Coexistence under Hierarchical Resource Exploitation: The Role of the $R^*$-Preemption Trade-Off

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Abstract: Resource competition theory predicts coexistence and exclusion patterns based on species’ $R$’s, the minimum resource values required for a species to persist. A central assumption of the theory is that all species have equal access to resources. However, many systems are characterized by preemption exploitation, where some species deplete resources before their competitors can access them (e.g., asymmetric light competition, contest competition among animals). We hypothesized that coexistence under preemption requires an $R^*$-preemption trade-off—that is, the species with the priority access should have a higher $R$ (lower “efficiency”). Thus, we developed an extension of resource competition theory to investigate partial and total preemption (in the latter, the preemptor is unaffected by species with lower preemption rank). We found that an $R^*$-preemption trade-off is a necessary condition for coexistence in all models. Moreover, under total preemption, the trade-off alone is sufficient for coexistence. In contrast, under partial preemption, more conditions are needed, which restricts the parameter space of coexistence. Finally, we discuss the implications of our finding for seemingly distinct trade-offs, which we view as special cases of the $R^*$-preemption trade-off. These trade-offs include the digger-grazer trade-off, the competition-colonization trade-off, and trade-offs related to light competition between trees and understories.

Keywords: resource competition, competition-colonization trade-off, coexistence theory, asymmetric competition, interference competition, $R^*$ theory.

Introduction

Explaining the tremendous diversity of plants and animals is a major challenge in ecology (Gauze 1934; Hutchinson 1959; Hardin 1960; Tilman 1982; Chesson 2000; Pennisi 2005; Vellend 2016). Classical resource competition theory (Volterra 1928; MacArthur 1972; Armstrong and McGehee 1980; Tilman 1982) provides a simple means for predicting diversity patterns from a mechanistic description of resource exploitation. This theory predicts patterns of competitive exclusion and coexistence on the basis of species’ $R$’s, the minimum resource values required for a species to persist (also equivalent to the resource levels in a monoculture at equilibrium; Tilman 1982).

A central assumption of resource competition theory is equal access exploitation, that is, all species have identical access to resources (Volterra 1928; MacArthur 1972; Armstrong and McGehee 1980; Tilman 1982). Equal access exploitation (also known as “scramble competition” or “symmetric competition”) is a reasonable approximation for well-mixed systems, such as algae species in an aquatic ecosystem (Tilman 1977). However, some systems are characterized by preemption exploitation (“contest competition” or “asymmetric competition”), where species deplete their resources before their competitors can access them (Schoener 1976; Grime 1977; Huston and DeAngelis 1994; Schwinning and Weiner 1998; Craine and Dybzinski 2013; DeMalach et al. 2016). Common examples include fast-moving animal species that deplete resources before slow-moving competitors arrive (Richards et al. 2000; Kneitel and Chase 2004) and tall plants that deplete light for shorter plants (Tilman 1988; Schwinning and Weiner 1998; DeMalach et al. 2016).

Regardless of the specific mechanisms by which species are competing for resources, as long as species get equal access to a resource, coexistence requires each species to specialize on a different resource, that is, there is a trade-off in...
Here, we propose that coexistence under preemption requires a trade-off between preemption rank and $R'$. In a simple two-species scenario, it implies that one species has a lower $R'$ (hereafter, "gleaner") while the other has priority in accessing the resource (hereafter, "preemptor"). We argue that seemingly distinct trade-offs among organisms can be viewed as specific cases of this trade-off.

The grazer-digger trade-off (also known as the "exploiter-explorer" or the "cream-skimmer–crumb-picker" trade-off) suggests that animals with fast movement (i.e., grazers) can reach the resource preemptively before slow-moving species (i.e., diggers) arrive. However, the more efficient diggers can persist on the leftovers (Richards et al. 2000; Kneitel and Chase 2004). According to the body size trade-off (Basset 1995), large animals are more aggressive, which allows them to preempt resources, but smaller species are more efficient foragers. Likewise, the dominance-discovery trade-off in ants (Adler et al. 2007) suggests that foraging in large groups allows preemption (by aggressive behavior), while foraging efficiency is higher when ants have a more scattered spatial spread. Similarly, the $R'$-preemption trade-off lies at the heart of the leaf economy trade-off (Onoda et al. 2017) and trade-offs between allocation to height growth versus other functions (e.g., crown growth, reproduction, and shade survival; see Givnish 1982; Falster and Westoby 2003; Onoda et al. 2014; Detto et al. 2022).

Here, we investigated the effect of the $R'$-preemption trade-off on coexistence and relative abundance patterns under the different types of preemption. First, we examine a model with total preemption, where the gleaner uses only the leftovers of the better preemptor and therefore does not affect the latter. This model describes competition for light between trees and understory herbs. Then, we investigate a model with partial preemption, where a preemptor can partially preempt the resource because of its faster discovery rate. Still, once discovered by the gleaner, the resource is accessible to both species.

### Methods

Our models follow the simplifying assumptions of the classical models (Tilman 1982), including no age structure and lack of spatial and temporal heterogeneity in environmental conditions. Although simple, our models are mechanistic in the sense that all interactions are mediated by resource depletion instead of assuming direct interactions, as in phenomenological models (for details, see Letten et al. 2017).

For simplicity, we examined a scenario of a single type of resource (e.g., light, specific food type) and two competitors. However, we show that under total preemption, an arbitrary number of species can coexist under the $R'$-preemption trade-off (supplement S1).

#### A Light Competition Model

In this model, the preemptor is a canopy tree (species 1), and the gleaner is an understory herb (species 2). The following function describes the population dynamics of both species:

$$\frac{dN_i}{dt} = (a_i w_i I_i - m_i) N_i,$$

where $N_i$ is population density, $m_i$ is the mortality rate, $a_i$ is the resource depletion rate, and $w_i$ is a conversion factor of light depletion to population growth. The term $I_i$ is the amount of unused light experienced by the $i$th species; that is, the unused light determines population growth (table 1). Light levels are denoted by $I$ rather than $R$ to highlight that we describe a flux rather than concentration, as for most other resources (following Dybzinski and Tilman 2007).

The amount of unused light experienced by species 1 ($I_1$) is directly related to its density:

$$I_{1(i)} = \max(g - a_1 N_{1(i)}, 0),$$

where $g$ is the resource influx and $a_1 N_1$ is light consumption by established trees. The amount of unused light

### Table 1: Variables and parameters of the models

| Symbol | Description | Type |
|--------|-------------|------|
| $N_i$  | Population density | Variable |
| $R_i$  | Resource concentration (grazer-digger model) | Variable |
| $I_i$  | Unused light level (light competition model) | Variable |
| $m_i$  | Mortality rate | Parameter |
| $a_i$  | Resource depletion rate | Parameter |
| $w_i$  | Conversion factor from resource depletion to population growth | Parameter |
| $g$    | Resource influx | Parameter |
| $q$    | Resource decay rate (grazer-digger model) | Parameter |
| $d$    | Resource discovery rate of the gleaner (grazer-digger model) | Parameter |

Note: The subscript $i$ indicates species-specific (except for $R_i$) variable or parameter values.
available for the population growth of understory herbs \((I_2)\) equals the total light influx \((g)\) minus light consumption by established adults of its own species \((a_1N_2)\) and that of the trees \((a_1N_1)\):

\[
I_{2(0)} = \max(g - a_1N_{1(0)} - a_2N_{2(0)}, 0).
\]  

A Grazer-Digger Model

In this model, the preempper is an animal with a fast movement (grazer), and the gleaner is an animal with more efficient resource use (digger). The model includes a resource \((R_1)\) that is available only to the grazer (has not been discovered by the digger) and a resource \((R_2)\) that is available to both species. Population growth in this model is affected by resource concentration:

\[
dN_1 \over dt = [a_1w_1(R_1 + R_2) - m_1]N_1, \tag{4}
\]

\[
dN_2 \over dt = (a_2w_2 - m_2)N_2. \tag{5}
\]

The following equations describe the dynamics of the two resources:

\[
dR_1 \over dt = g - a_1R_1N_1 - dR_1 - qR_1, \tag{6}
\]

\[
dR_2 \over dt = dR_1 - a_1R_1N_1 - a_2R_2N_2 - qR_2, \tag{7}
\]

where \(g\) is the resource influx of \(R_1\), \(a_1R_1N_1\) is resource consumption by the preempper, and \(d\) is the rate by which \(R_1\) is “transforming” into \(R_2\) (i.e., the discovery rate of the gleaner). Unlike \(R_1\), \(R_2\) is consumed by both species \((a_1R_1N_1, a_2R_2N_2)\). The decay rate \((q)\) is assumed to be equal for both resources (table 1).

Results

Light Competition Model

To be consistent with the classical terminology of \(R^*\) in Tilman (1982), we define \(I^*\) of each species as the amount of unused light leading to zero net growth (or the amount of unused light of a monoculture). Thus, \(I^*\) can be calculated by assuming a quasi-steady approximation of \(dN_i/\over dt = 0 \rightarrow (a_iw_i - m_i)N_i = 0:\)

\[
I^*_i = \frac{m_i}{a_iw_i}. \tag{8}
\]

We define the unused light in the absence of consumers as \(I^*_{1} = I^*_{2} = g\). An abiotic extinction (i.e., when the population growth rate is negative in the absence of competitors) occurs if \(I^*_i > I^*\). When both species’ values are lower than \(I^*_i\), coexistence and exclusion are determined by the difference among species in their \(I^*\) values (fig. 1; supplement S1). When \(I^*_i < I^*\), the tree (species 1) excludes the herb (species 2). When \(I^*_i > I^*\), coexistence is possible because the herb can persist on the leftovers of the tree. This rule can be generalized to any number of species: a species with a lower preemption rank and lower \(I^*\) than resident species can always invade a community in equilibrium. Since the invader cannot affect the resident species, a theoretically infinite number of species can coexist on a single type of resource under total preemption (see the invasion analysis in supplement S1). Obviously, in reality, the number of species will be limited by energetic constraints on the requirements for species persistence under extremely low resource availability.

Patterns of relative abundance are more complex than coexistence (fig. 1; supplement S1). They are affected by both species’ traits \((I^*)\) and resource availability \((I^*)\). The condition for herbs to exceed the abundance of the trees is

\[
\frac{m_2}{a_2w_2} < \left(1 + \frac{a_2}{a_1}\right) \frac{m_1}{a_1w_1} - g \frac{a_2}{a_1} \quad \text{and} \quad \frac{m_1}{a_1w_1} < g, \tag{9}
\]
which can be rewritten as

\[ I_1' < \left(1 + \frac{a_2}{a_1}\right) I_1' - g \frac{a_2}{a_1} \quad \text{and} \quad I_1' < g. \quad (10) \]

These equations imply that an increase in resource influx \( g \) increases the relative abundance of the preemptor but does not affect the gleaner (see supplement S1, eqq. [S1-1]–[S1-4]).

**Grazer-Digger Model**

We define \( R \) for each species here as the resource level of zero net growth (equivalent to the equilibrium resource concentration of a monoculture, sensu Tilman 1982). Thus, while the biological interpretation of \( I \) and \( R \) is different (Dybinski and Tilman 2007), they are equally affected by the same parameters \( dN_i/dt = 0 \rightarrow (a_i, R_i - m_i)N_i = 0 \):

\[ R_i^* = \frac{m_i}{a_i w_i}. \quad (11) \]

Furthermore, the conditions for abiotic extinctions are similar though quantitatively different. An abiotic extinction of \( N_i \) occurs when \( R_i^* > R_i^w \), where \( R_i^w \) is the steady-state resource concentration available for grazers in the absence of consumers and \( R_i^w = g/q \) (i.e., \( R_i^w = R_i^m + R_i^s \) in supplement S2, eq. [S2-1]). An abiotic extinction of \( N_i \) occurs when \( R_i^* > R_i^s \), where \( R_i^s \) is the steady-state resource concentration available for diggers in the absence of consumers and \( R_i^s = dg/[(q + d)q] \) (supplement S2, eq. [S2-1]).

Nonetheless, the conditions for exclusion and coexistence are qualitatively different for partial preemption exploitation. The gleaner can exclude the preemptor under the condition \( R_i^* < R_i^* - g/(d + q) \), limiting the parameter space of coexistence to \( R_i^* - g/(d + q) < R_i^* < d(R_i^s)^2/(dR_i^s + g) \) (fig. 2).

The condition for the gleaner to exceed the abundance of the preemptor is (supplement S2, eq. [S2-5])

\[ R_i^* < \frac{-\zeta + \sqrt{\zeta^2 + 4d(d + q)a_2^2(R_i^s)^2}}{2(d + q)}, \quad (12) \]

where

\[ \zeta = \left(\frac{a_1}{a_2} + 1\right)g + \left(\frac{a_1}{a_2}d - d - q\right)R_i^*. \]

These equations imply that an increase in resource influx \( g \) increases the relative abundance of the preemptor and that an increase in the discovery rate \( d \) of the gleaner increases the relative abundance of the gleaner. Therefore, while an increase in \( q \) decreases the abundance of the preemptor, it does not affect the gleaner when the preemptor exists (see details in supplement S2, eq. [S3-4]).

Figure 2: Competition outcome for a grazer/preemptor (\( N_i \)) and a digger/gleaner (\( N_j \)). The four qualitative outcomes are abiotic extinction of either species (for any species with \( R \) higher than \( R^* \)), competitive exclusion of \( N_i (R_i^* \leq R_j^* - g/(d + q) \) and \( R_i^* < R_j^* \)), competitive exclusion of \( N_j (R_j^* \geq d(R_i^s)^2/(dR_i^s + g) \) and \( R_j^* < dR_j^*/[(q + d)q] \), and coexistence (\( R_j^* < dR_j^*/[(q + d)q] \) and \( R_j^* > R_i^* - g/(d + q) \)). The coexistence region is divided on the basis of the relative abundance of the species. The lines represent the transition between a higher abundance of the grazer (above each line) and a higher abundance of the digger (below each line). Different lines represent different \( a_i/a_j \) values based on equation (12). In the graph, \( g = 10 \), \( d = 0.2 \), and \( q = 0.1 \).

In sum, the light competition and grazer-digger models differ in three interrelated aspects. First, only in the grazer-digger model can the gleaner exclude the preemptor. Second, the coexistence region is much smaller in the grazer-digger model than in the light competition model, where the \( R \)-preemption trade-off is insufficient for coexistence. Last, unlike the light competition model, the grazer-digger model cannot be extended for an arbitrary number of species using invasion analysis (because invading species can lead to the extinction of the resident species).

**Discussion**

Within our models, the trade-off between preemption ability and \( R \) is a necessary condition for coexistence under preemption exploitation. Furthermore, in the light competition model, this trade-off alone is sufficient for coexistence. In contrast, coexistence in the grazer-digger model requires additional conditions because the gleaner species can exclude the preemptor in some parameter spaces.

We attribute the differences between the two models to differences between partial and total preemption because
the other difference between the models (concentration vs. flux resource types) has a negligible effect on the outcomes (supplement S3). Below, we discuss the implications of our model for different organisms and the new questions arising from our findings.

**Preemption in Plant Communities**

Asymmetric competition for light is a classic example of preemption exploitation in plants (Schwinning and Weiner 1998). Theoretical (DeMalach et al. 2016) and empirical (Lamb et al. 2009; DeMalach et al. 2017; Hautier et al. 2018) studies demonstrate that transition from relatively symmetric competition belowground to asymmetric competition for light is a major driver of species loss in various grasslands. Many grassland species are not efficient enough to grow under low light levels, and therefore preemption competition results in the extinction of short-statured species (Dickson et al. 2014; DeMalach et al. 2017). More broadly, in the absence of the $R'$-preemption trade-off, preemption exploitation can lead to lower diversity than equal access exploitation because of large ecological fitness differences (sensu Chesson 2000).

However, in many well-established forests, there is a layer of understory herbs that persist despite light preemption by trees (De Frenne et al. 2013). We use these phenomena as an example to illustrate how the model’s parameters relate to biological attributes (fig. 3). The primary condition for coexistence between trees and understory species is that the understory species (gleaner) will have a lower $R'$ than the trees. Thus, coexistence is impossible in a dense forest without highly efficient understory species (fig. 3a). In contrast, in some systems high light capture efficiency (high $a$) and ability to perform photosynthesis under low light conditions (high $w$) of understory species (Valladares et al. 2002) enables them to survive on the unused light (fig. 3b). Additionally, a low population density of trees (as affected by $m$, $w$) may allow sufficient radiation for the persistence of herbaceous vegetation (fig. 3c). Coexistence can also occur when the per capita effect of trees on light availability ($a$, which is closely related to leaf area index) is small (fig. 3d).

The $R'$-preemption trade-off can be relevant to the coexistence of species varying in phenology. For example, in the Mediterranean annual communities of California, some species grow and deplete water much earlier than others (Godoy and Levine 2014; Alexander and Levine 2019). Theoretically, a late-phenology species can persist on the leftovers of the early-phenology species by withstanding lower water potential (lower $R'$). However, since there is often an overlap of the growing seasons, it implies partial (rather than total) preemption, which restricts the conditions for coexistence. Furthermore, empirical evidence suggests that phenology also affects many other processes. Therefore, it is difficult to merely attribute coexistence patterns among species varying in phenology to the parameters of our model (Godoy and Levine 2014; Alexander and Levine 2019).

One of the most common explanations for coexistence among plants and other sessile organisms is a trade-off between competition and colonization abilities (Hastings 1980; Tilman 1994; Calcagno et al. 2006). Interestingly, this trade-off could also be viewed as a special case of the $R'$-preemption trade-off, where space is the limiting resource and $R'$ is the fraction of empty patches in a monoculture at equilibrium. The better competitor is analogous to the pre- emptor in the model of total preemption because it is not affected by the other species. Additionally, the colonizer without priority access to space is restricted to the pre- emptor’s leftovers (empty patches). In these models, coexis- tence requires the colonizer to have a lower “$R'$” than the preemption in the sense that its monoculture should have fewer empty patches at equilibrium.

Although we propose that the competition-colonization trade-off is a particular case of the preemption-$R'$ trade-off, the specific models of the competition-colonization trade- off (Hastings 1980; Tilman 1994; Calcagno et al. 2006) are different from our models because space is not consumed similarly to other resources. Moreover, within our model $R'$ and $I'$ are related to resource depletion ($a$) and conversion ($w$) rather than dispersal or fecundity, as in the competition-colonization models.

**Preemption in Animal Communities**

Several trade-offs that enable coexistence on a single resource type have been proposed for animal communities, including the body size trade-off, the grazer-digger trade-off, and the dominance-discovery trade-off (Basset et al. 1995; Richards et al. 2000; Adler et al. 2007; Basset and DeAngelis 2007). We argue that all of these trade-offs are special cases of the preemption-$R'$ trade-off.

More broadly, animal ecologists have long recognized that preemption exploitation (“contest competition”) is a common phenomenon in animal communities (Nicholson 1954; Lawton and Hassell 1981). However, to date contest competition has not been incorporated into mechanistic models and has been described only by phenomenological models, where the effects of competition are assumed to be direct instead of mediated by resource consumption (Hassell 1975; Brannstrom and Sumpter 2005). Mechanistic models often provide a better understanding of the underlying processes (Letten et al. 2017; Koffel et al. 2021). Additionally, the number of parameters scales linearly rather than quadratically with species number in mechanistic models, making them less data demanding for multispecies communities (Tilman 1982).
Comparison between Preemption and Equal Access Exploitation

Under equal access exploitation, a single type of limiting resource does not permit coexistence (the competitive exclusion principle; Volterra 1928; Hardin 1960; MacArthur and Levins 1964; Levin 1970; Armstrong and McGehee 1980). However, under preemption exploitation, each species experiences different resource availability, and therefore the number of effective resources always equals the number of species.

Figure 3: Illustration of the conditions of coexistence for trees (preemptor) and understory herbs (gleaner) competing for light. 

(a) No coexistence

A dense canopy of trees (as affected by $m$, $w$, and $a$) can prevent the growth of understory species by reducing light availability.

(b) High efficiency

Understory species can persist despite low light availability when they have high conversion efficiency ($w$).

(c) Low population density

Low tree density (higher $m$ or lower $w$ of tree) can enable the persistence of understory species in the gaps.

(d) Low preemption

Low per capita depletion ($a$) by the trees (driven by low canopy density here) increases the trees’ $I^*$, thereby enabling the persistence of understory herb.
of species. Notably, our findings do not refute the competitive exclusion principle but demonstrate that what is a single resource under equal access exploitation (e.g., light) effectively acts as distinct resources under preemption exploitation, thereby allowing more opportunities for coexistence (for a thorough discussion of how resources should be counted, see Abrams 1988).

The classical theory assumes that all species experience equivalent levels of resource. In contrast, our model assumes a hierarchy of resource acquisition, where species with lower preemption ranks have better access to resources. This hierarchy can be strict where the preemptor is not affected by other species (total preemption) or not (partial preemption). Partial preemption lies between total preemption and completely equal access exploitation. As a result, the parameter space of coexistence enlarged from completely equal access exploitation to partial preemption and total preemption exploitation. Although we did not extend the partial preemption model for an arbitrary number of species using invasion analysis, this does not mean that multispecies coexistence is impossible in that model. For example, Lyapunov functions (Guo et al. 2006) can be used to demonstrate multispecies stability in future investigations.

The continuum between preemption and equal access exploitation was investigated in animal ecology using phenomenological models (Hassell 1975). Still, equal access exploitation was assumed when seeking a mechanistic explanation for the models (Geritz and Kisdi 2004). In plant ecology, the continuum was described within the context of size asymmetry, a quantitative measure of the degree of size-related differences in resource acquisition (Schwinnig and Weiner 1998; DeMalach et al. 2016). Notably, the continuum between equal access exploitation and hierarchical preemption is not necessarily affected only by the size of plants nor restricted to the plant communities. We therefore hope that future mechanistic models will investigate this continuum in various other contexts.

Concluding Remarks

In this contribution, we built a simple model to demonstrate a general concept. Hence, we used the simplifying assumption of resource competition theory. Such a simple approach, however, raises new questions that require more complex and system-specific approaches. First, how does spatial and temporal variability affect preemption exploitation? Second, what happens when multiple types of resources are involved in preemption exploitation? Answering these questions is a challenge for future models and empirical tests of the current model.

A central open question is how important is the R*-preemption trade-off as a coexistence mechanism. In contrast with our initial expectation, we found that partial preemption allows coexistence only under a narrow range. These findings suggest that partial preemption alone is probably not a major mechanism for maintaining biodiversity. Nonetheless, this trade-off, together with spatial heterogeneity in the abiotic environment, may promote coexistence where different strategies are favored in different microsites.

In contrast with partial preemption, total preemption enables multispecies coexistence in vast parameter space. The assumption of amensalism can be met when species differ in their life form/life history attributes. Under these conditions, we expect the R*-preemption trade-off to be a crucial coexistence mechanism in various ecosystems. Furthermore, the R*-preemption trade-off could be a mechanism of character displacement that promotes the divergence of different life forms.

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Statement of Authorship

M.Q., N.D., and T.S. developed the modeling framework. M.Q. and Y.D. solved the model. M.Q. and N.D. wrote the first draft. All authors provided comments on the modeling framework and substantially contributed to the drafts.

Data and Code Availability

The R code used to generate figures 1 and 2 is available on Zenodo (https://doi.org/10.5281/zenodo.5833193). The R code used to generate competition outcomes of pairwise species under the R*-preemption trade-off is also available on Zenodo (https://doi.org/10.5281/zenodo.5833193).

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'The larval development of *Apus* ([figured], *A. æqualis* Packard, in Hayden’s Report) has been studied by Zaddach. We know nothing of the embryology of this animal. I have, however, been able to discover that the blastodermic skin, like that of *Limulus*, consists of a single layer of moulted cells.” From “Life-Histories of the Crustacea and Insects” by A. S. Packard Jr. (*The American Naturalist*, 1875, 9:583–622).