# 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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## 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 Europe (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).

Like the Rosetta Stone, in this article we aim to decipher Robert H. MacArthur's consumer-resource model (equation 1 & 2; (MacArthur 1969, 1970, 1972)) for a broad audience, highlighting key misinterpretations. We focus on MacArthur's model for two reasons. First, we view this 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 (e.g., r/K selection, priority effects) 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 important 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.

### 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 (Holt 2007). 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" (his 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.

## (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, as first presented in (MacArthur 1969):

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

$$\frac{1}{R_k}\frac{dR_k}{dt} = r_k\left[1 - \frac{R_k}{K_k}\right] - \sum_{i=1}^{n} a_{ik}X_i \tag{2}$$

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 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). More consumer individuals means more drawdown of resources, slowing the resource's per capita growth rate. In equation 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 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 each individual eats 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)—they emerge from equation 1 based on how attack rates are distributed among m resource types. 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 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 or integral calculus if continuous). 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[1]

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). 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 can be used to characterize a consumer's fundamental and realized niche (Hutchinson 1957; Carscadden et al. 2020), as well as niche similarities among consumers (or what Lawlor (1980) refers to as 'consumer similarity' (i.e., overlap of attack rate functions between consumers)). 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 environments given that species will be equivalent regardless of context (whereas the inverse is not necessarily true).

### (b) Utilization functions[2]

For reasons that will become clear, 'utilization', represented in MacArthur (1970) and May (1974) by the following equation:

$$U_{ik} = \sum_{k=1}^{m} a_{ik} \sqrt{w_k K_k / r_k} \tag{3}$$

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 in a given resource environment, 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

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[1] Sometimes referred to as 'utilization curves' (MacArthur 1970), 'utilization efficiency' (MacArthur 1969), 'harvesting ability' (MacArthur 1970), and 'consumer electivity' (Schoener 1974; Lawlor 1980)

[2] Sometimes referred to as 'total', 'actual' or 'weighted' utilization (Schoener 1974)

**Table 1. Description of parameters in MacArthur's consumer-resource model, including their units, assumptions, 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 |
|---|---|---|---|---|
| $C_i$<br>$(0 < Ci < \infty)$ | $\text{grams}_{\text{Daphnia}} \times$ $\text{Joules}^{-1}$ | **Definition:** Conversion efficiency of turning combined nutritional weight (eg. Joules or grams) of all excess substitutable resources acquired to grams of individuals (offspring). Represented as a constant.<br>**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)<br>**II.** Conversion efficiency is identical between all resources | **I.** Perrson et al. 1998; Weitz & Levin 2006<br>**II.** Leibold 1988; Abrams & Cortez 2015 |
| $a_{ik}$<br>$0 \leq a_{ik} < \infty$ | flask × $\text{Daphnia}^{-1}$ × $\text{Day}^{-1}$ | **Definition:** Attack rate represents the probability the consumer i both encounters and consumes the resource k in a unit time. This can be thought of as what portion of the experimental unit (eg. "50ml flask") a consumer can encounter and consume a resource in a unit time (day).<br>**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 entire resource k. | **I.** Independent of resource density. Representing a Type 1 (linear) functional response (consumption is instantaneous, no handling time)<br>**II.** Independent of consumer density (eg. no Allee effects, interference, or mutualisms)<br>**III.** Independent of environmental conditions (eg. temperature independent, no optimal foraging)<br>**IV.** Resource competition occurs only over (constantly) limiting resources<br>**V.** Attack rate is constant over time<br>**VI.** Resources depleted by consumers are used for consumer growth (i.e. no wastage) | **I.** Stewart & Levin 1973; Real 1977; Armstrong & McGehee 1978, Abrams 1980<br>**II.** Beddington 1975; DeAngelis et al. 1975; Holland & DeAngelis 2010<br>**III.** Betini et al. 2019; Orlando et al. 2012; Vasseur 2020<br>**IV.** Mazancourt & Schwartz 2012<br>**V.** Wiens 1977; Persson et al. 1998<br>**VI.** (Hernández-García et al. 2009; Leimar et al. 2013) |
| $w_k$<br>$-\infty < w_k < \infty$ | Joules × $\text{Plankton}^{-1}$ | **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).<br>**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 |
| $R_k$<br>$0 < R_k < \infty$ | Plankton × $\text{flask}^{-1}$ | **Definition**: Abundance (density) of resource k, usually defined under a logistic growth model as either individuals or biomass.<br>**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). Eg. if resource k abundance is defined as individuals set in a "50ml flask", then the units for $R_k = N_k /$ "50ml flask". Likewise, carrying capacity of a population must be defined per unit area to constitute a 'density'. | **I.** Resources are depletable<br>**II.** Resources are equally accessible (resources and consumers are homogeneously distributed in space)<br>**III.** Resources are not interacting<br>**IV.** Resources cannot go extinct if used for Q or L-V translation<br>**V.** Resources renew logistically<br>**VI.** Resources are defined per unit of space.<br>**VII.** Resource and consumer dynamics operate on separate time scales if used for Q or L-V translation<br>**VIII.** Resources can be ordered along one dimension if used for gaussian utilization functions | **II.** Sasaki 1996<br>**III.** MacArthur 1970; Levine 1976<br>**IV.** Hsu & Hubbell 1979; Abrams 1980<br>**V.** MacArthur 1972; Abrams 1980<br>**VII.** O'Dwyer 2018 |
| $T_i$<br>$0 < T_i < \infty$ | Joules × $\text{Daphnia}^{-1}$ × $\text{Day}^{-1}$ | **Definition**: Per capita resource requirement for species i such that the population is not growing or shrinking (not induced by resource competition).<br>**Comments**: Can be thought of as the metabolic requirement to maintain one individual. This includes the physiological resource requirements for that individual under the given time frame (day) and also turnover i.e. the averaged added 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 unnecessarily impedes understanding. Subscripts, 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, J, and m.

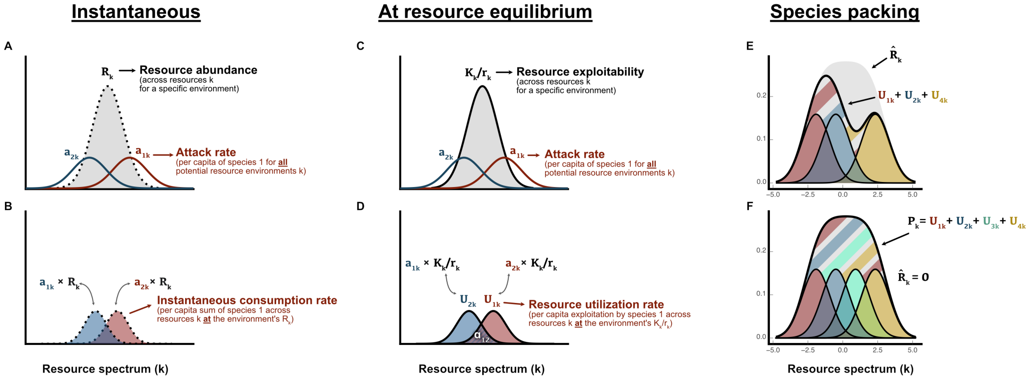

**Fig. 1.** Clarifying confusion about differences between attack rates, consumption rates, and utilization (panels A-D). Panels (A, C) depict the attack rate functions of two consumers, red (consumer $i$) and blue (consumer $j$), for any given level of resource abundance (A), which determines how many 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)).

persist. However, if the resource is non-renewing, resources will eventually be depleted to zero, resulting in the eventual extinction of the consumer[3].

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[4] (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, thus, 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, say, of 100 individuals. Let's say each resource is attacked ($a_{ik}$) with a probability of 0.1 and the rate of resource re-supply ($r_k$) is 2.0, in other words, resources are replenished 20x faster than they are removed. Even though 10% of resources are attacked and used to grow new consumers, after accounting for resource re-supply, only 5% of the 100 resources are unavailable to future consumers, resulting in a utilization of 5. If $r_k$ was instead 1.0 (a slower rate of re-supply), utilization would double to 10.

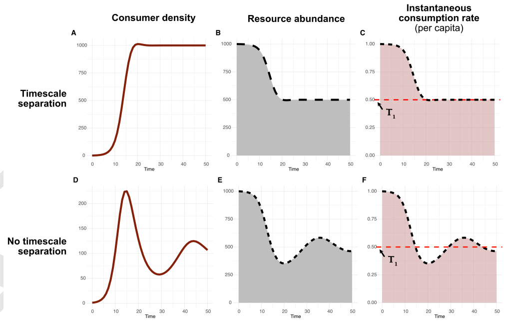

**Fig. 2.** Comparison of population dynamics of a consumer and its resource with (A-C) and without (D-F) a separation of timescales (see section iii(c)). Panels A-C show the approximate logistic growth of the consumer generated by the timescale separation, modeled by giving the resource a fast low-density 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)[5]. More precisely, competition is highest for resources that have what we will call the highest 'exploitability' ($K_k/r_k$). Exploitability is 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

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[3] Although we only raise this specific scenario only as an illustrative example, it suggests the existence of what we will call "pseudo-source" populations (i.e., populations that appear to persist but that are doomed for extinction), the inverse of "pseudo-sinks" (Holt 2009). One might expect to find pseudo-sources in environments where resources are deposited in a pulsed, periodic fashion, or if resources with a very slow resupply rate have had a long time to accumulate before the arrival of a consumer.

[4] Note that some authors (Ackermann and Doebeli 2004; Abrams et al. 2008) use $K_k$ instead of re-supply to calculate utilization, which does not aim to diminish the importance of re-supply, but rather, to makes the simplifying assumption that resources replenish fast enough to always return to $K_k$.

[5] Although rates of re-supply may sound familiar to those familiar with Tilman's graphical model, Tilman assumes that exploitability ($K_k/r_k$) is equal for all resources in order for his concept of supply points to be useful (Tilman 1982).

(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. Taken 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.

***(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):

$$\mathcal{Q} = \underbrace{\sum_k \frac{w_k K_k}{r_k}\left[r_k - \sum_j a_{jk} X_j\right]^2}_{\mathcal{U}} + \underbrace{2\sum_j T_j X_j}_{\mathcal{B}} \qquad (4)$$

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 $U$) 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[6]; gray portion of figure 1E), then the community is susceptible to invasion by new species or new genotypes—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 $K$ (instead of the more familiar symbol, $r$), and nowhere in that paper does he actually refer to $K$ as the intrinsic rates of increase[7]. 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., $r$, $\alpha$, and $K$) are not independent, as they share mechanistic underpinnings, and (2) that every parameter is affected by the resource environment.

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., $X_j$):

$$\frac{1}{X_i}\frac{dX_i}{dt} = r_i\left[1 - \frac{X_i}{K_i} - \frac{\sum_{j=1}^{j} a_{ij} X_j}{K_i}\right] \qquad (5)$$

This version of the Lotka-Volterra equation forces the intraspecific interaction coefficient ($\alpha_{ii}$) to be 1, thus, $\alpha_{ij}$ is relative to $\alpha_{ii}$. 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 $\alpha_{ij} < 1$ . Note: in our discussions below, keeping track of the subscripts is essential given that similar

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[6] 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 (Ti = 0) is biologically implausible.

[7] In fact, for these reasons, it was not clear to us that these translations were ever reported in the literature, and it was not until we derived them all ourselves to populate table 2 that we were able to identify them in the classical literature.

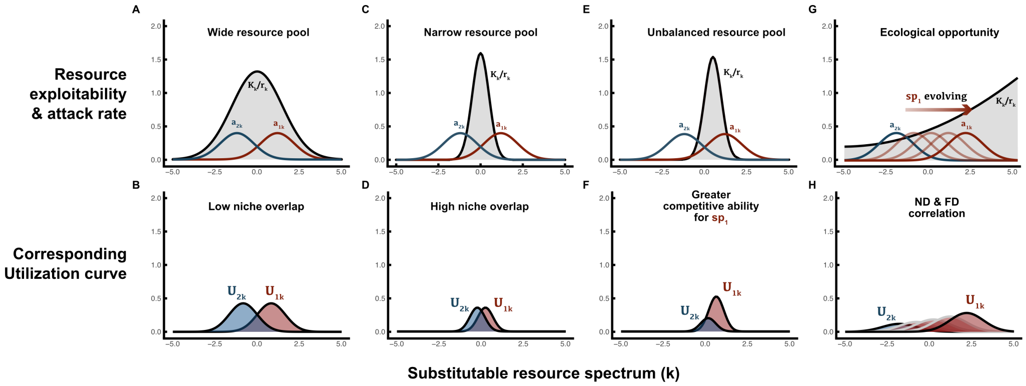

**Fig. 3.** Effect of the resource environment on competitive differences among consumers. Panels (A,C,E) depict the same two consumers, red (consumer $i$) and blue ($j$), in three different years. In years with a wide and more even distribution of resources (A), utilization closely mirrors the consumer's 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 efficiency curve), 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.

parameters appear in different contexts (e.g., parameter $K$ in equation 2 vs. equation 5)—we only ever use subscript $k$ to refer to resources, subscripts $i$ and $j$ to refer to consumers.

First we examine the mechanisms underlying Lotka-Volterra parameter $r_i$ (table 2(a)), which describes how quickly a consumer population can grow from low densities (i.e., when all $X \approx 0$). Intuitively, $r_i$ 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, $r_i$ can be calculated by setting $R_k$ in equation 1 to $K_k$. Doing so means that energy available for growth is simply the difference between energy gained by consumption ($a_{ik}w_kK_k$) and energy lost to metabolism ($T_i$). $C_i$ converts this excess energy gain or loss into gain or loss of consumer individuals. So, the consumer's growth rate at low densities ($r_i$) 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 ($C_i$). $r_i$ is unaffected by rates of resource resupply. Note that energy gain is summed across all k resource types, so to generalize, $r_i$ increases with the area under the attack rate function.

As consumer populations grow, Lotka-Volterra's competition model includes two quantities that describe how consumers impact each other's growth as consumer densities increase: $K_i$ and $\alpha_i j$. Consumers reach carrying capacity ($K_i$) when at least one resource is drawn down to a density low enough that any energy captured ($a_{ik}w_kR_k$) is just enough to meet metabolic requirements ($T_i$)—this resource density, calculated as $T_i/(a_{ik}w_k)$, is the consumer's $R*$. $R*$ is also the resource's equilibrium density when the consumer is at $K_i$—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"[8].

Together, $r_i$, $K_i$, $\alpha_{ii}$, and $\alpha_{ij}$ 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 $r_i$ 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 $\alpha_{ij}$ and $\alpha_{ji}$—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 $r_i$ (e.g., if $K_k$ increases), this is not always the case—the rate of resource re-supply has no impact on $r_i$ whereas it is key to the interaction coefficients (so long as $K_k$ is unchanging).

One of the biggest limitations of Modern Coexistence

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[8] Note that "useful production" is distinct from resource exploitability (equation 5), with the latter being an intrinsic characteristic of the resource agnostic to consumer densities.

**Table 1.** Translating MacArthur’s consumer-resource model into terms of Lotka-Volterra’s competition model

| Lotka-Volterra and related quantities | MacArthur | Biological interpretation |
|---|---|---|
| A.<br>Intrinsic rate of increase<br>($r$) | $C_i\left(\sum_{k=1}^{m} a_{ik} w_k K_k - T_i\right)$ | $r_i$is 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 ($a_{ik} w_k K_k$) 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.<br>Carrying capacity<br>($K$) | $\frac{C_i(\sum_{k=1}^{m} a_{ik} w_k K_k - T_k)}{C_i \sum_{k=1}^{m} a_{ik}^2 w_k K_k / r_k}$ | The numerator is the equation for $r_i$, whereas the denominator is the unscaled version of $a_{ik}$ (see note in table 2(d)). Can be simplified to a single resource as $K_i = (r_k / a_{ik})(1 - R_k^* / K_k)$ |
| C.<br>Interspecific interaction coefficient<br>($\alpha_{ij}$) | $\frac{C_i \sum_{k=1}^{m} a_{ik} a_{jk} w_k (K_k / r_k)}{C_i \sum_{k=1}^{m} a_{ik}^2 w_k (K_k / r_k)}$<br>$= \frac{\sum_{k}^{m} U_{ik} U_{jk}}{\sum_{k}^{m} U_{ik}^2}$ | How much energy available ($w_k K_k / r_k$) 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).<br>Note that this version of Lotka-Volterra quantifies interspecific competition scaled relative to intraspecific competition. This can be undone (as in equation 6) by removing the denominator. |
| D.<br>Intraspecific interaction coefficient<br>($\alpha_{ii}$) | $\frac{C_i \sum_{k=1}^{m} a_{ik}^2 w_k (K_k / r_k)}{C_i \sum_{k=1}^{m} a_{ik}^2 w_k (K_k / r_k)}$ , or 1 | The interpretation is the same as for $\alpha_{ij}$ except now between conspecific individuals.<br>This version of Lotka-Volterra, which MacArthur uses, sets $\alpha_{ii}$ to 1. This can be undone (as in equation 6) by removing the denominator. |
| E.<br>Resource at consumer equilibrium<br>($R_{ik}^*$) | $\frac{T_i}{a_{ik} w_k}$ | The resource density when both a single consumer and resource 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 apparent competition among resources and lowers $R_{ik}^*$ in comparison to isolation such that (reformulated from Holt 1977):<br>$R_{ik}^* = \frac{\frac{T}{a_{ik} w_k} - \sum_{l \neq k}^{m} K_l \times \frac{a_{il} w_l}{a_{ik} w_k} \times \left(1 - \frac{a_{il} / r_l}{a_{ik} / r_k}\right)}{1 + \sum_{l \neq k}^{m} \frac{a_{il}^2 w_l}{a_{ik}^2 w_k} \times \frac{w_l K_l / r_l}{w_k K_k / r_k}}$ |
| F.<br>Resource density at any given level of consumers<br>($\hat{R}_k$) | $K_k - \sum_{i=1}^{n} \frac{(K_k a_{ik} X_i)}{r_k}$ | Resource density that is in equilibrium with any given density of consumers. This assumes a separation of timescales between resources and consumers. |
| G.<br>"Useful" production<br>($P_k$) | $r_k - (\frac{r_k}{K_k})(\frac{T}{a w_k})$ | 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., $a_{ik} K_i$) so the net difference is 0 (i.e., both consumer and resource are in equilibrium). Can be simplified to $r_k(1 - R_k^* / K_k)$ given that $R_{ik}^* = T_i / (a_{ik} w_k)$ if we apply MacArthur’s assumption that all consumers have equivalent $a_{ik}$ and $T_i$, hence no consumer subscripts. |

Theory is how sensitive outcomes are to environmental context. Consider how competitive differences change between the exact same two species competing in three different years (figure 2), even though the species have attack rate functions that allow them to specialize on different resources. In a year with a broad pool of resources, each species' utilization (figure 2B) largely reflects 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[9] (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 [10]

An important assumption MacArthur uses to analyze his model is a complete separation of timescales[11] between consumer and resource dynamics (MacArthur 1970). What does this mean, exactly, why is this assumption needed, and what are its consequences? 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 2) are exactly equal to rates of resource removal by consumers (the second term in equation 2). We present the equation to solve for this density, which we call $\hat{R}_k$, in table 2(f). 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.

**(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 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 resource dimensions, we envision expanding equation 1 to multiple dimensions ($D$):

$$C_i \prod_{d=1}^{D} \sum_{k=1}^{m} a_{ikd} w_{kd} R_{kd} - T_{id} \tag{6}$$

In this way, the equation is multiplicative, meaning that requirements of every dimension ($T_id$) must be met in order for the population to grow. In addition, this means that every non-substitutable resource dimension may still be made up of substitutable resource types, as opposed to categorizing consumers as competing for substitutable, non-substitutable, or a combination of resources (Tilman 1980).

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[9] For example, (Abrams 2022) explores the consequences of breaking the assumption of linear functional responses.

[10] 'Quasi-steady state' is a common term used in biochemistry (Srinivasan 2022), meaning that one state variable (e.g., resources) are at an equilibrium even if the other state variable (e.g., consumers) are not.

[11] Although many articles state this assumption, finding a clear description of what this assumption means, why it is made, and what consequences it has for interpretation is difficult.

**(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 $\alpha_{ij}$ without corresponding increases $\alpha_{ji}$ or $\alpha_{ii}$. In other words, in this example, consumer $i$'s response to ($\alpha_{ji}$) and effect on ($\alpha_{ij}$) 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. For 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 both are theoretically possible, without considering dynamics of the resource environment, we cannot predict which outcomes will be most likely, as these outcomes critically depend on how rates of resupply vary among resource types to shape ecological opportunities (Germain et al. 2024). 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). Additionally, predicting the likely consequences of various 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 (section (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.

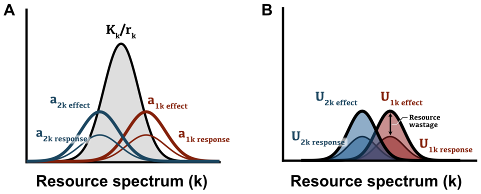

**Fig. 4.** How resource wastage affects competition. Here, we now show two kinds of attack rate and utilization functions. The curves with thinner lines represent what we refer to here as "effective" attack rate/utilization functions, i.e., resources that are consumed and actually contribute to a consumer's 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).

***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:*** 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 $r_i$ in equation 5) 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 at-

## 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 & 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). In other words, it is incorrect to state that $r_i$ is under selection in low density environments without more information on what keeps those densities low. 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 that is deviation 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 2 (b)) given that individuals that capture more resources will outcompete others; this creates a Red Queen dynamic favoring the evolution of increased competitive ability. We believe that these misconceptions have arisen in part due to their 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) Priority effects*** [a]

'Priority effects' are a competitive outcome that arises when competition is stronger among heterospecifics than conspecifics (Ke and Letten 2018). With priority effects, species increasingly gain an advantage as they outnumber their competitors, resulting in positive frequency-dependent population growth that leads to exclusion of the rarer species (e.g., the species that arrived after the other established a population). To ecologists, the causes of priority effects are often debated (Fukami 2015; Zou and Rudolf 2022; Stroud et al. 2024) and remain mysterious to many. How can priority effects arise in MacArthur's model[b]? Tilman proposed that consumers may sometimes impact resources they do not strongly require (Tilman 1982). Priority effects then arise 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?

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 a priority effect, 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 applies 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 priority effects tend to be a rare occurrence in coexistence studies relative to other competitive outcomes (Buche et al. 2022).

[a] We use a definition of priority effects based on unstable coexistence equilibria, aligning with definitions from coexistence theory, as opposed to a definition of priority that encompasses exclusion due to differences in timing of individuals (e.g., due to germination, dispersal) within any given year, where wastage would play a less obvious role.

[b] One will quickly find that priority effects cannot be represented using simple niche cartoons, in contrast to coexistence or competitive asymmetries.

tack 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 resource supply is equal to $X_iT_i$ (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 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 $a_ik$ can be estimated by dividing $T_i$ by $R_k$ (by rearranging equation (E) in table 2). 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

Like the Rosetta Stone, which eased translation between ancient languages, here we have deciphered Robert MacArthur's consumer-resource model and its connection to the behavior of a phenomenological model 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 among species in resource niches
- made accessible complex concepts, such as timescale separation and MacArthur's minimization principle, 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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(c) No resources are wasted

*Photo of the Rosetta Stone as it is currently held in the British Museum. © The Trustees of the British Museum*