MacArthur's consumer-resource model: a 'Rosetta Stone' for competitive interactions

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Recent developments in competition theory, namely, Modern Coexistence Theory (MCT), have aided empiricists in formulating tests of species persistence, coexistence, and evolution from simple to complex community settings. However, the parameters used to predict competitive outcomes, such as interaction coefficients, invasion growth rates, or stabilizing differences, remain biologically opaque, making findings difficult to generalize across ecological settings. Here, our article is structured around five goals, towards clarifying MCT by first making a case for the modern-day utility of MacArthur's consumer-resource model, a model with surprising complexity and depth: (i) to describe the model in uniquely accessible language, deciphering the mathematics towards cultivating deeper biological intuition about competition's innerworkings regardless of what empirical toolkit one uses, (ii) to provide translation between biological mechanisms from MacArthur's model and parameters used to predict coexistence in MCT, (iii) to make explicit important but understated assumptions of MacArthur's model in plain terms, (iv) provide empirical recommendations, and (v) to examine how key ecological concepts (e.g., r/K selection) can be understood with renewed clarity through MacArthur's lens. We end by highlighting opportunities to explore mechanisms in tandem with MCT and to compare and translate results across ecological currencies towards a more unified ecological science.

coexistence theory | competition theory | contemporary niche theory | Lotka-Volterra | R* |resource utilization

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******Note: There may be minor discrepancies between this version and the submitted version******

Introduction

The Rosetta Stone, a slab carved by Egyptian clergy in 196 BC to translate between hieroglyphic, Demotic, and Greek script, was lost for tens of hundreds of years until it was discovered during Napoleon's invasion of Egypt (Ray 2014). Prior to this discovery, no one knew how to interpret hieroglyphics—hieroglyphics were often interpreted literally, as pictographs representing ideas or events (e.g., 𓄿 represents a vulture) rather than symbols representing sounds of language (i.e., 𓄿 represents "ah"), and as a result, ancient Egypt remained a mystery. Much like ancient civilizations, ecology is a field of many languages in the form of theoretical frameworks each depicting some aspect of how organisms interact with each other and their environments. Some theories deal with flows of matter and energy (Loreau 1995; Sterner and Elser 2002; Brown et al. 2004), others with population abundances and dynamics (Hutchinson 1978) or the distribution of species within and among communities (Leibold and Chase 2017). Although these theories are interrelated and sometimes even involve or describe similar variables or phenomena (e.g., low density growth rates (Roff 1993; Arendt 1997; Saavedra et al. 2017)), like languages, each is rich with tradition (e.g., notation style) and history (e.g., how meaning of parameters has changed over time (Barabás et al. 2018)), has a unique system of assumptions and symbolic representations, and is complex in ways that make translation between theories difficult (Grainger et al. 2022; Ou et al. 2022).

To help translation between seemingly disparate theories in ecology, we focus here on deciphering Robert H. MacArthur's consumer-resource model (equation 1; (MacArthur 1969a, 1970, 1972)) for a general audience while highlighting key misinterpretations. We focus on MacArthur's model for two reasons. First, we view MacArthur's model as an intermediary with potential to connect and better understand ecological theories, including modern theories that simplify prediction by skipping the biological details (Box 1). Second, for some, MacArthur's model is intuitive—it is easy to picture, for example, birds requiring, consuming, and growing populations in response to available seed resources—and thus, can be used to better intuit outcomes in a broad range of ecological scenarios. However, as we will discuss, there are important nuances to interpreting MacArthur's model that are easy to get wrong in ways that are consequential.

Our article is structured around four primary goals: (i) to describe MacArthur's model in biological terms using best practices of accessible writing (e.g., numerical examples, relatable analogies (Shoemaker et al. 2021; Grainger et al. 2022; Ou et al. 2022)), (ii) to present a mathematical translation between parameters of MacArthur's model and parameters more familiar to practitioners of phenomenological models of competition, (iii) to make explicit important (mis)interpretations, assumptions, and limitations, and (iv) provide empirical recommendations. In doing so, we also make a case for the modern-day utility of MacArthur's model (Box 1) and examine how key ecological concepts (i.e., r/K selection, positive frequency-dependent competition) can be better understood through MacArthur's lens (Box 2). Importantly, our contribution here is not simply a review of concepts that can be gathered from any handful of source articles or textbooks—it is the result of 5 years of discussion, puzzlement, and discovery. Much of what we say here is a synthesis of material scattered across hundreds of articles published across decades, and throughout, we make explicit interpretations of the model that have only ever been made implicitly, shedding new light even on concepts that might feel well-understood at first glance.

(i) MacArthur's consumer-resource model: building biological intuition

To aid our discussions, we necessarily begin by first walking the reader through the fundamentals of MacArthur's consumer-resource model, first presented in (MacArthur 1969):

$$\frac{1}{X_i}\frac{dX_i}{dt} = C_i\left[\sum_{k=1}^{m} a_{ik} w_k R_k - T_i\right] \tag{1.1}$$

$$\frac{1}{R_k}\frac{dR_k}{dt} = r_k\left[1-\frac{R_k}{K_k}\right] - \sum_{i=1}^{n} a_{ik} X_i \tag{1.2}$$

The model describes dynamics that arise as populations of consumer species i of density X_i consume and grow in response to resource species k of density R_k. Two features are worth highlighting. First, competition among consumers and predator-prey dynamics are modeled simultaneously, unlike phenomenological models that must treat these two types of interactions separately. Second, this model can be extended to any number of consumer species (denoted by n), resource species (denoted by m), and in subsequent work by others (Chesson and Kuang 2008; McPeek 2022) to more than two trophic levels.

In the absence of consumers (i.e., setting X_i to 0), resources in equation 1.2 grow logistically; they recover from low densities at rates described by r_k, reaching an equilibrium population size at K_k. In the presence of a single individual of consumer species i ($X_i = 1$), each individual of resource k has a probability of being removed of a_{ik} (the per capita attack rate) per unit time. More consumer individuals means more drawdown of resources, decreasing the resource's per capita growth rate. In equation 1.1, parameter w_k "weights" each resource type by its overall nutritional quality to consumers, essentially converting resource intake into usable energy (or consumer biomass, henceforward referred to as 'energy' for brevity). Thus, $\sum a_{ik} w_k R_k$ in equation 1.1 represents total energy intake by each individual of consumer species i (on average at an instance of time) by consuming resources of different weights, adding to growth, whereas term Ti represents each individual's baseline energetic requirements (on average at an instance of time). Populations grow ($(1/X_i)(dX_i/dt) > 0$) when individuals eat more than they require (on average) and shrink ($(1/X_i)(dX_i/dt) < 0$) when they require more than they eat. The exact rate of population growth or decline is set by C_i, the conversion of net energy gain/loss into gain/loss of consumer individuals. For example, if an individual consumes 100 more energy units than it needs and each offspring costs 20 energy units to produce, then the individual can afford to produce five offspring. Although this model feels intuitively familiar in ways that ease understanding, as we will discuss, it harbors a surprising complexity and nuance.

Resource utilization': an ecological hieroglyph One of ecology's most widely used symbolic representations is the Gaussian curve depicting resource utilization, a dimension of the niche that contributes to the outcome of competition. Generally speaking, resource utilization functions depict the ability of an individual, population, or species to consume or usurp certain resource types relative to other resource types (Roughgarden and Feldman 1975). Utilization functions are often drawn cartoonishly to simplify communication of complex concepts (e.g., (Araújo et al. 2011; Brodersen et al. 2018; Ponisio et al. 2019)) and support verbal arguments in presentations or research papers. For example, in devising predictions for how competition coefficients might change as competing species coevolve in sympatry (i.e., a phenomenological approach), it can be helpful to consider changes in the strength and direction of selection on resource utilization felt by each species (e.g., figure 1 in (Germain et al. 2020)). However, utilization curves have a precise theoretical meaning—we will keep the meaning of "utilization" vague for now because, as we will describe, there are several variants of how utilization has been presented in the literature with important consequences for interpretation. Note that these functions need not be ordered on a one-dimensional axis (i.e., seeds based on size), Gaussian, or continuous: they can take on any shape (although the math becomes more complex (see (Roughgarden 1974; Pigolotti et al. 2010; Leimar et al. 2013)), with the area under the curve representing total utilization across all resource types (using summations if discrete (as per equation 1.1) or integral calculus if continuous). Although equation 1.1 deals with discrete resources, we default to continuous (ordered) Gaussian curves in our figures due to their familiarity to most readers. Here we aim to unpack different variants of "utilization", their interpretation, how they relate to one another, and streamline inconsistencies in terminology. In all cases, the height at each point of each curve in figure 1 depicts the magnitude of a given response variable for a given resource type.

(a) Attack rate functions Attack rate functions describe how attack rates (a_{ik} in equation 1) are distributed across k resources (solid lines in figure 1A,C). These rates are assumed in equation 1 to be constant over time and space (unless specified otherwise) and spatially implicit, meaning that every resource item in a given unit of space has an equal probability of being consumed by every consumer individual (see table 1) — by virtue of describing rates of resource removal, some ecologists prefer to refer to attack rates as '(space) clearance rates' (Narwani and Mazumender 2010; DeLong et al. 2018). Attack rate functions reflect traits (e.g., behavioral, morphological) of both the consumer (e.g., different search strategies) and resources (e.g., any countermeasures (Beardsell et al. 2021)). Attack rate functions can be used to predict how a consumer would perform in any hypothetical resource environment (Lawlor 1980), both alone and in competition with other consumers. For example, a consumer may be capable of consuming a given resource, but if that resource is absent, the consumer will be unable to meet its requirements and will not persist (MacArthur 1969). As such, attack rate functions

Box 1. MacArthur's centrality in modern-day ecology

One might wonder why MacArthur's model is worth revisiting at this point in time. No one would argue against MacArthur's central place in ecology's history—his model is well known (at least in terms of its existence) and is understood in great depth by some subset of ecologists, particularly, some theoreticians (Barabás et al. 2018; Chesson 2020; Abrams 2022). At the same time, many modern-day ecologists consider "classical" mechanistic models like MacArthur's to be antiquated given the empirical intractability of measuring all necessary parameters for all relevant resource dimensions (Letten et al. 2017), to the extent that the current generation of ecologists rarely are exposed to this older body of theory as part of their training. "Modern" Coexistence Theory (MCT) has been offered as a popular solution (Hart et al. 2018; Grainger et al. 2019b). Where competition between consumers in mechanistic models largely emerges as an indirect consequence of resource consumption, MCT instead models competition as though it were a direct interaction (McPeek 2022). In doing so, population-level parameters important to competition (e.g., competition coefficients) can be measured by manipulating densities of consumers (Hart et al. 2018) without needing to know the biological details of what consumers are competing for and how—this is often referred to as a more "phenomenological approach" to studying competition (McPeek 2022). This, however, comes at a cost: we have learned from our own experience that it can be challenging to decipher how parameters in a phenomenological model of competition arise biologically (in general and in a specific experimental context), making it hard to predict how parameters (and thus outcomes of interest) might translate across different ecological settings.

Why now? One might argue that to revisit MacArthur's models is to repeat history (Graham and Dayton 2002). Indeed, MacArthur's motivation for developing a mechanistic theory of competition stemmed from a dissatisfaction with phenomenological models, such as Volterra's equations, which may be "hopelessly far" (MacArthur's words) from the reality of nature in many situations (appendix of chapter 2 in (MacArthur 1972)); this is in part why MacArthur's theory and theories derived from it (e.g., (Tilman 1982)) are referred to as "contemporary niche theory" (Leibold 1995)—at the time, a mechanistic approach was the modern one. How can we make progress if we simply keep repeating ourselves? We argue that timing and packaging is everything (hence, the motivation for this special issue). Now more than ever, empiricists are looking to engage with theory, both to motivate and refine experiments (Hart et al. 2018; Grainger et al. 2019b) and to help solve applied problems (e.g., restoration (Aoyama et al. 2022)). This desire is being met with an interest in making theory accessible to a wider audience (Shoemaker et al. 2021; Ou et al. 2022), especially mathematical representations of theory (Grainger et al. 2022)—this in our opinion has been the greatest roadblock: texts aligning phenomenological and mechanistic approaches to competition theory exist (e.g., (Letten et al. 2017)) but are written at a level that may be difficult for most readers to fully grasp.

At the same time, over the past 50 years, ecology has matured as a more synthetic science; revisiting old models with a new lens and new tools (e.g., computational methods (Bolker 2008), experimental techniques (Jolliffe 2000)) can lead to new research avenues. Importantly, we are not advocating for the re-adoption of mechanistic approaches over phenomenological ones (but see (Abrams 2022; McPeek 2022))—in many ways, the phenomenological approach offered by MCT opens up lines of inquiry that would not be feasible to test otherwise, for example, of how overall competitive ability varies among species based on evolutionary history (Sakarchi and Germain 2023), order of arrival (Grainger et al. 2019a), or environmental context (Lanuza et al. 2018; Van Dyke et al. 2022). Rather, we advocate for a deeper understanding of MacArthur's model so that it could be used to help build biological intuition when using other approaches, such as MCT.

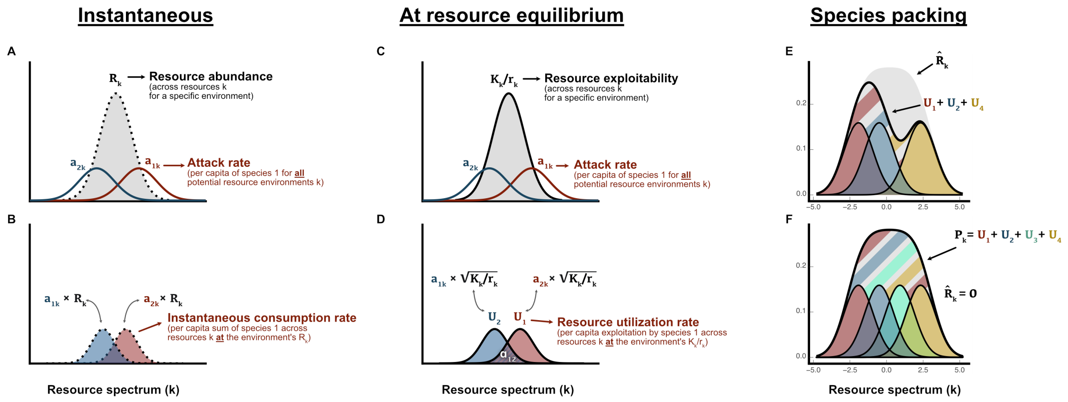

Fig. 1. Clarifying confusion about differences between attack rates, consumption rates, and utilization (panels A-D). Panels (A, C) depict the attack rate functions of two consumers, red (consumer i) and blue (consumer j), for any given level of resource abundance (A), which determines how many resources are consumed by each species at any moment in time (B), or based on relative to rates of resource exploitability (see section i(b)) to determine utilization rates (D). Panel (E) shows an underpacked community where some resources are underutilized, leaving the community susceptible to invasion, whereas panel (F) presents a community of species that fully utilize available resource production (see section i(c)), and thus are fully "packed". The gap in gray between R_k and the summed utilization functions represents the $\mathcal{U}$ component of $\mathcal{Q}$ (described section i(c)).

can be used to characterize a consumer's fundamental and realized niche (Hutchinson 1957; Carscadden et al. 2020), In addition, the degree of overlap in attack rate functions between consumers describes similarities in those consumers' resource niche, or what Lawlor (1980) refers to as 'consumer similarity'. Quantifying attack rate functions can help understand phenomena such as niche evolution (MacArthur and Wilson 1967; Lawlor 1980) or potential spread of species to new areas (Usui et al. 2023). Confusingly, attack rate functions are often referred to as 'utilization functions' (Levins 1968; Schoener 1974; Chesson 1990; Ackermann and Doebeli 2004). For reasons that will become clear (see subsection (b) 'utilization functions' below), attack rate functions are distinct from utilization and cannot be used to predict (i) a consumer's performance, (ii) how many resources a consumer will consume, or (iii) the outcome of competition in the absence of information about the resource environment. However, as Lawlor (1980) argues, if consumers overlap perfectly in attack rate functions, they will also overlap perfectly in all resource environments given that species will be equivalent regardless of context (whereas the inverse is not necessarily true).

(b) Utilization functions For reasons that will become clear, 'utilization' (sometimes referred to as 'total', 'actual' or 'weighted' utilizations (Schoener 1974), represented in MacArthur (1970) and May (1974) by the following equation:

$$U_i = \sum_{k=1}^{m} a_{ik}\sqrt{w_k K_k / r_k} \tag{2}$$

can be thought of as a consumer's ability to impact the amount of resources available to other consumers in the immediate future (a description that sounds vague but is theoretically precise)—these rates are not to be confused with the actual amount of resources each consumer eats at a given point in time (calculated as $\sum_{k=1}^{m} a_{ik} R_k$), a quantity Tilman (1980) instead refers to as the 'instantaneous consumption rate' (figure 1B). Although instantaneous consumption rates determine if a population of consumers will instantaneously grow or shrink given resource abundances at a given point in time, they cannot be used to predict whether or not the population will persist or how strongly a population will experience competition. To understand why, consider a consumer entering an environment replete with resources. At first, the population would grow, giving the impression that the population will persist. However, if the resource ceases to be renewed (e.g., a resource patch formed by a pulsed event), resources will eventually be depleted to zero, resulting in the eventual extinction of the consumer.

In contrast to instantaneous consumption rates, utilization is not necessarily based on consumption itself but on the consequences of consumption for future growth in ways that can be used to predict the outcome of competition. Specifically, for utilization, what matters most is how attack rates align with the rate of resource "re-supply" (i.e., the $w_i K_k / r_k$ portion of the utilization equation (figure 1C vs D)). Consider two resources: mice and rabbits, which both serve as prey for an aerial predator. Because mice have shorter generation times than rabbits (approximated under continuous time for simplicity), their populations are "re-supplied" at a faster rate ($r_{mice} > r_{rabbit}$), rabbits are unavailable for consumption more frequently. In other words, if prey populations have not recovered from consumption by the time the predator returns, then the predator will experience competition. Thinking about this problem mathematically, imagine a single consumer entering an environment where a resource with a nutritional weight (w_i) of 1 is at its carrying capacity of 800 resource individuals per enclosure. Let's say one resource is attacked (a_{ik}) with a rate of 0.1 and the rate of resource re-supply (r_k) is 2.0, in other words, the resource is replenished 20x faster than it is removed per unit time. Even though 10% of resource is attacked and used to grow new consumers, after accounting for resource re-supply, only 5% of the 800 resources are unavailable to future consumers, resulting in a utilization of 2. If r_k was instead 1.0 (a slower rate of re-supply), utilization would increase to $\tilde{2}.83$.

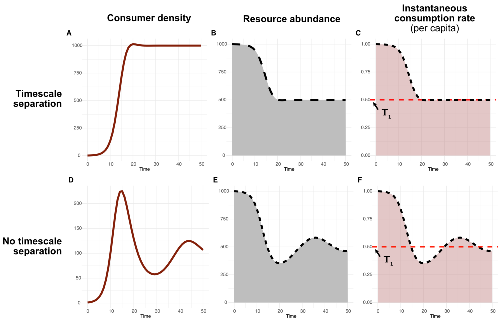

Fig. 2. Comparison of population dynamics of a consumer and its resource with (A-C) and without (D-F) a separation of timescales (see section iii(c)). Panels A-C show the approximate logistic growth of the consumer generated by the timescale separation, modeled by giving the resource a fast low-density growth rate ($r_k = 2$). This fast resource growth corresponds to a consumer utilization (U_{1k}) of 0.5. Panels D-F now show dynamics (e.g., oscillations) when the assumption of timescale separation is broken, with slow resource growth ($r_k = 0.2$) leading to a high consumer utilization ($U_{1k} = 5$). Notably, with timescale separation, resources never fall below a density that fails to meet each individual's minimum requirements (T1; panels C vs. F). All other parameters are held constant: $K_k = 1000$, $a_{1k} = 0.001$, $T_1 = 0.5$.

The effect of r_k on utilization is important in a competitive context because it means that competition is weaker for resources that are resupplied at faster rates ($r_{mouse} > r_{rabbit}$), i.e., resources that are less scarce or less limiting, which is a central tenet of competition theory (Tilman 1984). More precisely, competition is highest for resources that have what we will call the highest 'exploitability' (K_k/r_k). Exploitability corresponds to the time each resource takes to return to its carrying capacity, which is highest for resources that are more abundant (higher K_k) or that are resupplied more slowly (lower r_k). Taken to the extreme, as noted by MacArthur (1972), if resources were to renew instantaneously ($r_k \to \infty$), consumers would not experience competition. Inversely, if resources were increasingly non-renewing ($r_k \to 0$, such that $K_k/r_k \to \infty$), competition would intensify and be destabilized (see section iii(a) about timescale separation) until the resource is entirely expended. Taken

Table 1. Description of parameters in MacArthur's consumer-resource model, including their units, assumptions, and extensions where assumptions are relaxed

Parameter (& Domain)	Example units	Biological definition and comments	Notable assumptions (Special cases are underlined)	Examples of papers that relax these assumptions
C_i $(0 < Ci < \infty)$	grams$_{\text{Daphnia}}$ × Joules^{-1}	**Definition:** Conversion efficiency — a constant that turns combined nutritional weight (e.g., Joules or grams) of substitutable resources acquired in excess of requirement to grams of new individuals (offspring). **Comments:** Often depicted as unitless (as it would be g_i / g_k), unless w_k is better defined with different units like Joules (see w_k)	**I.** Conversion of energy to grams of individuals is linear (proportional to resources obtained) **II.** Conversion efficiency is identical between all resources	**I.** Perrson et al. 1998; Weitz & Levin 2006 **II.** Leibold 1988; Abrams & Cortez 2015
a_{ik} $0 \leq a_{ik} < \infty$	flask × Daphnia^{-1} × Day^{-1}	**Definition:** Attack rate represents the probability the consumer i both encounters and consumes resource *k* per unit time. This can be thought of as what portion of the experimental unit (e.g., "50ml flask") a consumer can encounter and consume a resource in a unit time (day). **Comments**: If the attack rate is 10% per day, this would represent 0.1 "50ml flask"/day. However, if probability is greater than 100% (i.e. $a_{ik} > 1$), this suggests the consumer would take less than the unit time (one day) to encounter and consume the resource *k*.	**I.** Independent of resource density. Representing a Type 1 (linear) functional response (consumption is instantaneous, no handling time) **II.** Independent of consumer density (no Allee effects, interference, or mutualisms) **III.** Independent of environmental conditions (temperature independent) **IV.** Resource competition occurs only over (constantly) limiting resources **V.** Attack rate is constant over time (no optimal foraging) **VI.** Resources depleted by consumers are entirely used for consumer growth (no wastage)	**I.** Stewart & Levin 1973; Real 1977; Armstrong & McGehee 1978, Abrams 1980 **II.** Beddington 1975; DeAngelis et al. 1975; Holland & DeAngelis 2010 **III.** Betini et al. 2019; Vasseur 2020 **IV.** Mazancourt & Schwartz 2012 **V.** Wiens 1977; Persson et al. 1998; Orlando et al. 2012 **VI.** (Hernández-García et al. 2009; Leimar et al. 2013)
w_k $-\infty < w_k < \infty$	Joules × Plankton $^{-1}$	**Definition**: Nutritive weight of a specific resource, often considered to be its 'quality' or 'nourishing value' (not to be conflated with C_i, which is a constant conversion rate across all resources). **Comments**: Usually represented in physical weight (g_k/N_k) but can be converted to other units (e.g., Joules, mg of a specific micronutrient) if physical weights of different resources are not equally nutritious. This would carry over to the conversion efficiency to become a unit-less constant (g_i / g_k). When negative, $w_k < 0$, the resource requires more energy to consume than it provides.	**I.** Each resource is equal in 'nutritive weight' to all consumers	**I.** Schoener 1974
R_k $0 < R_k < \infty$	Plankton × flask^{-1}	**Definition**: Abundance (density) of resource *k*, usually in units of either individuals or biomass per unit area. **Comments**: Sometimes the units are presented without an explicit spatial extent, in which case the spatial unit is equivalent to the experimental unit (e.g., enclosure, pond, island, erlenmeyer flask)--or with explicit space (square meters, gallons). This also extends to the concept of carrying capacity — capturing the 'density' of a population per unit area.	**I.** Resources are depletable **II.** Resources are equally accessible (resources and consumers are homogeneously distributed in space) **III.** Resources are not interacting **IV.** Resources cannot go extinct if used for Q or L-V translation **V.** Resources renew logistically **VI.** Resources are defined per unit of space **VII.** Resource and consumer dynamics operate on separate time scales if used for Q or L-V translation **VIII.** If Gaussian utilization functions are used, resources can be ordered along one dimension	**II.** Sasaki 1996 **III.** MacArthur 1970; Levine 1976 **IV.** Hsu & Hubbell 1979; Abrams 1980 **V.** MacArthur 1972; Abrams 1980 **VII.** O'Dwyer 2018
T_i $0 < T_i < \infty$	Joules × Daphnia^{-1} × Day^{-1}	**Definition**: Per capita resource requirement for consumer *i*; if resource intake just meets this requirement, the population will not grow or shrink. **Comments**: Can be thought of as the metabolic requirement to maintain one individual per unit time. This includes the physiological resource requirements for that individual and also demographic turnover, i.e., resources needed to replace death with birth per unit day. "T" stands for threshold.	**I.** Resource requirement is density independent	**I.** Schoener 1974; Holt 1985; Aubier 2020

Note: Citations in this table are relegated to the Supplementary Materials due to space constraints. Although different symbols for MacArthur's consumer-resource model are used by different authors (e.g., m_i "mortality" instead of T_i and c_{ij} instead of a_{ij} in Chesson (1990)), we adhere to MacArthur's original symbology given that inconsistency across the literature can impede understanding. Scripts, *i*, *j*, and *k* refer to consumer species, heterospecific consumers in the Lotka-Volterra equations, and resource species, respectively, each with a total species pool of *n* and *m*.

together, most ecologists recognize that resource availability (perhaps in a vague sense) is key to determining the outcome of competition. Here, we make the notion of 'availability' more precise in terms of resource exploitability, which emphasizes the importance of dynamic fluxes of resources as opposed to standing stocks. In doing so, we better clarify what competition is fundamentally: it is not simply the impact consumers have on each other's growth, but rather, how rates of consumption affect the amount of time a renewable resource is made unavailable to future consumers. Note that some authors (Ackermann and Doebeli 2004; Abrams et al. 2008) use K_k instead of K_k/r_k to calculate utilization, which does not aim to diminish the importance of re-supply, but rather, makes the simplifying assumption that resources have equal r_k.

(c) Community utilization MacArthur's interest in characterizing resource utilization also served an additional purpose: to formulate his 'minimization principle' (MacArthur 1969; MacArthur 1970). MacArthur's minimization principle states that communities should assemble such that resource competition (and its evolution) minimizes inefficiencies in resource utilization at the community level. He labeled these inefficiencies $\mathcal{Q}$, a quantity that MacArthur himself admitted is "not easy to interpret biologically" (MacArthur 1970):

$$\mathcal{Q} = \underbrace{\sum_k \frac{w_k K_k}{r_k}\left[r_k - \sum_j a_{jk} X_j\right]^2}_{\mathcal{U}} + \underbrace{2\sum_j T_j X_j}_{\mathcal{B}} \tag{3}$$

This equation has been summarized by others (Gatto 1990; Ghedini et al. 2018)) as a sum of two parts: the unutilized productivity of the environment ($\mathcal{U}$, not to be confused with utilization 'U' in (2)) and productivity lost to the basal metabolic maintenance of the consumer population ($\mathcal{B}$). Broken down in into $\mathcal{U}$ and $\mathcal{B}$, it becomes clearer that $\mathcal{Q}$ represents inefficiencies in energy flow from lower trophic levels to higher ones: if a population of consumers used resources in their entirety, consuming new resources as fast as they are produced (i.e., when $a_{jk}X_j = r_k$, such that $R_k \to 0$ and $\mathcal{U} = 0$; figure 1F), and had infinitesimally small metabolic requirements (i.e., $T_i \to 0$, causing $\mathcal{B} = 0$), then inefficiencies (i.e., $\mathcal{Q}$) would be 0. Of course, it is biologically impossible for populations to subsist with next to zero requirements, and more efficiently utilizing productivity (decreasing $\mathcal{U}$) would typically come at the cost of increasing metabolic requirements (increasing $\mathcal{B}$)—thus, every community is inefficient to some degree.

$\mathcal{Q}$ is ecologically important for several reasons. First, if $\mathcal{Q}$ decreases over time ($d\mathcal{Q}/dt < 0$) it tells us that the community of consumers is not at an equilibrium ($X_j \neq X_j*$). Second, and perhaps more importantly, if the community is at an equilibrium and $\mathcal{Q}$ is still not minimized (i.e., alternative combinations of species that reduce $\mathcal{Q}$ further are biologically possible; gray portion of figure 1E), then the community is susceptible to invasion by new species or new genotypes — by "biologically possible", we mean species that are closer to an optimized form given realistic biological constraints — for example, a species with zero metabolic requirements ($T_i = 0$) is biologically impossible. In other words, $\mathcal{Q}$ is closely tied to conditions for coexistence in multi-species communities (MacArthur 1969). Additional details on species packing with an emphasis on communities assembled by evolution can be found in Germain et al. (2024).

(ii) Translating MacArthur to Lotka-Volterra

Modern coexistence theory has become a popular tool for testing hypotheses of how species persist, coexist, and evolve in simple to complex community settings, however, there remains concern over how phenomenological 'mechanisms' of coexistence underlying modern coexistence theory can be interpreted biologically (Box 1 (Abrams 2022; McPeek 2022)). We argue that these concerns could be addressed in part by making explicit the mechanistic underpinnings of the parameters found in phenomenological models of coexistence, both verbally and mathematically (table 2), which we provide here in one place for the first time. Although these mathematical translations can be found scattered throughout the classical literature, they are easy to miss—for example, MacArthur (1970) represents a consumer's intrinsic rate of increase using $\mathcal{K}$, and nowhere in that paper does he actually refer to $\mathcal{K}$ as the intrinsic rates of increase. In addition, MacArthur was a champion of brevity, presenting the equations with little biological interpretation. We focus on the Lotka-Volterra competition model given its widespread use in ecology, including in the coexistence literature (e.g., (Broekman et al. 2019)) — other commonly encountered models, such as the Beverton-Holt annual plant model, make slightly different assumptions but share many general features with Lotka-Volterra (Weigelt and Jolliffe 2003). By providing a translation to mechanisms, this section will make clear two important take-home messages about the Lotka-Volterra competition model: (1) that its parameters (e.g., r, α, and K) are not independent, as they share mechanistic underpinnings, and (2) that every parameter is affected by the resource environment (albeit in different ways). To avoid confusion, symbols 'r' and 'K' will continue to represent the **resources'** intrinisic growth rate and carrying capacity (as per equation (1.1)); to clearly distinguish the consumer from the resource, we will use symbols 's' and 'L' to refer to the intrinsic growth rate and carrying capacity of the **consumer**, respectively (note: 's' and 'L' are one-letter. shift from 'r' and 'K').

We begin by walking through the Lotka-Volterra competition model (see table 2 for a quick reference of parameters), a model which describes the growth of different consumer species i as they compete with conspecifics (i.e., X_i) and heterospecifics (i.e., X_j):

$$\frac{1}{X_i}\frac{dX_i}{dt} = s_i\left[1 - \frac{X_i}{L_i} - \frac{\sum_{j=1}^{n} a_{ij} X_j}{L_i}\right] \tag{4}$$

This version of the Lotka-Volterra equation forces the intraspecific interaction coefficient (α_{ii}) to be 1, thus, α_{ij} is

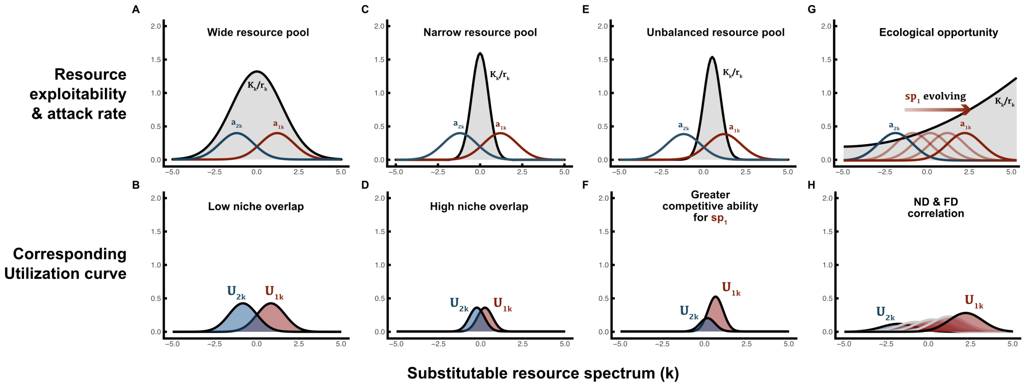

Fig. 3. Effect of the resource environment on competitive differences among consumers. Panels (A,C,E) depict the same two consumers, red (consumer i) and blue (j), in three different years. In years with a wide and more even distribution of resources (A), utilization closely mirrors the consumer's attack rate function (B). By contrast, differences among consumers collapse (i.e., increased overlap (D)) or result in a competitive asymmetry (i.e., an asymmetry in total utilization (F)) when resources are more narrowly distributed (C) and favor one consumer (E). Panels (G,H) illustrate how the resource environment can create ecological opportunities that consumers can evolve to better exploit (i.e., a shift in the red consumer's attack rate function), here, illustrating how competitive asymmetries ("fitness differences", or FD, to mirror the MCT literature) and niche partitioning ("niche differences", or ND) can evolve to increase in tandem.

relative to α_{ii}. As a consequence, a necessary condition for coexistence in this model is that intraspecific competition must be greater than interspecific competition; this condition is met when all $\alpha_{ij} < 1$.

First we examine Lotka-Volterra parameter s_i (equation (4), table 2(A)), which describes how quickly a consumer population can grow from low densities (i.e., when all $X \approx 0$). Intuitively, s_i should increase with resource densities, but why and by how much? When $X \approx 0$, resource densities grow to carrying capacity (K_k) as no consumption takes place. As such, s_i can be calculated by setting R_k in equation 1.1 to K_k. Doing so means that energy available for growth is simply the difference between energy gained by consumption ($\sum a_{ik}w_kK_k$) and energy lost to metabolism (T_i). Parameter C_i converts this excess energy gain or loss into gain or loss of consumer individuals. So, the consumer's growth rate at low densities (s_i) is higher in environments where resources have a higher K_k or nutritional value (w_k) or for consumers with higher overall attack rates (a_{ik}), lower metabolic requirements (T_i), or a higher conversion efficiency (C_i); s_i is unaffected by rates of resource resupply.

As consumer populations grow, the Lotka-Volterra competition model includes two quantities that describe how consumers impact each other's growth as consumer densities increase: L_i and $\alpha_i j$. Consumers reach carrying capacity (L_i) when resources are drawn down to a density low enough that any energy captured ($\sum a_{ik}w_kR_k$) is just enough to meet metabolic requirements (T_i). When assessed separately for each resource species k, the exact resource density corresponding to L_i is the consumer's $R*$ for that resource, calculated as $T_i/(a_{ik}w_k)$ (see table 2E for calculation of $R*$ when multiple resource species are present). $R*$ is also the resource's equilibrium density when the consumer is at L_i — i.e., it represents the standing productivity of the system that cannot be used by consumers, which helps illustrate exactly why consumers with higher requirements (T_i) are inefficient from an energetic perspective (see section i(c)). At this $R*$, because the resource is below its own carrying capacity (i.e., $R_k < K_k$), the resource begins every moment in time by growing logistically, producing what MacArthur referred to as "useful production".(table 2G (MacArthur 1972)). This productivity is "useful" in the sense that 100% of resource growth will be consumed to maintain the consumer at its current density. Note that "useful production" is not to be confused with resource exploitability (equation (2)), as the latter is an intrinsic characteristic of the resource agnostic to consumer densities. By substituting $R*$ into the left-hand side of the equation shown in table 2F, we can solve for X_i, which is the consumer density that corresponds to resources at R* (table 2B)—this solution is the equation for the consumer's carrying capacity from Lotka-Volterra except represented by the parameters of MacArthur's model.

α_{ij} describes the interspecific interaction coefficient, or, the change in a consumer *i*'s per capita population growth rate for each individual of consumer *j* added—resource competition results in positive values of α_{ij}. In MacArthur's model, interspecific competition is described by the equation shown in table 2C, or how much of an individual's potential utilization will be usurped by an individual of consumer*j*(i.e., another species, numerator) relative to an individual of consumer*i*(i.e., its own species, denominator). As a side note, unlike MacArthur, many ecologists prefer to work with the Verhulst version of the Lotka–Volterra model (Mallet 2012; Broekman et al. 2019):

$$\frac{1}{X_i}\frac{dX_i}{dt} = s_i - \alpha_{ii}X_i - \sum_{j=1}^{n}\alpha_{ij}X_j \tag{5}$$

In this version, L_i emerges naturally as intraspecific competition (α_{ii}) causes per capita growth rates to decrease from s_i to 0. In this version, α_{ii} can take on any value and α_{ij} is no longer relativized by α_{ii}.

Together, s_i, L_i, α_{ii}, and α_{ij} provide everything one needs to calculate Modern Coexistence Theory's mechanisms of coexistence, for example in non-fluctuating environments, niche differences that act to stabilize coexistence and competitive ability differences that destabilize it. From our descriptions above, we can see why these two mechanisms may not necessarily vary independently of one another, as has been demonstrated by others (Kuno 1991; Mallet 2012; Barabás et al. 2018; Song et al. 2019). For example, imagine a scenario where a new beneficial mutation rises to fixation in a population that allows for more efficient resource extraction across all resource types. This singular change would lead to an increase in s_i as each individual would have access to more resources at low densities at the cost of simultaneously increasing the intensity of intraspecific interactions, causing shifts in the relative strengths of α_{ij} and α_{ji}—this specific scenario would mean that competition is strongest in ideal environments, strengthening competition-environment covariance, a key contributor to coexistence in fluctuating environments (Johnson and Hastings 2022). Note, however, that even though niche and competitive ability differences are not mechanistically independent, they can still vary in an uncorrelated fashion, as has been obvious in empirical research (Kraft et al. 2015; Buche et al. 2022; Yan et al. 2022) given the diversity of ways mechanistic parameters may change across species and environments (Vincent et al. 1996; Abrams 2022). Even more, although changes in the resource environment can simultaneously impact interaction coefficients and s_i (e.g., if K_k increases), this is not always the case—the rate of resource re-supply has no impact on s_i whereas it is key to the interaction coefficients (so long as K_k is unchanging).

One of the biggest limitations of Modern Coexistence Theory is how sensitive empirical outcomes are to environmental context. Consider how competitive differences between a pair of species change among years depending on interannnual variation in resource exploitability (figure 2), even though the species have fixed attack rate functions. In a year with a broad pool of resources, each species' utilization (figure 2B) largely mirrors its attack rate function (figure 2A)—each species utilizes a similar total amount of resources (i.e., areas under the curves are equivalent), meaning that their competitive abilities are similar (MacArthur and Levins 1967), and the area of overlap is small, suggesting the presence of niche differences. If this pool of resources narrows (figure 2C) or becomes biased in favor of one species (i.e., species j; figure 2E), coexistence becomes less stable as niche differences collapse (figure 2D) and competitive asymmetries emerge (figure 2F). Often, empirical tests of Modern Coexistence Theory lack information about the resource environment or about how species are using or requiring resources, leading to a common conclusion that responses to, say, an environmental manipulation, are "idiosyncratic" across species (Germain et al. 2018). In other words, Modern Coexistence Theory can reveal how species competitive hierarchies shift in different contexts (experimental or natural), but without knowing why they shift, predicting and forecasting outcomes in new contexts, such as when environments change or when new species are added, is not possible.

(iii) Less understood but important assumptions of MacArthur's model

As with any model, MacArthur's model is replete with assumptions. Exploring the consequences of breaking these assumptions has been an enduring focus of empirical (Ayala et al. 1973; Miller et al. 2005) and theoretical (e.g., (Fronhofer et al. 2018)) research, including subsequent work by MacArthur (MacArthur 1972) and Tilman's well-known exposition in the 1980s (Tilman 1980). Assumptions are important to be aware of because they tend to constrain a model's generality, for example, of what kinds of study systems the model can and cannot be applied to. Assumptions may apply to individual parameters in the model (see table 1), to the model as a whole, and to the techniques used to analyze the model to arrive at analytical solutions. However, assumptions are not always easy to intuit unless they are explicitly and unambiguously stated (Ou et al. 2022), although an intuition does become easier as one becomes more familiar with a model, an aim of this article. Here, we do not wish to provide an exhaustive review of the model's assumptions given the availability of other excellent reviews (but see table 1, where we have compiled the most extensive list of assumptions of MacArthur's model to date). Rather, we wish to highlight three consequential but lesser known or understood assumptions.

(a) A complete separation of timescales (also referred to as a 'quasi-steady state' assumption An important assumption MacArthur uses to analyze his model is a complete separation of timescales between consumer and resource dynamics (MacArthur 1970). Although many articles state this assumption, descriptions of what it means, why it is needed, and what its consequences are remain difficult to interpret biologically. Timescale separation means that, at every point in time, resources are assumed to start at a density that is in equilibrium with the density of consumers. At this resource density, rates of resource growth (the first term in equation 1.2) are exactly equal to rates of resource removal by consumers (the second term in equation 1.2). We present the equation to solve for this density, which we call $\hat{R}_k$, in table 2F. Importantly, consumer densities are still free to change, thus, $\hat{R}_k$ exists in a quasi-steady state, constantly adjusting to track the consumer population (figure 3B). If consumers were to instantaneously vanish from a system, the resource population would reach its carrying capacity effectively instantly regardless of the resource's density when consumers were present.

Assuming a complete separation of timescales is made purely for mathematical ease, although theoreticians argue that it is biologically reasonable in systems where resources have short generations relative to consumers (e.g., plankton growing faster than planktivores). Without this separation, consumer-resource interactions become more complex (Reynolds and Brassil 2013; O'Dwyer 2018), generating consumer dynamics that no longer follow logistic growth (e.g., predator-prey cycling as seen with lynx and hare; figure 3A,B vs 3D,E) — biologically this is not a problem, but mathematically it complicates attempts to analyze MacArthur's model, for example, when attempting to align parameters from MacArthur's model with parameters from the Lotka-Volterra competition model as shown in section (ii) (O'Dwyer 2018). Additionally, without timescale separation, resources may be consumed to extinction, whereas this is much less likely with timescale separation (i.e., resource abundances bottom out as consumers reach their equilibrium).

(b) Resources are substitutable Although rarely explicitly stated, MacArthur's model only applies to substitutable resources. Non-substitutable (or 'essential') resources refer to different resource types that cannot be consumed interchangeably to meet a similar metabolic need. For example, a plant requires both water and nitrogen—consuming more nitrogen does not make up for any shortcomings in the supply of water. By contrast, substitutable ('non-essential') resources can be consumed interchangeably. Resources need not have the same nutritional quality in order to be considered substitutable, for example, if a hawk can simply eat more mice to make up for a lack of rabbits. Note that equation 1.1 only has a single requirement term, T_i, for all resources; each resource type contributes to meeting this T_i, which would not be the case for non-substitutable resources.

To extend MacArthur's model to include non-substitutable resources, we envision that each unique class of non-substitutable resources (e.g., food, water, shelter) represents a non-substitutable resource dimension (d) that may still be composed of substitutable subtypes. Equation (1.1) then becomes:

$$\frac{1}{X_i}\frac{dX_i}{dt} = C_i \min_{d}\Big(\sum_{k=1}^{m} a_{ikd} w_{kd} R_{kd} - T_{id}\Big) \qquad (6)$$

In this way, the equation applies Liebig's law of the minimum (von Liebig 1855), meaning that growth is dictated by the resource dimension that is least available ($\sum a_{ikd} w_{kd} R_{kd}$).relative to the consumer's requirement (T_{id}; hence the $\min_d$. In practical terms, equation (6) allows us to holistically consider a wider array of resources and predict if changes in abundance of any one resource within a given dimension will ultimately influence competition.

(c) No resources are wasted MacArthur's model implicitly assumes that resource consumption always contributes to consumer growth—in nature, however, resources are sometimes wasted (i.e., made unavailable by a consumer without contributing to its growth). Resource wastage can occur via many mechanisms. For example, brown bears have been known to only consume the fattiest parts of a salmon, leaving 75% of the body that is now unusable to other consumers of live salmon (Lincoln and Quinn 2018). Alternatively, resource wastage may also take the form of interference competition, including territoriality, allelopathy, environmental modification via metabolic, or apparent competition for 'enemy free space'(MacArthur and Levins 1967; Holt 1977; Jeffries and Lawton 1984). Here, a consumer may monopolize resources in a territory even if the consumer is that it is unable to consume those resources (Leimar et al. 2013).

Resource wastage has interesting consequences for competition. For example, wastage might cause a consumer (say, consumer i) to increase its impact on another (consumer j), increasing α_{ij} without corresponding increases α_{ji} or α_{ii}. In other words, in this example, consumer i's response to (α_{ji}) and effect on (α_{ij}) consumer j become decoupled (Goldberg 1990; Leibold 1995; Hart et al. 2018; Sakarchi and Germain 2023) while tipping the balance between the relative magnitudes of intraspecific and interspecific competition, creating a competitive asymmetry (but see figure 4 for an alternative scenario). For this reason, several authors (Hernández-García et al. 2009; Leimar et al. 2013) have proposed that, when necessary, utilization functions can be decomposed into two parts (figure 4): 'effective utilization', which represents the fraction of utilization that contributes to growth, and 'total utilization', which also includes wastage.

(iv) Empirical recommendations

Throughout this article, we have shown how considering resource dynamics in tandem with consumer dynamics can reframe our biological intuition about the inner workings of competition. Here, we highlight fruitful applications and avenues for empirical research inspired by these intuitions.

Strengthening hypotheses: As ecological theory becomes increasingly abstract, we risk detaching our decisions of what we manipulate and measure in experiments from the underlying biology. As one example, competitors might coevolve to use different resources (character divergence) or to use the same resources (character convergence), or might not evolve at all. Although all are theoretically possible, we cannot predict which outcomes will be most likely without considering the dynamics of the resource environment, as these outcomes critically depend on how rates of resupply vary among resource types to shape ecological opportunities (Germain et al. 2024). As another example, one might want to test whether a focal species can persist in different parts of a landscape. However, if resources in that landscape were deposited in a pulsed, periodic fashion, or if the resources with a very slow resupply rate have had a long time to accumulate before the experiment was initiated, the species may at first appear to persist only until resources are wholly depleted, spurring a crash (as discussed in section (i)). Such scenario illustrates what we will call a "pseudo-source" population, the inverse of a "pseudo-sink" (Holt 2009). Similarly, we might draw stronger inferences about the likely winners and losers of competition based on experimental manipulations of, say, increased resource supply (as in figure 2) or temperature (that increases metabolic demands); this contrasts studies that instead conclude that competitive responses are "idiosyncratic" across species, as we describe in section (ii). Lastly, predicting the likely consequences of broken assumptions (listed in table 1) is itself the basis for entire research programs, for example, to test how often resources are wasted, in what ways, and with what consequences for competitive outcomes (sec-

(c) No resources are wasted

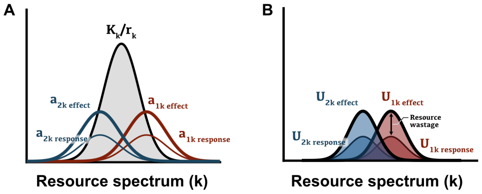

Fig. 4. How resource wastage affects competition. Here, we now show two kinds of attack rate and utilization functions. The curves with thinner lines represent what we refer to here as "effective" attack rate/utilization functions, i.e., resources that are consumed and actually contribute to a consumer's growth—these are no different from the regular curves presented in figure 1A. By contrast, the curves with the thicker lines represent "total" attack rates/utilization, which includes the "effective component" as well as extra resources impacted through wastage (see section iii(c))—thus, wastage is the difference between these two curves. If only one species wastes resources, this can cause an asymmetry in competitive impact even if those consumers are otherwise competitively equivalent. This figure and the effective vs. total terminology is summarized from Leimar et al. (2013).

tion (iii)). In Box 2, as examples, we unpack two specific research topics in ecology that can be understood with renewed clarity through the lens of MacArthur's model. This is where we feel this paper will make its biggest impact: by cultivating a stronger biological intuition for the mechanisms underlying competition, stronger hypotheses will naturally follow.

Converting biological currencies across scales: Because MacArthur's model describes the consumption and conversion of exploitable resources into more consumers, it provides a natural link between biological scales: lower levels, such as metabolism/energetics and stoichiometry of individuals (which includes movement and behavior), to higher levels, such as communities or ecosystems. Reflecting our own expertise, here we have focused on the upwards translation: from individuals to populations to communities. However, we believe that the deeper understanding of MacArthur's model that our article provides should similarly ease future translations by others to lower levels (e.g., the metabolic, behavioral, and biophysical traits that determine the parameters in MacArthur's model). Once those connections are made, we imagine being able to examine the cascading consequences of changes at any level to all others, analytically, or more practically, using individual-based simulations. Doing so would reveal the biological cause of fundamental constraints and tradeoffs in biological responses.

Modifying competition experiments to estimate consumer traits and resource dynamics: A common approach to parameterizing phenomenological models of competition is to measure the growth rates of competitors when introduced at low densities in an environment that either lacks competitors (to isolate s_i in equation 4) or that contains resident species at an equilibrium—this approach is called an 'invasibility trial' (Grainger et al. 2022). For organisms with simple resource requirements, such as flour beetles, these experiments present an unappreciated opportunity: to estimate each consumer's attack rates (a_{ik} in equation 1) and resource requirements (T_i) by explicitly considering resource dynamics in tandem with population dynamics. Specifically, when consumers are at their carrying capacity, which is usually the case for the resident population in an invasibility trial, the rate of the total resource supply is equal to $X_i T_i$ (i.e., the total amount of resources required to sustain the population of consumers at their equilibrium size). In other words, by dividing the rate of total resource resupply by the size of the consumer population, we can estimate T_i. If the experimenter is also able to estimate R_k at this equilibrium, then $a_i k$ can be approximated by dividing T_i by R_k (by rearranging equation E in table 2 assuming a linear functional response). In the interest of brevity, in the Supplementary Materials, we provide two detailed case studies of how an experiment could be designed to estimate T_i and a_{ik}. There are many reasons why an ecologist might be interested in a consumer's resource requirements and attack rates. For example, the distribution of attack rates across resource types constitutes the fundamental niche (section i(a)), and trade-offs between resource requirement and attack rates may represent a fundamental constraint on resource acquisition and coexistence (Box 2(a)).

Conclusions

Here we have showcased Robert MacArthur's consumer-resource model's centrality to the theory of competitive interactions and its connection to phenomenological models commonly used to quantify competition and predict coexistence.

In doing so, we:

- made clear the distinction between attack rates, consumption rates, and utilization, quantities that have been conflated in the literature for >40 years
- moved beyond vague notions of "resource availability", emphasizing "resource exploitability" as a key determinant of competitive outcomes
- clarified exactly what competition is (i.e., the action of making a renewable resource unavailable for a prolonged period of time)
- showed when and why coexistence outcomes are expected to change across resource environments, and sometimes might even give the appearance that species are ecologically equivalent in certain resource environments despite underlying differences in resource niches among species (figure 2)
- made accessible complex concepts, such as timescale separation, "useful production", and MacArthur's minimization principle (and the meaning of $\mathcal{Q}$ (eq. 4), that are of broad importance to biodiversity studies

As described in Box 1, two excellent books have highlighted a range of concerns (Abrams 2022; McPeek 2022) which they use to stake their opposition to phenomenological approaches. Our stance is more balanced (Germain et al. 2022), instead providing a guide for researchers to endeavor to understand mechanistic models enough to guide hypotheses, to think through assumptions, and to potentially stimulate new research at the intersection of approaches and biological scales.

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Box 2. Resolving misconceptions about core ecological concepts through the lens of MacArthur's model

Ecology is a science of how organisms and their environments interact, however, linkages between many concepts and mechanisms that underlie them is not always obvious. Here, we expand upon two core concepts, describing how common misconceptions of each can be resolved by viewing them through the lens of MacArthur's consumer-resource model. Of course, there are many concepts in ecology—we view these specific (and closely related) two as examples of how the inner workings and applications of core concepts could be more easily intuited by being placed within MacArthur's model.

(a) r/K life history theory "r/K selection", as originally envisioned by MacArthur and Wilson (MacArthur and Wilson 1967), refers to the selective environment populations experience when they are kept at densities far below carrying capacity (i.e., in their exponential "r" phase of growth) vs in competition at carrying capacity (i.e., the "K" phase of growth). Instead of focusing on traits, such as investment in many small vs. few large offspring (Pianka 1970); (Reznick et al. 2002), it is useful and perhaps more general to consider how these life history syndromes map onto resource utilization (MacArthur and Wilson 1967). Importantly, increasing overall utilization of resources comes at a cost, as individuals are burdened with increased resource requirements (i.e., higher T_i) to fuel the machinery and increased energetic demands of more efficiently capturing resources (e.g., through enhanced mobility). Consider a population at low density, nowhere near its carrying capacity. Each individual has access to a surplus of resources, even with very low effort. Although increasing utilization efficiency would further increase access each individual has to resources, net fitness benefits may be balanced out by the costs of increasing requirement, and thus, may not evolve. At carrying capacity, individuals are still bound by these tradeoffs. However, even if an increase in utilization comes at the cost of increased requirement, there remains a net benefit as these individuals would outcompete others for scarce resources. By rooting r/K selection by MacArthur's model, several misconceptions become more apparent. First, r-selection only makes sense in environments where populations fall far below K_i, for example, due to disturbances or predators (Reznick et al. 2002) and not environments that simply cannot support a high population density (Taylor et al. 1990). Second, numerous ecology textbooks define K-selection as selection for increasing population size over time as populations adapt to competition (Vandermeer and Goldberg 2013; Hutchings 2021), suggesting that K-selected species interact less strongly with each other compared to r-selected species (that simply never reach high enough densities to compete), a statement also found in the primary literature (Roughgarden 1971)—this seems backwards. Instead, one might expect carrying capacity to shrink over time as populations adapt to increase their attack rate (a_{ik}, thereby lowering K_i, table 2B given that individuals that capture more resources will outcompete others; this creates a Red Queen dynamic favoring the evolution of increased competitive ability, or more generally, a "tragedy of the commons" over shared resources. A systematic review of the r/K-selection literature with a focus on studies that directly measure the evolution of carrying capacities (as opposed to growth rates or selection gradients, as is most common) are needed to weigh evidence for or against these expectations. We believe that these misconceptions have arisen in part due to drift in terminology: that the term 'K-selected' has been interpreted as meaning selection **for** K_i under competition, as opposed to referring to populations evolving **at** K_i, as MacArthur initially envisioned when he first coined these terms (MacArthur 1962) and expanded upon in MacArthur & Wilson (1967) in terms of resource utilization. These misconceptions might also explain why r/K selection has fallen out of fashion.

(b) Positive frequency-dependent competition An interesting competitive dynamic arises when heterospecifics compete more strongly than conspecifics (Ke and Letten 2018): species increasingly gain a fitness advantage as they outnumber their competitors, resulting in positive frequency-dependent population growth that leads to exclusion of the rarer species. As a consequence, competition may result in alternative stable states depending on which species is able to gain a numerical advantage, for example, by arriving first or due to random fluctuations in density, a dynamic sometimes referred to a 'priority effect' in the coexistence literature (but see (Zou and Rudolf 2023) for a commentary on terminology). How can positive frequency-dependence arise in MacArthur's mode? Tilman proposed that consumers may sometimes impact resources they do not strongly require (D. Tilman 1982). Positive frequency dependence then arises when competing species reciprocally impact resources their competitors require most, relative to resources they themselves require. Why would an individual invest time and energy impacting resources for which it does not strongly require? One quickly finds that this kind of dynamic cannot be represented using simple niche cartoons, in contrast to coexistence or competitive asymmetries (e.g., as per figure 2). We contend that 'resource wastage' (see section iii(c)) is an overarching explanation, which occurs when a resource is consumed (in the broad sense) which is not critical for growth, which can inflate interspecific competition relative to intraspecific competition (figure 4). In order for wastage to confer alternative stable states, both species must waste each other's resources. For example, a wild pig digging through soil to find food might destroy habitat for groundhogs; groundhogs, in the process of digging their tunnels, may destroy food resources for wild pigs. If wild pigs are more abundant than groundhogs, groundhogs are at a disadvantage and vice versa. Although examples are most easily conceived of for non-substitutable resources, where each species requires something very different from the environment, the same reasoning should apply to substitutable resources if resource types differ in how nutritious they are to different consumers (i.e., $w_{ik} \neq w_{jk}$). As one might imagine, the probability of two species who reciprocally waste each other's resources coming into contact is likely low (though they may be common in some systems, for example, microbial systems with waste by-products), explaining why positive frequency dependence tends to be a rare occurrence in coexistence studies relative to other competitive dynamics (Buche et al. 2022).

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(c) No resources are wasted

Table 2. Translating MacArthur's consumer-resource model into terms of Lotka-Volterra's competition model

Lotka-Volterra and related quantities	**MacArthur**	**Biological interpretation**
A. Consumer intrinsic rate of increase (s_i)	$C_i\left(\sum_{k=1}^{m} a_{ik}w_kK_k - T_i\right)$	s_i is derived from the conversion of consumed energy to new consumers when there are no consumers present, i.e., when the resource is at its carrying capacity (K_k). Under these conditions, energy acquired through consumption ($\sum a_{ik}w_kK_k$) is as high above requirement as is possible in a given environment. Conversion rate C_i determines how energy gains are converted into new consumer individuals. Referred to as "$\mathcal{K}_i$ " in MacArthur (1970).
B. Consumer carrying capacity (L_i)	$\frac{C_i(\sum_{k=1}^{m} a_{ik}w_kK_k - T_k)}{C_i\sum_{k=1}^{m} a_{ik}^2 w_kK_k/r_k}$	The numerator is the equation for s_i, whereas the denominator is the unscaled version of a_{ik} (see note in table 2D. Can be simplified in terms of useful production as $\frac{r_k}{a_{ik}}(1-\frac{R^*_{ik}}{K_k}) = \frac{P_k}{a\ }_{ik}$(see table 2G).
C. Interspecific interaction coefficient (α_{ij})	$\frac{C_i\sum_{k=1}^{m} a_{ik}a_{jk}w_k(K_k/r_k)}{C_i\sum_{k=1}^{m} a_{ik}^2 w_k(K_k/r_k)}$ $= \frac{U_iU_j}{U_i^2}$	How much energy available (w_kK_k/r_k) for growth is lost per individual of consumer *i*for each individual of consumer *j* added (numerator), relative to losses due to competition with conspecifics (denominator). Note that this version of Lotka-Volterra quantifies interspecific competition scaled relative to intraspecific competition. This can be undone (as in equation 3) by removing the denominator.
D. Intraspecific interaction coefficient (α_{ii})	$\frac{C_i\sum_{k=1}^{m} a_{ik}^2 w_kK_k/r_k}{C_i\sum_{k=1}^{m} a_{ik}^2 w_kK_k/r_k}$ $= \frac{U_i^2}{U_i^2}$ $= 1$	The interpretation is the same as for α_{ij} except now between conspecific individuals. This version of Lotka-Volterra, which MacArthur uses, sets α_{ii} to 1. This can be undone (as in equation 3) by removing the denominator.
E. Resource at consumer equilibrium (R^*_{ik})	$\frac{T_i}{a_{ik}w_k}$	The resource density when consumer species i and resource species k are in equilibrium. This is as low as the resource concentration will go, and is the point at which consumer energy gain = energy loss. Note: introducing more than one substitutable resource creates conditions for apparent competition among resources and can affect R^*_{ik} in comparison to isolation such that (reformulated from Holt (1977)): $R^*_{ik} = \frac{\frac{T}{a_{ik}w_k} - \sum_{l\neq k}^{m} K_l \times \frac{a_{il}w_l}{a_{ik}w_k} \times \left(1 - \frac{a_{il}/r_l}{a_{ik}/r_k}\right)}{1 + \sum_{l\neq k}^{m} \frac{a_{il}^2}{a_{ik}^2} \times \frac{w_lK_l/r_l}{w_kK_k/r_k}}$
F. Resource density at any given level of consumers ($\hat{R}_k$)	$K_k - \sum_{i=1}^{n} \frac{(K_ka_{ik}X_i)}{r_k}$	Resource density that is in equilibrium with any given density of consumers. This assumes a separation of timescales between resources and consumers.
G. "Useful" production (P_k)	$r_k - (\frac{r_k}{K_k})(\frac{T}{aw_k})$	Per capita growth rate of the resource at the consumer's R*, prior to consumption. This amount should equal total consumption by all consumers at their carrying capacity (i.e., $a_{ik}L_i$) so the net difference is 0 (i.e., both consumer and resource are in equilibrium). Note: this assumes that all consumers have equivalent a_{ik} and T_i, hence, no consumer subscripts. We can simplify this to $r_k(1 - R^*_k/K_k)$ given that $R^*_{ik} = T_i/(a_{ik}w_k)$ (see table 2E).

Photo of the Rosetta Stone, also known as the "Stone of Rashid" (حجر رشيد) in Arabic, as it is currently held in the British Museum. © The Trustees of the British Museum