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RESEARCH HIGHLIGHTS

Temporal niche partitioning: Mechanism of coexistence or competitive exclusion via priority effects?

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Abstract

Research Highlight: Ekrem R., de Vries, C., Kaiser, T., & Kokko, H. (2025). Temporal niche differentiation often leads to priority effects rather than coexistence: Lessons from a marine midge. *Journal of Animal Ecology*, https://doi.org/10.1111/1365-2656.70094. Temporal niche partitioning has always been hypothesized as a key mechanism in maintaining species coexistence. By utilizing resources or habitats at different times, each species will occupy distinct 'temporal niches', thereby reducing overlap in resource use and the potential for competitive exclusion. However, to what extent temporal niche partitioning can explain coexistence remains contested, as increasing theoretical and experimental evidence finds weak contributions of such temporal mechanisms to community dynamics. In a recent study, Ekrem et al. (2025) shed new light on this debate by studying the complex life history of coexisting strains of the marine midge, *Clunio marinus*. Using mathematical models based on empirical processes, they found that the temporal differentiation of breeding phenology between strains does not always lead to coexistence. Instead, the first strain that emerges and breeds will benefit from a positive frequency dependence, leading to priority effects that promote the exclusion of other strains. These results highlight the nuanced role of temporal niche partitioning and related mechanisms in contributing to coexistence, emphasizing the importance of system-specific knowledge in considering the consequences of temporal differentiations in resource and habitat use.

KEYWORDS
Clunio marinus, coexistence, priority effect, temporal niche, temporal storage effect

The coexistence of many ecologically similar species has always puzzled ecologists. In nature, ecologically similar species often rely on a small number of fundamental resources that, according to classic theoretical prediction, cannot support more species than the number of resources (Gause, 1934; Hutchinson, 1961; MacArthur, 1969; Tilman, 1982). Theory has since focused on finding alternative mechanisms that promote species coexistence by partitioning the limited resources or ecological niche on the spatial and temporal dimensions. For instance, species may use the same resource or habitat at different times, minimizing direct competition (Albrecht & Gotelli, 2001). This idea of temporal niche partitioning is further developed into the so-called temporal storage effect, where different species may have higher fitness in some years but not others; on a broader scale, this mix of 'good' and 'bad' years balances the performance of all species such that no species has a distinct advantage (Barabás et al., 2018; Chesson & Warner, 1981; Stump & Vasseur, 2023; Figure 1a). On the other hand, empirical evidence has revealed that temporal differentiation may not necessarily promote

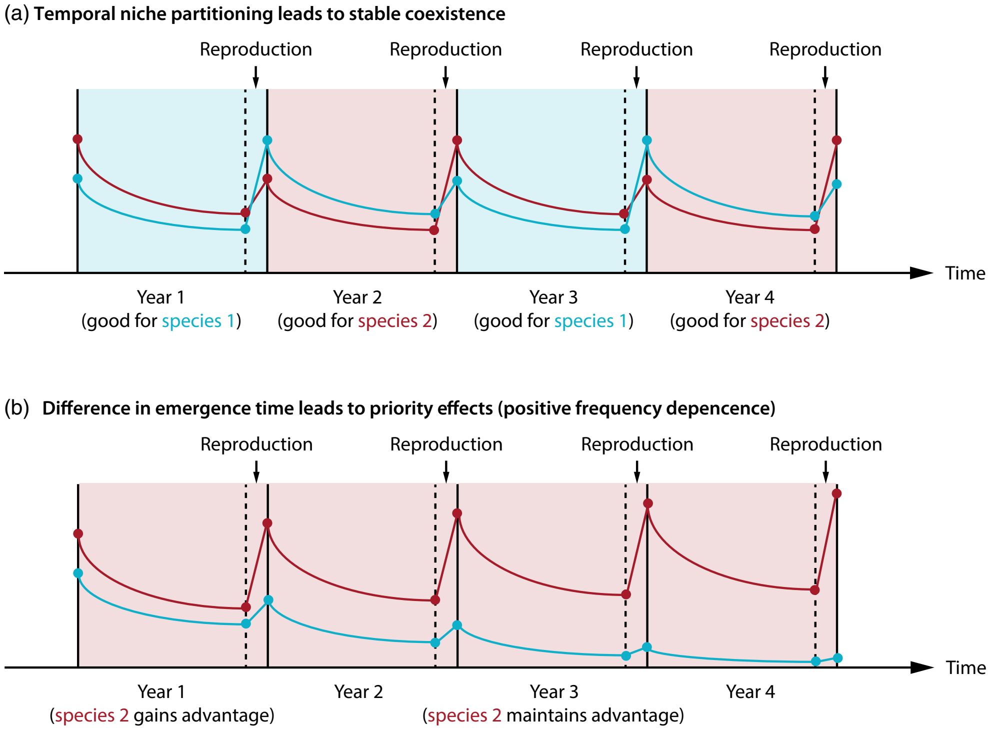

FIGURE 1 Conceptual figure of how temporal niche partitioning could promote species coexistence or priority effects. In a two-species community, the species share the same habitat (resources), reproduction happens at the end of each year, and during the year, both species are subject to density-dependent mortality. In (a), species alternate to use the habitat, leading to alternate 'good' and 'bad' years for each species and stable coexistence. In (b), species 2 first utilizes the resource and gains an advantage, and this numeric advantage is maintained over time, driving the other species extinct (i.e. a priority effect). In Ekrem, de Vries, et al. (2025), the first strain of the marine midge *Clunio marinus* that emerges during low tide gains an advantage, leading to a priority effect.

coexistence. Rather, species that occupy the habitat first can negatively impact the later inhabitants, creating a 'priority effect' that could undermine coexistence (Fukami, 2015; Zou & Rudolf, 2023; Figure 1b). Instead of a general mechanism that always promotes coexistence, temporal niche partitioning may lead to vastly different dynamics in specific ecological communities.

In a recent study, Ekrem, de Vries, et al. (2025) further tipped the scale of temporal niche partitioning towards priority effects by modelling the dynamics of a unique marine midge system. Larvae of the midge *Clunio marinus* develop in the benthic intertidal zone, and adults only emerge during the lowest tides to reproduce, meaning that the midge's lifecycle is closely related to the lunar phase (Kaiser et al., 2021). The population consists of strains that either emerge at the new or full moon (monthly or once per 4 weeks) or both (fortnightly), leading to three distinctive strains that are genetically determined (Kaiser et al., 2021). Hybridization is maladaptive because any intermediate timing is not synchronous with low tide and leads to low success in finding mates, leading to reduced reproduction. These characteristics essentially create a strong Allee effect, where rare strains face extra penalties by the lower probability of encounters during their short lifespan or encountering adults of other strains and producing maladaptive hybrids. Therefore, each strain creates its own 'good tides' when it emerges and reproduces. During development, larvae compete for identical resources, and the longer they stay in the larval stage, the more likely they are to be subject to predation, but the more offspring they will produce after emergence, leading to a potential growth-survival trade-off. If present, this trade-off penalizes the fortnightly strain, which spends less time in the larval stage.

The unique and complex life history of *Clunio* seems to have all the ingredients for the temporal storage effects between the three strains (Stump & Vasseur, 2023). First, there is strong temporal niche partitioning because each strain uses different tides to emerge and reproduce. Second, population growth is buffered because larvae of one strain produced during its 'good tides' can remain at larval stages during its 'bad tides' (i.e. tides where the other strains emerge *en masse*). Third, a 'good tide' produces more offspring that should lead to more intense competition, fulfilling the requirement of an 'environment-density dependence covariance'. However, results from simulations do not support the promotion of coexistence, but rather competitive exclusion from priority effects: the first strain to reproduce usually gains an advantage and excludes one or both other strains. These priority effects do not change with the addition of the growth-survival trade-off and become even stronger with the Allee effect, where the rare strains are more disadvantaged. The only case where the temporal niche differentiation leads to stable coexistence is with ontogenetic niche shift, where larvae above a certain age use a different resource and therefore do not compete with younger larvae. When two monthly strains compete, an ontogenetic niche shift at 2 weeks can concentrate larval competition

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within single strains, promoting the coexistence of these strains. However, when a monthly strain competes with a fortnightly strain, the ontogenetic niche shift at 2 weeks no longer promotes coexistence because it overwhelmingly benefits the fortnightly strain, unless the growth-survival trade-off offsets this advantage. Similarly, ontogenetic niche shift also does not promote coexistence when all three strains are present. Together, Ekrem, de Vries, et al. (2025) provide compelling evidence that temporal niche partitioning more likely leads to competitive exclusion via priority effects, not coexistence, in the *Clunio* midge system.

This study adds to a series of recent challenges to the causal link between temporal niche partitioning and species coexistence. For instance, Stump and Vasseur (2023) found that models of temporal storage effects rely on four assumptions in addition to the three requirements listed above; these additional assumptions are rarely met in empirical systems. Failure to meet these assumptions leads to a much smaller impact of temporal storage effects on species coexistence in empirical studies. Indeed, evidence from nectar microbiomes (Letten et al., 2018), planktons (Descamps-Julien & Gonzalez, 2005; Ellner et al., 2019), aquatic plants (Armitage & Jones, 2019) and terrestrial plants (Hallett et al., 2019; Zepeda & Martorell, 2019) all found weak contributions of temporal storage effects in maintaining coexistence. In these systems, coexistence is often promoted by other fluctuation-dependent mechanisms (i.e. mechanisms that arise from environmental fluctuations; Barabás et al., 2018; Chesson, 2000). In the *Clunio* midge system, coexistence among different strains is, in fact, promoted by the interaction between time and space: the different reproduction timing between the new moon strain and the full moon strain leads to oviposition at different water levels, leading to spatial niche differentiation (Ekrem, Jacobsen, et al., 2025). These theoretical and empirical explorations all add a cautionary note to assuming temporal storage effects as a general mechanism in maintaining coexistence.

More broadly, Ekrem, de Vries, et al. (2025), among other studies, touch on the foundation of considering time as a resource or niche axis that can be partitioned. Time is unidirectional and can only proceed forward. Therefore, past events are much more likely to affect the present. This argument is more obvious in systems where time is a proxy for other resources, such as nutrients: the previous inhabitants may deplete the resources required by later inhabitants, leading to inhibitory priority effects (niche preemption sensu Fukami, 2015) or modify the resource into a form that is no longer usable for the later inhabitants (niche modification). On the other hand, Ekrem, de Vries, et al. (2025) provide a unique example where time is not tied to a particular resource: the strain of *Clunio* that emerges first can still propagate via positive frequency dependence, leading to priority effects that undermine coexistence (Zou & Rudolf, 2023). Ekrem, de Vries, et al. (2025) join the vast literature on historical contingency and priority effects in raising the fundamental question about temporal niche partitioning: How can we meaningfully partition niche over time when the niche itself is constantly changing due to previous ecological dynamics? Exploring answers to this question will greatly improve our understanding of species coexistence and community dynamics over time and drive ecology one step closer to a predictive science.

AUTHOR CONTRIBUTIONS

H.-X.Z. wrote the manuscript and prepared the figure.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

No data or code were used.

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