and devote less energy to reproduction (slow life-history). The occurrence of this fast-slow life-history in nature is supported by several evidences. However, the predictions of this hypothesis may vary as a function of predator satiation. Here, we developed a predator-prey eco-evolutionary system with structured prey population to explore the intersections between the predator stage preference and satiation. By partitioning the gradient of selection in its r- and K-selection components, we were able to reproduce the fast-slow life-history continuum for a range of predator preference. Our results suggest that predator satiation can affect this continuum by changing the point where r- and K-selection are equal. We discuss the implications of our results for theory and empirical evidences interpretations.

Introduction

The fitness surfaces of prey species vary as a function of the overall predation risk imposed by predators in a given environment (Abrams 2000, Berryman 1992). Because of the limited amount of time and energy, prey species must reallocate energy from others biological functions to anti-predator traits in order to reduce their risk of getting caught (Khater et al. 2016, Magurran et al. 1992). Such energy reallocation may impact ecology and evolutionary trajectories of preys. Because preys are challenged with a variety of predator species with different foraging strategies, adaptation in anti-predator traits are expected to produce relevant effects in community structure (TerHorst et al. 2018). Besides predator characteristics, predation risk also varies with prey density. The predator satiation hypothesis predicts that if prey density is above the density necessary to satiate predators, predation risk decreases as prey density increases (Bogdziewicz et al. 2018, Eckrich Caren E.;Owens 1995, Farkas & Montejo-Kovacevich 2014, Sweeney & Vannote 1982, Zywiec et al. 2013). Several types of traits may evolve in response to predation risk, and they range from morphological traits such as body size (Basolo & Wagner 2004, Blumenshine et al. 2000) and brain size (Kotrschal et al. 2017), to more complex traits like boldness (Chang et al. 2017) and intelligence (Amodio et al. 2019). Because of the complex genetic architecture underlying anti-predator traits, modelling such interaction is usually made under the quantitative genetics framework (Abrams et al. 1993, Anderson 1995, Lande 1976).

Quantitative traits are complex traits with convoluted genetic background of interacting genes with many pleiotropic effects (Hansen 2006, Hansen & Wagner 2001). Pleiotropic interactions among genes are predicted to act as constraints to the evolutionary dynamics of organisms (Templeton 1980). Many of these constraints emerge not only as physiological effects, but also as changes in performance of ecological interactions (DeLong 2017, Flatt et al. 2005). In this sense, the overall selection acting on quantitative traits that affect many ecological functions may result from optimization processes constrained by the trade-offs produced by ecological pleiotropy. Because of the complexity involved in anti-predator traits, theory predicts that the adaptive dy-

namics of such traits may have a strong ecological component (McPeek 2017). In fact, the effect of predators on prey adaptation may be more a function of prey parameters than of predators parameters (Abrams 1990, Reznick et al. 2001). Which illustrates the context dependent nature of selection. In this sense, ecological context is a major driver of evolutionary dynamics, specially in the case of quantitative traits.

Life-history traits are usually quantitative traits (Lande 1982) intrinsically related to organisms ecological dynamics (de Roos 2018, Mueller et al. 1991). The life-history of an organism is a set of traits that, together, defines the patterns of reproduction, somatic maintenance and senescence (Vitt & Caldwell 2013). Since population growth results from the balance between reproductive and death rates, demographic dynamics may be affected by life-history traits (Promislow & Harvey 1990). Because predation is a major driver of mortality in prey populations, it is expected that predation pressure may play an important role in shaping prey life-history (Bronikowski et al. 2002, Stoks et al. 1999) as consequence of anti-predator adaptation (Benard & Fordyce 2003). One of the predictions of life-history theory is that predators will affect prey life-history when predation risk varies among the ages/stages of prey population (Reznick et al. 1982). This prediction is based on the relative importance of the environmental context faced by each age/stage to the overall selection. The stage-dependent mortality hypothesis (Franco et al. 1996, Persson & de Roos 2013, Reznick & Endler 1982) predicts that higher juvenile mortality may produce slow life-histories, with less energy allocated to reproductive effort, and late maturation. On the other hand, higher adult mortality may produce faster life-histories with greater reproductive effort and earlier maturation. If predation is the major driver of mortality, it is expected that life-history may adapt in response to the predation risk faced by each age/stage. Therefore, the position of a prey species in a fast-slow life-history continuum may be a function of the distribution of predation risk in each stage.

Several theoretical and empirical studies suggest that predator-induced life-history adaptation may be driven by rapid adaptation (Agrawal et al. 2013, DeLong & Luhring 2018, Han et al. 2018, Reznick & Endler 1982, Reznick & Bryga 1987, Reznick et al. 1996, Rodd et al. 1991, Stoks

et al. 1999, Walsh & Reznick 2011). Despite the recent increasing interest in eco-evolutionary dynamics, theoreticians have used the assumptions of rapid evolution and reciprocity between ecology and evolution in mathematical models for decades (Govaert et al. 2018, Pimentel 1961, 1967). The theory of r/K selection (MacArthur 1962, MacArthur & Wilson 1967), which was used to explain life-history diversity (Pianka 1970, Reznick et al. 2002), is one of the earliest predictive theories in ecology (Reznick et al. 2002) and it is based on density-dependent selection (Boyce 1984), the most common route of reciprocity (Kokko & López-Sepulcre 2007, Travis et al. 2013). During the last decades, many theoretical studies suggest that eco-evolutionary dynamics may drive predator-prey interactions (Abrams & Matsuda 1997, Cortez 2016, Jones & Ellner 2007, Yoshida et al. 2003). However, detecting reciprocity in nature is hard. The interplay among the various ecological functions related to the adaptive trait may obscure reciprocity (DeLong 2017). The lack of evidence for reciprocity associated with the potential importance of eco-evolutionary dynamics in a changing world (Carthey & Blumstein 2018) implies that it is a key field to understand biological processes and restore ecosystem functioning (Alberti 2014, Ferriere & Legendre 2013, Pelletier et al. 2009).

Because there are several ecological processes that may mimicry the effects of evolution, mechanistic models are useful to predict when reciprocity will be relevant (Luo & Koelle 2013). Theory predicts that the interplay between ecology and evolution may be detected by looking into how trait dynamics feed back to environment (Lion 2017), either by direct mechanisms such as density-dependent selection (Farkas & Montejo-Kovacevich 2014, Travis et al. 2013) or by indirect ecological interactions (Estes et al. 2013). In this paper, we explore the eco-evolutionary predictions of the interplay between two relevant predator-prey hypothesis: the stage-dependent predation hypothesis and the predator-satiation hypothesis. We present a mathematical model that captures the essence of the stage-dependent predation, and evaluate how predator satiation affects theoretical predictions. We show how to incorporate prey structure in a general predator-prey system, and how r/K selection theory can be used to evaluate the fast-slow life-history continuum. In the first section, we start by briefly reviewing the general predator-prey

eco-evolutionary system. Then we explain the necessary assumptions to track prey life-history adaptation. In the results section, we show the necessary assumptions to generate the fast-slow continuum and how the outcome of interaction depends on predator satiation. The implications of the results are discussed in the last section.

Methods

The General Approach

We use a system of ordinary differential equations that describes the eco-evolutionary dynamics of predator prey interaction. Here, we assume that prey vulnerability to predation is a quantitative trait that adapts in response to selection. We assume that prey population are structured in adults and juvenile stages. We use the quantitative genetics framework from Abrams et al. (1993), Lande (1976). We start by giving a brief explanation on the unstructured model. Next, we show how to incorporate stage structure. Then we show how to track the *r*- and *K*-selection terms on structured populations to track the fast-slow continuum. Finally, we describe the specific model used on the numerical analysis.

A General Predator-Prey Unstructured Eco-Evolutionary System

The basic concept underlying eco-evolutionary feedback loop is environmental feedback (Lion 2017). The environment is represented by any biotic and/or abiotic factor that interferes in the individual fitness of the evolving population. An environmental vector, **E**, of a system describing the eco-evolutionary dynamics of a predator-prey system can be written as:

$$\mathbf{E} = (N, \overline{\zeta}, P)^T$$

Where T denotes matrix transposition. Vector **E** is composed by the densities of preys and predators, N and P, respectively, and by the prey average vulnerability to predation, $\overline{\zeta}$. In this sense, the temporal dynamics of the ecological subsystem (N and P) can be described as functions

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of the **E**:

$$\frac{dN}{dt} = G_N(\mathbf{E})N \tag{1a}$$

$$\frac{dP}{dt} = b(\mathbf{E}). \tag{1b}$$

Where $G_N(\mathbf{E})$ stands for prey fitness and $b(\mathbf{E})$ stands for predator population growth.

We assume that preys vulnerability to predation, ζ, is a quantitative trait which temporal dynamics are described by the quantitative genetics framework (Abrams et al. 1993, Lande 1976). In this framework, trait dynamics equals the product between additive genetic variance and the selection gradient ($\partial G_N/\partial \zeta$). If trait variance is large, then the selection gradient must be calculated by integrating $\partial G_N/\partial \zeta$ over the trait distribution (Abrams & Matsuda 2004). To simplify our model, we assume a constant and relatively narrow trait variance. Under this assumption, the selection gradient may be approximated by the partial derivative of individual fitness with respect to trait value, and evaluated at the point where $\zeta = \bar{\zeta}$ (Abrams 2001). Trait dynamics is described by the following equation:

$$\frac{d\bar{\zeta}}{dt} = V\chi(\bar{\zeta}) \left. \frac{\partial G_N(\mathbf{E})}{\partial \zeta} \right|_{\zeta=\bar{\zeta}}. \tag{1c}$$

The function $\chi(\bar{\zeta})$ in equation 1c is a boundary function to prevent trait from trespass biological reasonable values. $\chi(\bar{\zeta})$ does not affect system stability (Abrams et al. 1993).

Incorporating Stage Structure in Prey Population

Life-history of an organism is a set of traits that, together, describe the patterns of reproduction, somatic maintenance and senescence (Vitt & Caldwell 2013). Because these patterns emerge at different times of an organism life, life-history is intrinsically related to population structure (de Roos 2018). To incorporate population structure in model 1, we assume that the environmental vector is now described by

$$\mathbf{E} = (\mathbf{N}, \bar{\zeta}, P)^T,$$

where vector $\mathbf{N}$ is a vertical vector with densities i of n stages, $\mathbf{N} = (N_i, ..., N_n)^T$. In this scenario, the overall population density is the sum of all stages densities in population, $N = \sum_{i=1}^{n} N_i$. To allow for simplicity, we arbitrarily assume that the prey population is composed by two stages, a juvenile stage and an adult stage, N_J and N_A, respectively. We assume that only adults reproduce, and that their reproduction varies as a function of ζ, $r_A(\zeta)$. Before maturate into adults, juveniles face an intrinsic death rate S_J as a consequence of energetic constraints generated by somatic maintenance costs. The maturation rate of the survivor juveniles is a function of ζ, $\mu(\zeta)$. If both functions $r_A(\zeta)$ and $\mu(\zeta)$ are qualitatively similar (both are increasing or decreasing functions of ζ), then trait dynamics can produce either a fast or slow life-histories strategies depending on the architecture of this ecological pleiotropy. Also, we assume that sensitivity for density regulation differs between adults and juveniles. Because life-history theory predicts a trade-off between the population growth rate and population carrying capacity (Aktipis et al. 2013), we assume that adult sensitivity to density is a function of ζ, $l_A(\zeta)$, which is qualitatively similar to $r_A(\zeta)$ (both are increasing or decreasing function of ζ). Assuming that $N = N_J + N_A$, the temporal dynamics of juveniles and adults can be written as

$$\frac{dN_J}{dt} = r_A(\overline{\zeta})N_A - S_J N_J - \mu(\overline{\zeta})N_J - l_J N_J N - P f_J(N, \overline{\zeta}) \tag{2a}$$

$$\frac{dN_A}{dt} = \mu(\overline{\zeta})N_J - l_A(\overline{\zeta})N_A N - P f_A(N, \overline{\zeta}). \tag{2b}$$

Where l_J in equation 2a stands for a constant juvenile sensitivity to density. The functions $f_J(N, \overline{\zeta})$ and $f_A(N, \overline{\zeta})$ are the predator functional response over juveniles and adults, respectively. We assume that predator numerical response is linear with conversion rate e and death rate d. Assuming that the overall functional response is given by $f(N, \overline{\zeta}) = f_J(N, \overline{\zeta}) + f_A(N, \overline{\zeta})$, predator population dynamics will be

$$\frac{dP}{dt} = P[ef(N, \overline{\zeta}) - d]. \tag{3a}$$

Individual fitness is composed by all the stages that the individual survived. Therefore, equations 2a and 2b must be summed and divided by the total population dynamics in order to

represent individual fitness. Assuming that the proportion of juveniles equals $\gamma = N_J/N$, prey individual fitness is:

$$\frac{dN}{Ndt} = r_A(\bar{\zeta})(1-\gamma) - S_J\gamma - N(l_A(\bar{\zeta})(1-\gamma) + l_J\gamma) - \frac{P}{N}f(N,\bar{\zeta}) \tag{3b}$$

From equation 3b we may derive the trait dynamics using equation 1c, which in this case will be:

$$\frac{d\bar{\zeta}}{dt} = V\chi(\bar{\zeta})\left[r'_A(1-\gamma) - Nl'_A(1-\gamma) - \frac{P}{N}\frac{\partial f(N,\bar{\zeta})}{\partial \zeta}\right] \tag{3c}$$

where the primes stand for derivatives in respect to ζ. Note that in absence of predators, selection over trait depends on the overall population density and on the frequency of juveniles in population. In this sense, equation 3c suggests that in absence of predators selection is both density-dependent and frequency-dependent. When predators are present, the overall selection will also depends on predator density and on its foraging strategy. Because the proportion of juveniles γ equals $N_J(t)/N(t)$, the temporal dynamics of γ will be given by the chain rule from calculus, which results in a type of replicator equation (Dingli et al. 2009, Lion 2017, Valdovinos et al. 2010)(Nowak n.d.):

$$\frac{d\gamma}{dt} = \frac{1}{N}\left(\frac{dN_J}{dt} - \gamma\frac{dN}{dt}\right)$$
$$= r_A(\bar{\zeta})(1-\gamma)^2 - \gamma(S_J(1-\gamma) - \mu(\bar{\zeta})) - N(1-\gamma)\gamma(l_J - l_A(\bar{\zeta})) - \frac{P}{N}(f_J(\bar{\zeta},N) - \gamma f(\bar{\zeta},N)) \tag{3d}$$

Together, equations 3a, 3b, 3c and 3d describe the eco-evolutionary dynamics of a predator-prey interaction with stage structure in prey population. If γ is at equilibrium, then the system stability will depend only on N, P and $\bar{\zeta}$.

Note that, in equation 3d, if $l_J = l_A(\bar{\zeta})$, $f_J(\bar{\zeta},N) = \gamma f(\bar{\zeta},N)$, $S_j = 0$ and $\mu(\bar{\zeta}) = \mu_1 r_A(\bar{\zeta})$ (where μ_1 stands for the linear coefficient between reproduction and maturation) the equilibrium value of γ will be the positive solution that satisfies

$$\gamma_e = \frac{(2+\mu_1) \pm \sqrt{\mu_1^2 + 4\mu_1}}{2}.$$

Therefore, in a symmetrical system the equilibrium density of proportion of juveniles depends only on $\mu 1$. In this sense, after the transient dynamics, system 3 will behave identically to the unstructured model (de Roos 2018).

The r/K Selection Gradients

The concept of fast-slow life-history continuum is intrinsically related to the r/K theory (Franco et al. 1996, Oli 2004, Pianka 1970). To evaluate how system dynamics behave in the fast-slow continuum, we first derive the r- and K-selection gradient from system 3. r/K theory is related to the logistic equation in its carrying capacity format (MacArthur 1962, Reznick et al. 2002), therefore, we must write equation 3b in this format. Because juveniles die at rate S_J, they do not reproduce. Therefore the population intrinsic growth rate r must be the amount of individuals born less the amount of juveniles that dies before reach maturation:

$$r(\bar{\zeta}, \gamma) = r_A(\bar{\zeta})(1 - \gamma) - S_J \gamma$$

Similarly, the overall sensitivity to density is found by adding juveniles and adults sensitivity, which leads to:

$$l(\bar{\zeta}, \gamma) = l_A(\bar{\zeta})(1 - \gamma) + l_J \gamma$$

Now, because the carrying capacity $K(\bar{\zeta}, \gamma)$ equals to $r(\bar{\zeta}, \gamma)/l(\bar{\zeta}, \gamma)$ (Rueffler et al. 2006), we may rewrite equation 3b in the following format:

$$\frac{dN}{dt} = Nr(\bar{\zeta}, \gamma)\left(1 - \frac{N}{K(\bar{\zeta}, \gamma)}\right) - Pf(N, \bar{\zeta}) \tag{4a}$$

Equation 4a suggests that individual fitness, $G_N(\mathbf{E})$ depends on functions $r(\bar{\zeta}, \gamma)$, $K(\bar{\zeta}, \gamma)$ and $f(N, \bar{\zeta})$. The selection gradient in this scenario will be

$$\frac{\partial G_N}{\partial \zeta} = \frac{\partial G_N}{\partial r}\frac{\partial r}{\partial \zeta} + \frac{\partial G_N}{\partial K}\frac{\partial K}{\partial \zeta} + \frac{\partial G_N}{\partial f}\frac{\partial f}{\partial \zeta} \tag{4b}$$

where the first and the second terms in the right hand side of equation 4b is the r- and K-selection gradients. Solving this equation and substituting K for r/l leads to the r- and K-selection terms,

(r_{sel} and K_{sel}, respectively)

$$r_{sel} = r'_A(1-\gamma)\left(1 - \frac{N(l_A(\bar{\zeta})(1-\gamma) + l_J\gamma)}{r_A(\bar{\zeta})(1-\gamma) - S_J\gamma}\right) \tag{5a}$$

$$K_{sel} = N\left(\frac{r'_A(1-\gamma)(l_A(\bar{\zeta})(1-\gamma) + l_J\gamma)}{r_A(\bar{\zeta})(1-\gamma) - S_J\gamma} - l'_A(1-\gamma)\right). \tag{5b}$$

Note that predator density does not affect the r- and K-selection terms. However, predators parameters will affect r_{sel} and K_{sel} through the equilibrium densities of the other variables.

Specific Models and Simulation Procedures

In all our numerical analysis, we assume that both $r_A(\bar{\zeta})$ and $l_A(\bar{\zeta})$ are simple linear functions of ζ, therefore:

$$r_A(\bar{\zeta}) = a + b\bar{\zeta} \tag{6a}$$

$$l_A(\bar{\zeta}) = k_0 + k_1\bar{\zeta} \tag{6b}$$

where a and b in equations 6a are the innate reproduction rate and the trait-dependent reproduction rate, respectively. Similarly, k_0 and k_1 in equation 6b are the innate and the trait-dependent adult sensitivity to density.

Because we are interested in life-history adaptation, we assume that the maturation rate, $\mu(\bar{\zeta})$, in equation 3d is also an increasing function of ζ. However, maturation rate must be bounded between 0 and 1, therefore:

$$\mu(\bar{\zeta}) = \frac{\mu_0(1-\mu_0) + \bar{\zeta}}{1 + \bar{\zeta} - \mu_0} \tag{6c}$$

where μ_0 is the trait independent maturation rate. Equation 6c implies that no matter how big ζ gets, maturation rate will never be greater than 1.

To evaluate the stage-dependent predation hypothesis, we assume that predator foraging effort on juveniles is given by f, which is bounded in $0 \le f \le 1$. Because f represents the amount

of energy and time spent foraging for prey N_J in relation to the total time spent foraging. In this sense, the foraging effort on adults will be $(1-f)$. The functional responses of predators on preys are given by the following set:

$$f(N,\bar{\zeta}) = f_J(N,\bar{\zeta}) + f_A(N,\bar{\zeta})$$

$$= \frac{\bar{\zeta}N\gamma f}{1 + h\bar{\zeta}N[\gamma f + (1-\gamma)(1-f)]} + \frac{\bar{\zeta}N(1-\gamma)(1-f)}{1 + h\bar{\zeta}N[\gamma f + (1-\gamma)(1-f)]}$$

$$= \frac{\bar{\zeta}N[\gamma f + (1-\gamma)(1-f)]}{1 + h\bar{\zeta}N[\gamma f + (1-\gamma)(1-f)]} \tag{7}$$

The interior equilibrium of system 3 as a function of γ, with equations functions from system 6 and equation 7 will be

$$N_e = \frac{a(1-\gamma) - S_J\gamma}{k_0(1-\gamma) + l_J\gamma} \tag{8a}$$

$$P_e = \frac{eb(1-\gamma)}{(e-dh)(f\gamma + (1-f)(1-\gamma))}\left(1 - \frac{(a(1-\gamma) - S_J\gamma)k_1}{(k_0(1-\gamma) + l_J\gamma)b}\right) \tag{8b}$$

$$\bar{\zeta}_e = \frac{d(k_0(1-\gamma) + l_J\gamma)}{(e-dh)(a(1-\gamma) - S_J\gamma)} \tag{8c}$$

Note that prey vulnerability to predation is the same for each stage, however, each stage generates different selective contexts (equations 2a and 2b). Since predators conversion rate e and handling time h are the same for each stage, the contribution of each selective scenario for the overall selection gradient will depend on the foraging effort of predators on each stage. In this sense, the fast-slow continuum will be represented by the r/K continuum (system 5) generated by predator foraging effort over juveniles.

Simulations

To evaluate the behaviour of r- and K-selection gradients for a range of parameters, we calculated the mean between the maximum and minimum values of the long term dynamics of the r_{sel} and K_{sel} terms. All the bifurcation diagrams were performed for a 0.1 parameter interval. To skip the transient dynamics, we used the last 5000 values from simulated time series of 80000 time-steps.

We performed all our numerical analysis in R (R Development Core Team 2011). The R codes for the models and figures of this paper are deposited at https://github.com/pbolanhom/C2.

To investigate if predator foraging effort in juveniles can generate a fast-slow life-history continuum we performed bifurcation diagrams of system variables for a range of f values. To access how the predator satiation hypothesis interplays with stage-dependent predation hypothesis, we evaluate how the fast-slow continuum varies as a function of h in five different cases. Case I happens when predators consume only adults ($f = 0$); Case II happens when predators consume both stages, but prefer adults ($f = 0.2$); In case III, predators do not discriminate adults and juveniles ($f = 0.5$); Case IV is when predators prefer juveniles ($f = 0.8$); and finally, case V is when predators consume only juveniles ($f = 1$).

We show a table with functions and parameters values and interpretations in the Appendix A.

Results

The Stage-Dependent Predation Hypothesis

In accordance with theory (Reznick et al. 2002), the r/K continuum over a range of predator foraging effort produced a fast-slow life-history continuum (figure 1 and figure 2). When predators spend more time foraging for juveniles ($f \approx 1$), system produced a predominant K-selection. On the other hand, when predators spend more time foraging for adults ($f \approx 0$), it produced a predominant r-selection. If predators spend approximately the same amount of time searching for both stages ($f \approx 0.5$), then $r_{sel} \approx K_{sel}$ (figure 1).

The intersection between r- and K-selection gradients ($r_{sel} = K_{sel}$) happens at the point where $f = 0.525$. Stable dynamic with predominant r-selection happens for a narrower range of f ($0.3 < f < 0.525$) than the stable dynamics for predominant K-selection ($0.525 < f < 1$). In cases where $f < 0.3$, system produced a runaway dynamics (figure 2). Figure 2 illustrates the system behaviour for densities, trait values and proportion of juveniles. When predators prefer

juveniles, selection gives advantage to more vulnerable phenotypes, which implies in higher reproductive effort and higher maturation rate (equations 6a and 6c, respectively). On the other hand, when predators prefer adults, selection gives advantage to less vulnerable phenotypes, and trait value is lower. The proportion of juveniles also decreases with f, implying that slower life-history results in a lower proportion of juveniles, and faster life-history in a higher proportion of juveniles.

Figure 3 shows the importance of juvenile somatic maintenance cost, S_J, and juvenile sensitivity to density l_J to the fast-slow continuum. If $l_J = 0$ and $S_J = 0.5$ (figure 3a), the point where $r_{sel} = K_{sel}$ happens when predators have preference of adult stages ($f = 0.15$), and the runaway happens for $f < 0.02$. Similarly, if $l_J = 0.5$, but $S_J = 0$ (figure 3b), $r_{sel} = K_{sel}$ happens where $f = 0.08$ and runaway for $f < 0.05$. When both S_J and l_J equals zero, negative K-selection brings trait value to s and predators can no longer persist. The maximum and minimum densities, trait value and proportion of juveniles are on Appendix A.
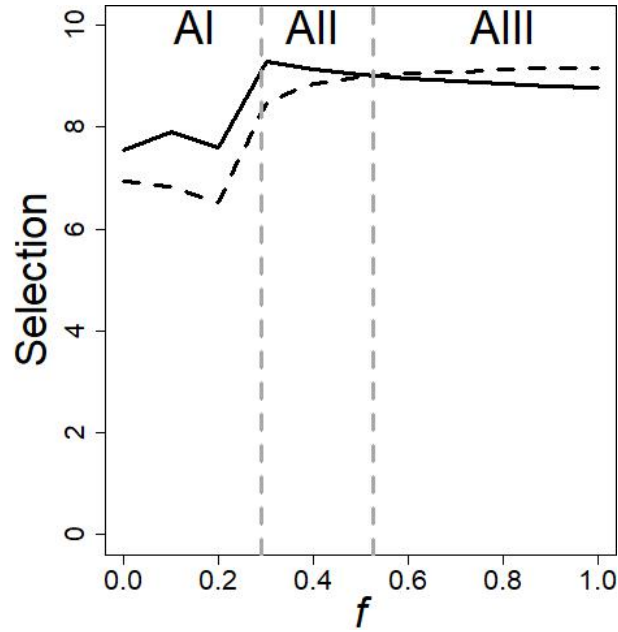
Figure 1: The behaviour of r- (solid black lines) and K-selection (dashed black lines) gradients (r_{sel} and K_{sel}, respectively) for a range of predator foraging effort, f, on juveniles. Vertical dashed grey lines separates the areas (AI, AII and AIII) in the plot. AI is the runaway dynamics ($0 < f < 0.29$); AII is the stable r-selection ($0.3 < f < 0.52$; and AIII is the stable K-selection ($0.52 < f < 1$). Parameters are: $a = 2.2$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $S_J = 0.5$, $l_J = 0.5$, $e = 1$, $h = 1$, $d = 0.5$, $\mu_0 = 0.5$, $s = 0.0001$ and $V = 0.05$. Initial conditions are: $N = 0.5$, $\gamma = 0$, $P = 0.5$ and $\bar{\zeta} = 1$.
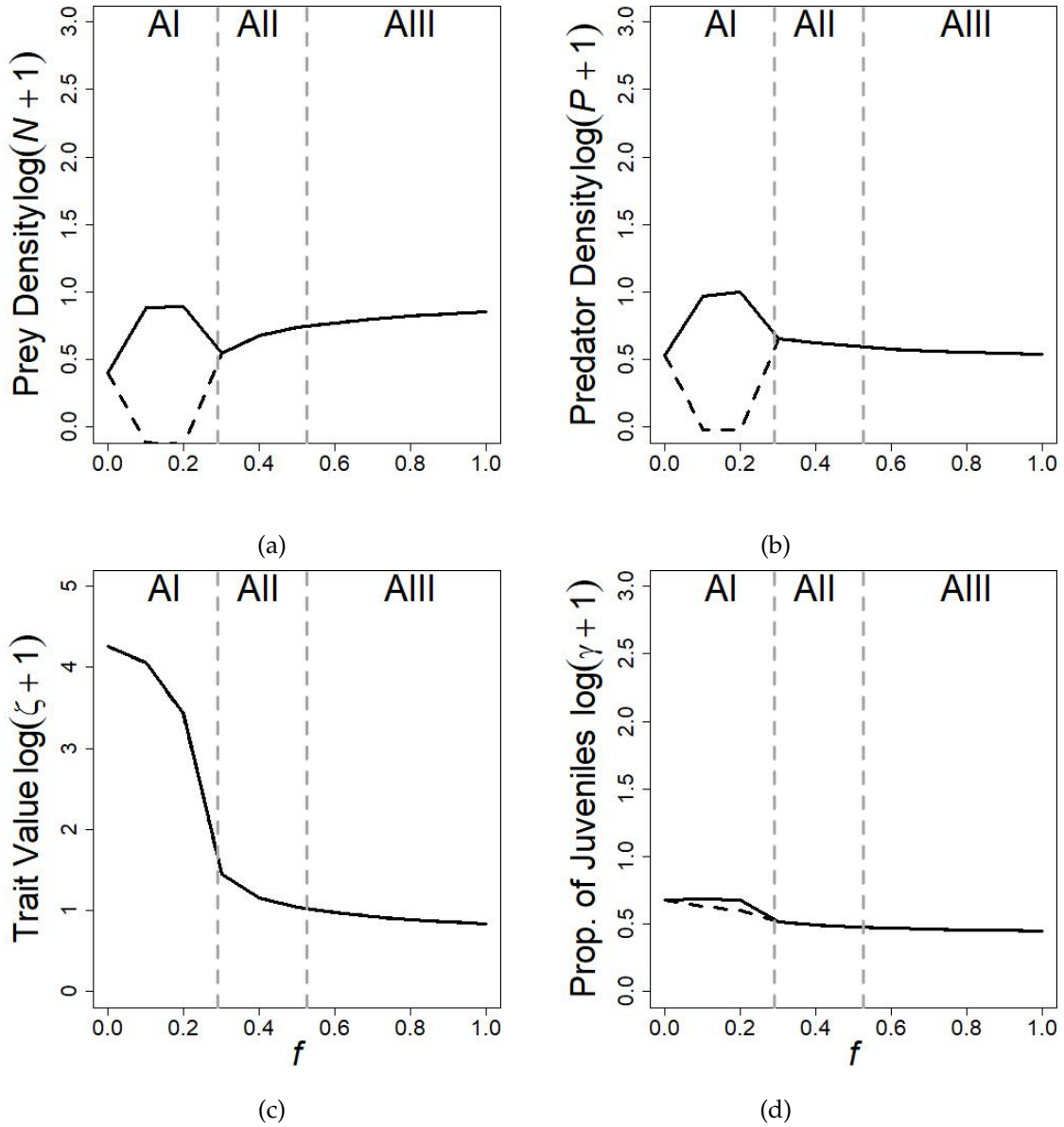
Figure 2: Maximum (solid black lines) and minimum (dashed black lines) of system dynamics for a predator foraging effort, f, on juveniles. a) Prey density; b) Predator density; c) Trait value; d) Proportion of juveniles. Vertical dashed grey lines separate the areas (AI, AII and AIII) in the plot. AI is the runaway dynamics ($0 < f < 0.29$); AII is the stable r-selection ($0.3 < f < 0.52$; and AIII is the stable K-selection ($0.52 < f < 1$). Parameters are: $a = 2.2$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $S_J = 0.5$, $l_J = 0.5$, $e = 1$, $h = 1$, $d = 0.5$, $\mu_0 = 0.5$, $s = 0.0001$ and $V = 0.05$. Initial conditions are: $N = 0.5$, $\gamma = 0$, $P = 0.5$ and $\bar{\zeta} = 1$.
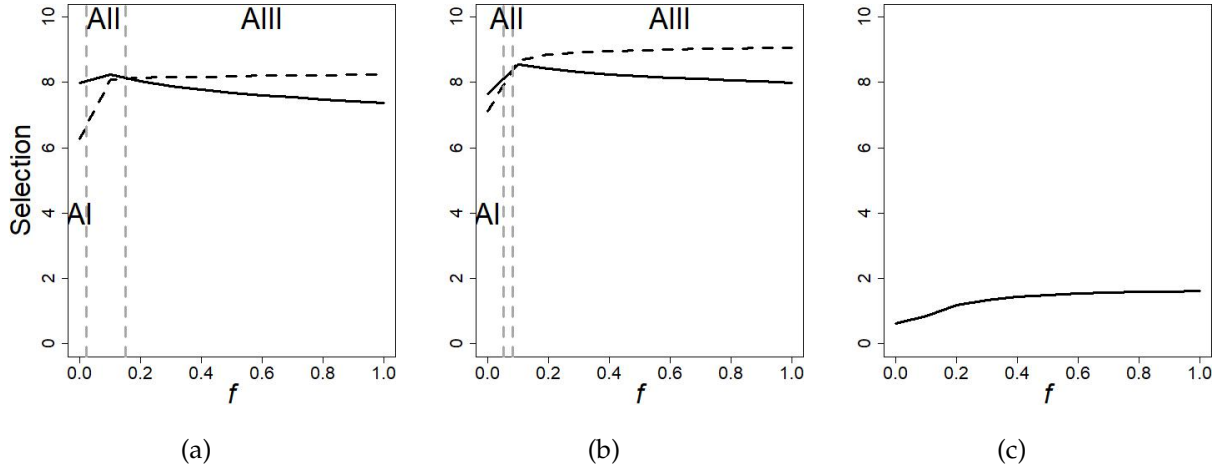
Figure 3: The behaviour of r- (solid black lines) and K-selection (dashed black lines) gradients (r_{sel} and K_{sel}, respectively) for a range of predator foraging effort, f, on juveniles in different scenarios. Vertical dashed grey lines separate the areas: AI (runaway dynamics); AII (stable r-selection); AIII (stable K-selection). a) $l_J = 0$ and $S_J = 0.5$. Areas: AI($0 < f < 0.02$), AII($0.02 < f < 0.15$) and AIII($0.15 < f < 1$); b) $S_J = 0$ and $l_J = 0.5$. Areas: AI($0 < f < 0.05$), AII($0.05 < f < 0.08$) and AIII($0.08 < f < 1$); c) $S_J = l_J = 0$. In this case, predators go extinct and K-selection is negative. Parameters are: $a = 2.2$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $e = 1$, $h = 1$, $d = 0.5$, $\mu_0 = 0.5$, $s = 0.0001$ and $V = 0.05$. Initial conditions are: $N = 0.5$, $\gamma = 0$, $P = 0.5$ and $\overline{\zeta} = 1$.

The Interplay Between Predator Satiation And Predator Foraging Effort

Our results suggest that predator satiation alternates the predominant selection and consequently, the fast-slow continuum. Figure 4 shows that, as predator shifts from specialists in adults ($f = 0$) to specialists in juveniles ($f = 1$), both r- and K-selection become stable for a larger range of predator handling time. When predators are specialists in adults, system is unstable for all values of h (figure 4a). Note that, in this case, increasing h values leads system dynamics from a runaway to predator extinction. The h value where $r_{sel} = K_{sel}$ increases as predators increase their preference for juveniles. Such increase enables a stable r-selection for large values of h. In all the cases, K-selection is produced when predator handling time equals

$h = e/d$. At this point, predators can no longer persist (see equation 8b). Note that, decreasing predator satiation and increasing preference for adults decrease the length of areas AII and AIII (stable r- and stable K-selection, respectively), but increase AI (runaway dynamics). The maximum and minimum values for densities, trait value and proportion of juveniles are at Appendix A.
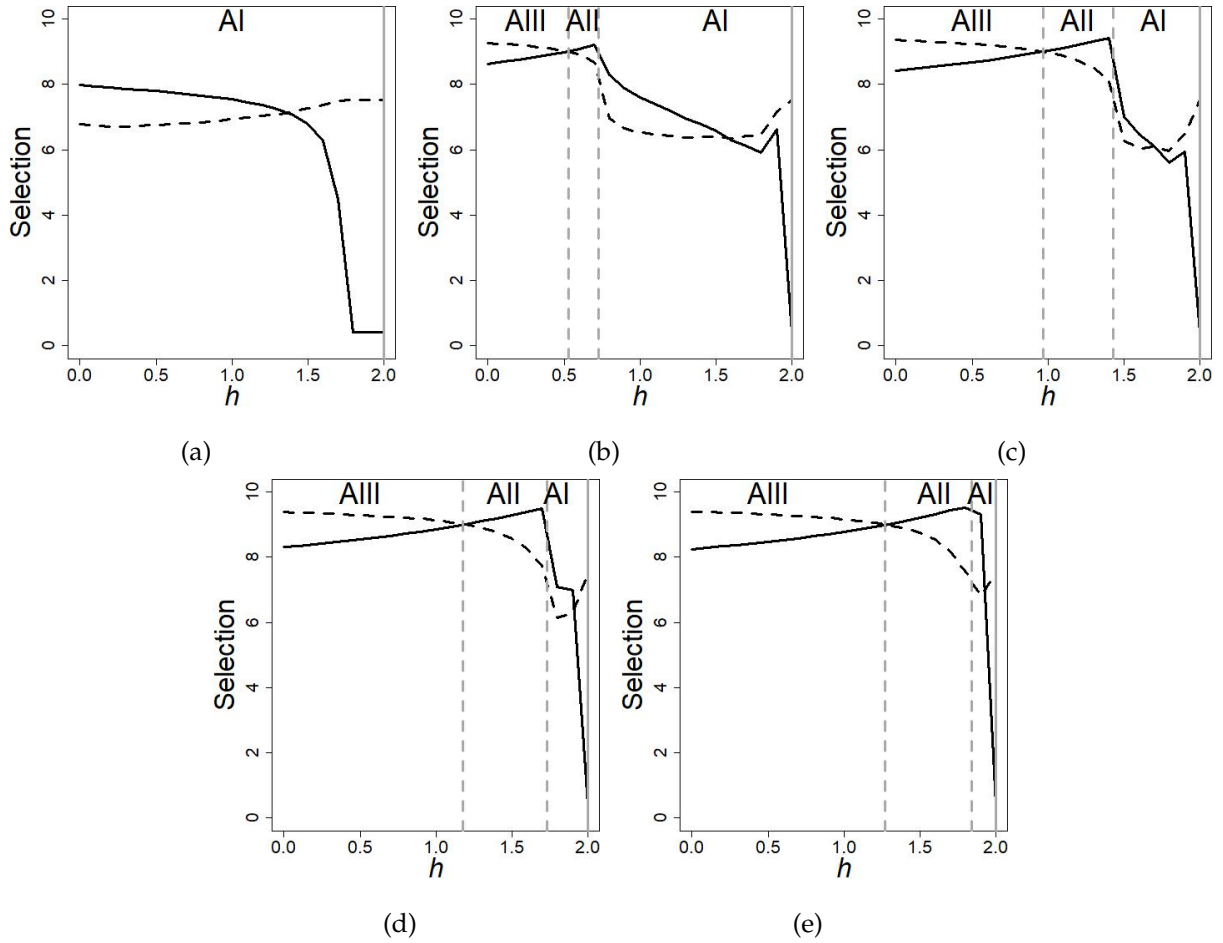
Figure 4: The behaviour of r- (solid black lines) and K-selection (dashed black lines) gradients (r_{sel} and K_{sel}, respectively) for a range of predator handling time, h, in different scenarios of f value. Vertical dashed grey lines separate the areas: AI (runaway dynamics); AII (stable r-selection); AIII (stable K-selection); Solid grey line represents the point where $h = e/d$ (unstable K-selection). a) Predators are specialists in adults ($f = 0$). Areas: AI($0 < h < 1.99$); b) Predators prefer adults ($f = 0.2$). Areas: AI($0.73 < h < 2$), AII($0.53 < h < 0.73$) and AIII($0 < h < 0.53$); c) Predators do not discriminate stages ($f = 0.5$). Areas: AI($1.4 < h < 1.8$), AII($1 < h < 1.4$) and AIII($0 < h < 1$); d) Predators prefer juveniles ($f = 0.8$). Areas: AI($1.73 < h < 2$), AII($1.18 < h < 1.73$) and AIII($0 < h < 1.18$); e) Predators are specialists in juveniles ($f = 1$). Areas: AI($1.8 < h < 2$), AII($1.27 < h < 1.8$) and AIII($0 < h < 1.27$)). Parameters are: $a = 2.2$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $S_J = 0.5$, $l_J = 0.5$, $e = 1$, $d = 0.5$, $\mu_0 = 0.5$, $s = 0.0001$ and $V = 0.05$. Initial conditions are: $N = 0.5$, $\gamma = 0$, $P = 0.5$ and $\bar{\zeta} = 1$.

Discussion

The interaction between preys and their predators is one of the conspicuous phenomena in nature. However, the mechanisms underlying the outcome of such interaction are not obvious. Understanding the relative importance of the components involving predator-prey interactions may improve our ability to understand and predict the outcome of ecological interactions. In this paper, we used a eco-evolutionary model of predator-prey to explore the stage-dependent predation hypothesis and the effects of predator satiation on the predictions of life-history theory.

Our model precisely described the fast-slow life-history continuum generated by the foraging effort of predators. Several field and experimental studies suggest that predator-induced adaptation is a major driver of prey life-history (Reznick et al. 1990, 2001, Rodd et al. 1991, Walsh & Reznick 2011). Nonetheless, these studies also suggest that the effect of predators on prey life-history may be dependent on how density regulation emerges in prey population (Bronikowski et al. 2002). Our model suggests the same. In equation 3d, for example, it is clear that, predator density, P, only affects the temporal dynamics of the proportion of juveniles, γ, when the functional response of predators over juveniles differs from $\gamma f(N, \bar{\zeta})$. However, if sensitivity to density is different between juveniles and adults, predators parameters may indirectly affect γ even if predator density does not. Our results also suggest that juvenile mortality due to somatic costs can affect the role of predator foraging effort (Appendix A). Juvenile intrinsic mortality due to somatic maintenance costs (S_J in our model) is known to affect life-history (Promislow & Harvey 1990). This occurs because, since juveniles do not reproduce, high maintenance costs may reduce population growth (Myers & Cadigan 1993), which affects adaptation if selection is density-dependent (Mueller et al. 1991). For example, Yu et al. (2018) investigated how the brain size affects the life-history of frogs. They found that the cost of maintenance of a larger brain correlated with later maturation. Another important aspect of our model is how juvenile sensitivity to density (l_J) also affects life-history continuum (Appendix A). If juveniles die due to increases in density, selection may give advantage to earlier maturation. In this sense, fast life-history

may evolve even in cases where juvenile predation is greater than adult predation (Appendix A). Therefore, our results suggest that the formation of a fast-slow life-history continuum depends on the ecological parameters of juvenile stage.

Our results indicate that predator satiation also plays a role in fast-slow continuum. Similarly to sensitivity to density regulation (function $l(\overline{\zeta}, \gamma)$ in our model), predator satiation also promotes density-dependent selection on preys (Bogdziewicz et al. 2018, Farkas & Montejo-Kovacevich 2014), but through a different mechanism. This is because while sensitivity to density is a measure of density-dependent mortality, predator satiation measures how predation risk changes with prey density, therefore, it causes mortality through an indirect mechanism. Since selection will optimize the prey energetic budget in order to reduce predation risk (Khater et al. 2016, Persson & de Roos 2013), predator satiation is expected to affect prey life-history. One known example is the reproductive synchrony in mayflies populations (Sweeney & Vannote 1982). Theory predicts that mayflies evolved to perform swarms in reproductive periods because in this way adult density remains greater than the necessary for predator satiation (Sweeney & Vannote 1982). Turtles also provide a good example. Evidences indicate that arribada nesting in turtles may have evolved to decrease predation risk in newborns because predators get satiated (Eckrich Caren E.;Owens 1995). Walsh & Reznick (2011) performed an experiment with guppies (*Poecilia reticulata*) and their prey killifish (*Rivulus hartii*) to evaluate the stage-dependent predation hypothesis. The results opposed to the theoretical predictions because guppies predation on young killifish correlated with the evolution of earlier maturation. Our model predicted that, if predator satiation is high, life-history may evolve towards the fast ending of the continuum even if predators are specialists in juvenile stage. Therefore, we argue that predator satiation could help explain killifish life-history evolution.

In our study, we define the evolving trait as vulnerability to predation. Such a definition may be applied to a broad range of traits such as body-size, speed, boldness, intelligence, or any quantitative trait with continuous distribution. However, specifying the trait of interest is a key point. For example, body size is a trait that also affects prey vulnerability to predation (DeLong &

Luhring 2018). Body-size is a bimodal trait, which means that prey can scape predation by either evolving larger or smaller body sizes (Scharf et al. 2000). On the other hand, traits such speed or toxicity are unimodal, which means that preys may only evolve towards one direction to scape predation. In a sense, any of the cited traits represent vulnerability to predation. However, the genetic architecture underlying each of these traits may differ. Because genetic architecture may change system stability (Schreiber et al. 2016), precisely describing the trait and its underlying genetic control may enhance biological realism of our model.

The eco-evolutionary outcome of ecological interactions may also depend on abiotic properties, such as seasonality and climate change (Carthey & Blumstein 2018, Ferriere & Legendre 2013). Since temperature affects physiological rates that help to define the outcome of predator-prey interaction (Bernhardt et al. 2018), it is expected that a gradual change in earth climate may alter system dynamics. In a theoretical study, Tyson & Lutscher 2016 found that increasing temperature affects predator behaviour, which shifted from generalist (Holling III) to specialist (Holling II) functional response. Predator preference may be intrinsically related to metabolic activity, which can vary seasonally. Similarly, temperature may also affect predator satiation. A empirical evidence is the change in foraging behaviour of bears prior to winter. Bears shift for more energetic resources (Unro et al. 2006), which in turn increases the amount of food supply needed to get satiated. Another example is experiments with *Chrysomya albiceps* that measured the handling time as a function of prey types (Faria et al. 2004). Later, the authors noted that predator satiation was higher in warmer days (personal communication). Such climate change may be assumed in a realist way by incorporating asymptotic environmentally determined trajectories (AEDT) (Chesson 2017) which assumes a gradual non-recursive in the long-term dynamics. We argue that, adopting this framework would help us to reformulate the assumptions of our model and to better predict the outcome of predator-prey interactions in a changing climate context.

In conclusion, our model behaviour is in accordance with the stage-dependent predation hypothesis. Nonetheless, for the model to behave as predicted, both juvenile somatic maintenance

cost and juvenile sensitivity to density must be considered. Also, our model predicts that predator satiation may affect the evolutionary route of predator-induced life-history. The increasing literature on rapid adaptation of predator-prey systems suggests that eco-evolutionary dynamics drives such interaction. We show that, assuming reciprocity between ecological and evolutionary dynamics allows to reproduce some of the relevant hypothesis underlying the effects of predation. Also, we would like to highlight the role that the r/K theory may play in helping to understand such mechanisms. Despite the long use of r/K theory to explain life-history (Gadgil & Solbrig 1972, Pianka 1970), it is not more than a density-dependent selection theory (Boyce 1984, MacArthur 1962). Still, when associated with population structure, the r/K theory precisely described the fast-slow continuum of prey life-history in our system.

Appendix A

The Fast-Slow Continuum

Figure A1 shows the densities, trait value and proportion of juveniles for a range of f values in three special cases: 1) $l_J = 0$; 2) $S_J = 0$; and 3) $S_J = l_J = 0$. This figure is complementary to figure 3 in the main text. The range for which predominant r-selection is stable is greater when $l_J = 0$, when compared to the case where $S_0 = 0$. When both rates are 0, predators go extinct (for our set of parameters; see table TA1) and consequently f does not affects stability.
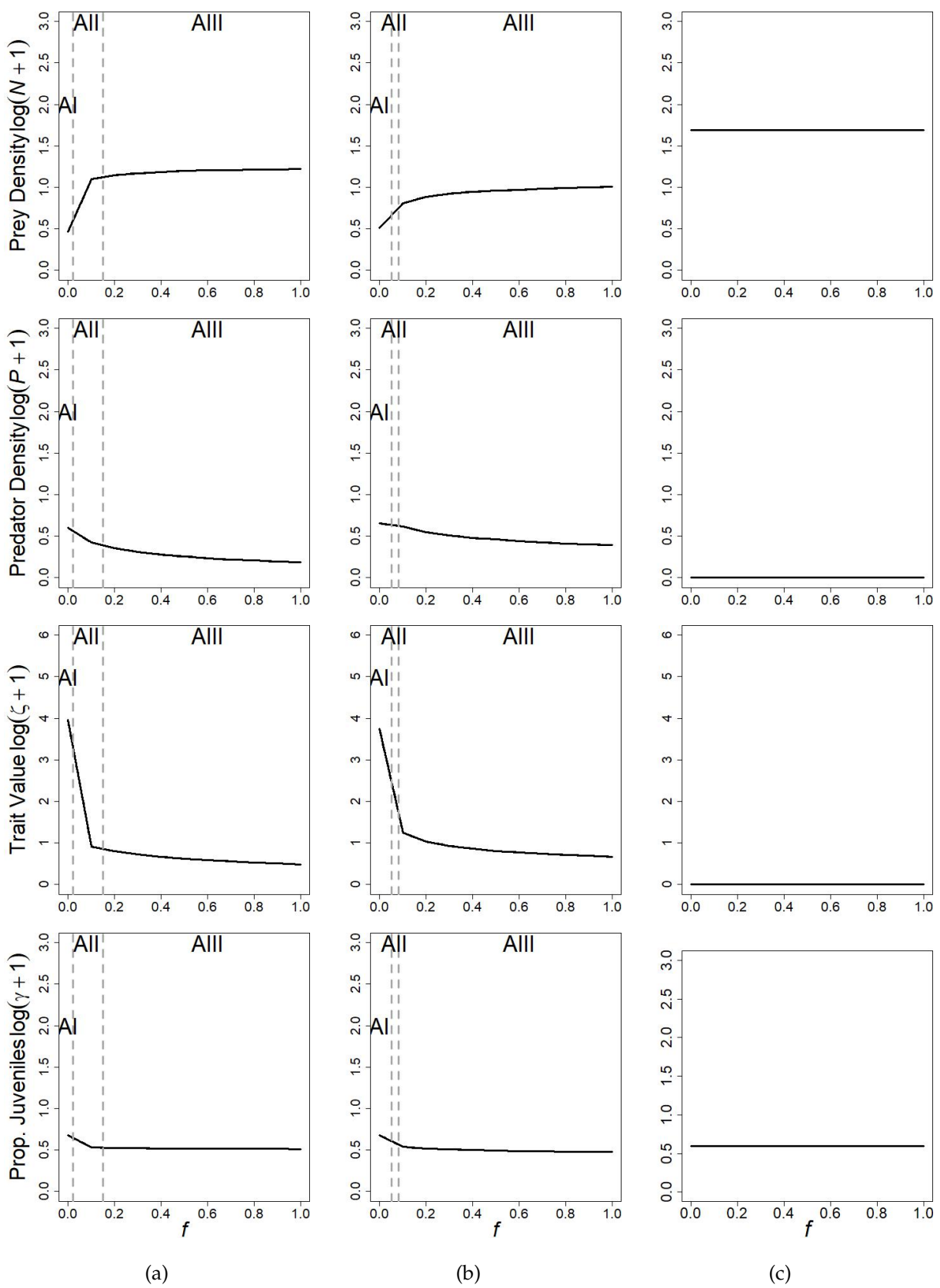
Figure A1: Maximum (solid black lines) and minimum (dashed black lines) of system dynamics for a range of predator foraging effort, f, on juveniles in different scenarios. Vertical dashed grey lines separates the areas: AI (runaway dynamics); AII (stable r-selection); AIII (stable K-selection). a) $l_J = 0$ and $S_J = 0.5$. Areas: AI($0 < f < 0.02$), AII($0.02 < f < 0.15$) and AIII($0.15 < f < 1$); b) $S_J = 0$ and $l_J = 0.5$. Areas: AI($0 < f < 0.05$), AII($0.05 < f < 0.08$) and AIII($0.08 < f < 1$); c) $S_J = l_J = 0$. In this case, predators go extinct and K-selection is negative. Parameters are: $a = 2.2$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $e = 1$, $h = 1$, $d = 0.5$, $\mu_0 = 0.5$, $s = 0.0001$ and $V = 0.05$. Initial conditions are: $N = 0.5$, $\gamma = 0$, $P = 0.5$ and $\bar{\zeta} = 1$.

Predator Handling Time

Figure A2 shows the densities, trait value and proportion of juveniles for a range of h values. This figure is complementary to figure 4 in the main text. Note that, greater the time spent foraging for adults, smaller is the predator satiation value that produces runaway dynamics. In the case where predators only forage for adults ($f = 0$), system presents a runaway dynamics for all values of h between the interval $0 < h < 2$.
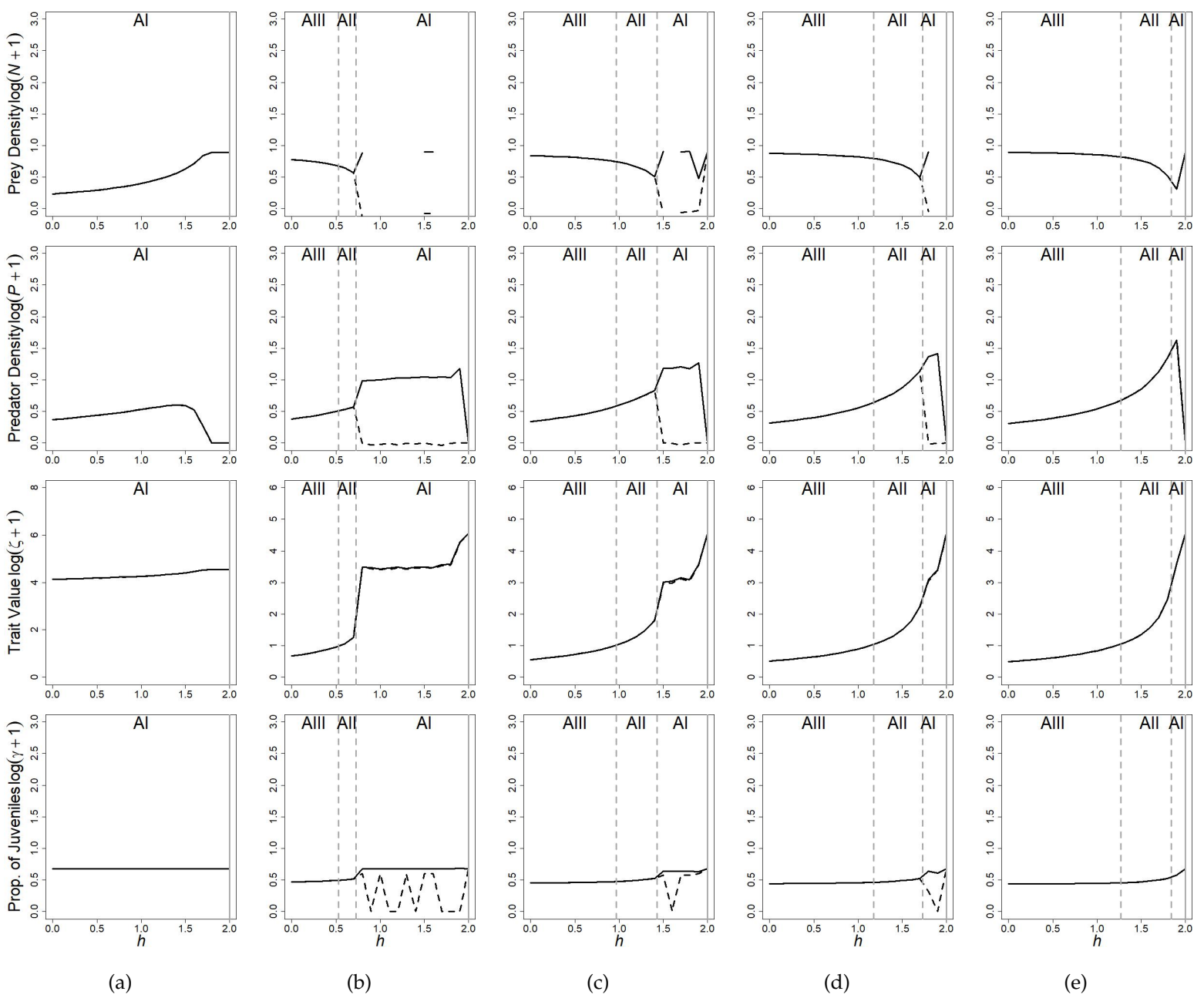
Figure A2: Maximum (solid black lines) and minimum (dashed black lines) of system dynamics for a range of predator handling time, h in different scenarios of f value. From top to bottom: Prey density, predator density, trait value and proportion of juveniles. Vertical dashed grey lines separates the areas: AI (runaway dynamics); AII (stable r-selection); AIII (stable K-selection); Solid grey line represents the point where $h = e/d$ (unstable K-selection). a) Predators are specialists in adults ($f = 0$). Areas: AI($0 < h < 1.99$); b) Predators prefer adults ($f = 0.2$). Areas: AI($0.73 < h < 2$), AII($0.53 < h < 0.73$) and AIII($0 < h < 0.53$); c) Predators do not discriminate stages ($f = 0.5$). Areas: AI($1.4 < h < 1.8$), AII($1 < h < 1.4$) and AIII($0 < h < 1$); d) Predators prefer juveniles ($f = 0.8$). Areas: AI($1.73 < h < 2$), AII($1.18 < h < 1.73$) and AIII($0 < h < 1.18$); e) Predators are specialists in juveniles ($f = 1$). Areas: AI($1.8 < h < 2$), AII($1.27 < h < 1.8$) and AIII($0 < h < 1.27$). Parameters are: $a = 2.2$, $b = 0.8$, $k_0 = 0.5$, $k_1 = 0.25$, $S_J = 0.5$, $l_J = 0.5$, $e = 1$, $d = 0.5$, $\mu_0 = 0.5$, $s = 0.0001$ and $V = 0.05$. Initial conditions are: $N = 0.5$, $\gamma = 0$, $P = 0.5$ and $\bar{\zeta} = 1$.

Parameter values

The parameters interpretations and values (when the parameter is not the one under analysis) is shown in table A1

Parameter	Interpretation	Values
a	Prey innate growth rate	2
b	Prey trait-dependent growth rate	0.8
k_0	Prey innate sensitivity to density	0.5
k_1	Prey trait-dependent sensitivity to density	0.25
e	Predator conversion efficiency	1
h	Predator handling time	1
d	Predator death rate	0.5
V	Trait additive genetic variance	0.05
s	Trait minimum value	0.0001
f	Predator foraging effort on juveniles	0; 0.2; 0.5; 0.8; 1
S_J	Juvenile somatic maintenance cost	0.5
l_J	Juvenile sensitivity to density	0.5
μ_1	Correlation coefficient between reproduction and maturation rate	-
μ_0	Trait-independent maturation rate	0.5

Table A1: Table with parameters values and their interpretation

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