Title

Diversity of biological rhythm and food web stability

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1 **Research Articles**

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4 # Diversity of biological rhythm and food web stability

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14 **Number of words:** abstract (142), main text (2419)

15 **Number of references:** 45

16 **Number of figures:** 2

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Abstract

How ecosystem biodiversity is maintained remains a persistent question in the field of ecology. Here I present a new coexistence theory, i.e., diversity of biological rhythm. Circadian, circalunar, and circannual rhythms, which control short- and long-term activities, are identified as universal phenomena in organisms. Analysis of a theoretical food web with diel, monthly, and annual cycles in foraging activity for each organism shows that diverse biological cycles play key roles in maintaining complex communities. Each biological rhythm does not have a strong stabilizing effect independently but enhances community persistence when combined with other rhythms. Biological rhythms also mitigate inherent destabilization tendencies caused by food web complexity. Temporal weak interactions due to hybridity of multiple activity cycles play a key role toward coexistence. Polyrhythmic changes in biological activities in response to the Earth's rotation may be a key factor in maintaining biological communities.

Introduction

Time and space, which are considered fundamental axes in nature, are responsible for the development of ecological communities. In early ecological studies, the spatial dimension was considered the major driver of the dynamics and structure of ecological communities, leading to the development of the field of spatial ecology [1]. However, while it has long been recognized that interactions between species change temporally, research on the temporal dynamics of ecological communities is still at a developmental stage [2,3]. Species interactions can change dynamically over time through environmental fluctuations [4], adaptive behavior [5], evolution [6], and changes in life-history traits [7], among other mechanisms.

In recent years, timing has received increasing attention as climate change threatens to shift phenology, seasonal timing of life-history events[8], which affects population persistence, and alter community compositions [9–12]. Because seasonality causes annual rhythms of species interactions[13], species interactions in active and non-active seasons should differ. For example, predation by a focal species in an active season will be weak or will completely vanish in a non-active season. Although recent studies have explored the roles of phenology in community dynamics and species coexistence [14–20], they typically consider primarily temporal variations, such as resource fluctuations at a particular trophic level, or focus on a simple community module comprising few species [21–23]. Examining the role of phenology on the dynamics and coexistence of diverse species in large ecological communities is a recent challenge [24].

Activity rhythms are not caused by phenology alone. While much research has focused on annual cycles and their role in species coexistence [14–19,22–25], diel and monthly cycles have received less attention. A well-studied empirical system with a diel cycle is the vertical migration of zooplankton [26], and such diel cycles should work in a wide variety of natural ecosystems because most species exhibit some form of circadian rhythm [27,28]. Nocturnal or diurnal activities are common in many species, and, as with annual cycles, interaction structures can change frequently, even within a day [27,28]. Similarly, a circalunar rhythm leads to monthly activity cycles [29,30]. A notable example is the dramatic change in reproductive activity of marine organisms during a full or new moon, a phenomenon known as a circasyzygic cycle. These remarkable circadian, circalunar, and circannual rhythms, which control organisms' activities over short and long periods, are widespread phenomena and may be considered adaptations to the Earth's rotation and orbit [31]. Nevertheless, how each biological rhythm affects the dynamics and stability of large ecological communities with diverse species remains largely unexplored. Here, I present a polyrhythmic community model incorporating diel, monthly, and/or annual cycles in foraging activity and further describe the role of diversity of biological rhythms in maintaining large ecological communities.

91   The proposed model is based on a food web comprising N species, any pair of which is

92   connected with the probability C (connectance). Population dynamics are driven by interspecific

93   interactions with a non-linear functional response (see Methods). A random food web was assumed to

94   reveal the effect of activity rhythms itself in the main text (two other network types are also tested). Diel,

95   monthly, and annual cycles in foraging activity are described by sine waves with cycles that have 1-, 30-,

96   or 365-day periods. The presence or absence of each rhythm (diel, monthly, and annual) is controlled by

97   γ_d, γ_m, and γ_y, respectively ($\gamma_i = 1$, where i = day, month, or year, in the presence of a focal rhythm;

98   otherwise, $\gamma_i = 0$).

99   Controlling the presence or absence of each biological rhythm, γ_i, allows for an examination of

100   the effects of diverse types of biological rhythms in foraging activities on the maintenance of ecological

101   communities. The degree of maintenance was evaluated using community persistence, an index of

102   stability defined as the probability that all species persist for a given time (see Methods for details).

Results

104   Consider an extreme case wherein foraging activity does not follow a biological cycle. In a complex

105   community with diverse species, such a system is unlikely to persist according to previous food web

106   models (Fig. 1). Although activity rhythms have been shown to improve the stability of such a fragile

107   system, the stabilization effects that a single rhythm has are weak (Fig. 1). Combining multiple rhythms

108   can increase community persistence. In particular, a system with all available rhythms, daily, monthly,

109   and annual foraging activity cycles, exhibits the highest degree of community persistence (Fig. 1). A

110   variety of biological rhythms can mitigate inherent destabilization due to community complexity (Fig.

111   2). Without biological rhythms, the increase in community complexity (N, C) dramatically decreases

112   community persistence. In contrast, diverse rhythms can prevent the destabilization associated with

113   community complexity.

114   The stabilization effect caused by a diversity of biological rhythms can be observed regardless

115   of the network type (Fig. S1). However, a non-linear functional response in foraging is key to exploiting

116   a strong stabilization effect due to the diversity of biological rhythms (Fig. S2, S3). In an extreme case

117   with a linear functional response, the stabilization effect due to a diversity of biological rhythms is found

118   to be weak (Fig. S2).

Discussion

120   This study describes a novel coexistence mechanism, i.e., diversity of biological rhythm. Diel, monthly,

121   and annual cycles in biological activity, known as circadian, circalunar, and circannual rhythms,

122   respectively, combine to play a crucial stabilizing role in large ecological communities. Although

123 coexistence is possible under temporal environmental fluctuations, as shown by earlier ecological

124 theories [21–23], multiple temporal fluctuations may lead to more stable coexistence.

125   Earlier theoretical studies explored the role of temporal fluctuation in environmental

126 conditions, such as seasonality in species coexistence [22]. For example, in competitive systems, temporal

127 variation in environmental conditions that affect the fitness of competing species can cause temporal

128 niche partitioning and determine coexistence patterns [21]. Timing of species interactions shaped by

129 phenology in the form of match/mismatch among species interaction also plays a key role in driving

130 community dynamics and species coexistence [17, 24]. Periodicity of resource fluctuations can affect

131 competitive coexistence, with longer periodicities promoting species coexistence. Through temporal

132 niche partitioning, weakened species interactions can promote species coexistence [23].

133   The present study shows that activity-level cycles can temporally weaken species interactions

134 [32], exerting an inherently stabilizing effect. However, a single activity-level cycle on its own has an

135 insufficient stabilizing effect for the following reasons. Inactive periods in a short cycle are unlikely to

136 be sufficient to ensure recovery in less-abundant and fragile species, and, while a long inactive period

137 may be able to rescue such species, an opposite active period in a long cycle may negate the rescue

138 effect or lead to the extinction of a fragile species. In short, because weak and strong interactions with

139 stabilizing and destabilizing effects are two sides of the same coin in a single active cycle [32], each active

140 cycle does not necessarily play an effective role in stabilizing community dynamics. However, if

141 multiple activity-level cycles coexist, an entirely different pattern can emerge. Hybridization of multiple

142 activity cycles contributes to a lower distribution of activity level (Fig. S4, S5), i.e., the skew toward low

143 activity reaches a maximum when all cycles are mixed. This skewed distribution of interaction strengths,

144 combined with a rescue effect resulting from a non-linear functional response (lower foraging rates to

145 less-abundant species), plays a key role in stability. This suggests that temporal low activity or "rest"

146 periods during multiple activity cycles can greatly reduce species interaction or cause temporal weak

147 interactions, which is essential for the maintenance of food webs [33]. It is important to note that

148 coexistence is not caused by a storage effect based on competition theory [34] because coexistence occurs

149 even if population dynamics are synchronized (not satisfying species-specific response to environments

150 [34]) (Fig. S6). Additionally, rhythmical changes in activity would be crucial for stability, because random

151 or non-rhythmical changes in activity do not seem to show stabilizing effects (Fig. S7). The temporal

152 weak interactions caused by hybrid activity cycles enable multiple species to coexist by the following

153 mechanism: Even if a short activity-level cycle cannot prevent extinction of a fragile species, a long

154 activity cycle can gradually reverse the species' prospects. This may result from a long-term increase in

155 activity levels or a long-term decrease in activity levels of the species' predators or competitors. Any

156 species that might face extinction because of a long-term unfavorable situation can recover by making

5

157   daily and/or monthly changes in its behavior. Activity cycles with different cycle periods may therefore

158   have complementary effects on stabilizing community dynamics.

159   The complementary effects of multiple activity cycles may have powerful implications for

160   biodiversity conservation. Artificial light at night [35] and temperature increases [36,37] can affect activity

161   levels or patterns in daily and monthly cycles, and climate changes, such as global warming, can affect

162   annual active periods [38]. If these changes prolong active phases in biological rhythms at various time

163   scales, activity cycles can be obscured, further preventing stabilization. Because of inherent links

164   between different activity rhythms [39], alterations in one activity cycle may cause alterations in another.

165   The present theory suggests that simultaneous alterations in multiple activity rhythms dramatically

166   decrease the stability of community dynamics. However, empirical tests of this theory are difficult to

167   conduct because creating a natural community without activity cycles is deemed problematic.

168   Nevertheless, a possible test of this hypothesis would involve controlling various types of rhythms in

169   environmental conditions, such as light and/or temperature, within a microcosm experiment. Comparing

170   the dynamics of communities before and after removing temporal factors, such as seasonality, using real

171   time-series data analysis [40] offers another option for testing this theory. Furthermore, since the present

172   theory emphasizes on the rhythmical change itself, a common stabilizing mechanism may be working in

173   other rhythmical changes, such as a burst-like activity pattern (i.e., short active states between long

174   inactive states) in animal behavior [41]. Future research should be aimed at understanding the relationship

175   between more general diverse rhythm types and higher system-level phenomena. Biological rhythms that

176   evolved in response to the Earth's rotational rhythms by changing the strengths of species interactions in

177   a polyrhythmic manner may play a key role in supporting biodiversity.

Methods

179   Consider a random food web in which pairs of species i and j ($i, j = 1,…, N$) are connected by a trophic

180   interaction with a probability of C, which is defined as the proportion of realized interaction links L in

181   the possible maximum interaction links L_{max} of a given network model ($L = CL_{max}$). To examine the

182   generalization of the main result, other types of food webs can be tested (Fig. S1). In a cascade model [42],

183   for each pair of species $i, j = 1,…, N$ with $i < j$, species i never consumes species j, whereas species j

184   may consume species i. The maximum link number L_{max} is calculated from $N(N-1)/2$ in both random

185   and cascade models. In a bipartite model [43], no interactions occur within the same trophic levels, and

186   species numbers in each of two trophic levels are the same, with $L_{max} = (N/2)^2$. The food web model is

187   defined by an ordinary differential equation:

188

189 $$\frac{dX_i}{dt} = (r_i - s_i X_i + \sum_{j=1}^{N} A_{ij} X_j) X_i \qquad (1)$$

190

191 where X_i is the abundance of species i, r_i is the intrinsic rate of change in a species i, s_i is the density-

192 dependent self-regulation of species i, and A_{ij} is the interaction coefficient between species i and j.

193 Interaction coefficients are defined as $A_{ij} = e_{ij}\alpha_{ij}$ and $A_{ji} = -\alpha_{ij}$, where e_{ij} (< 1) is the conversion

194 efficiency. Next, assume a type II functional response, $\alpha_{ij} = a_{ij}/(1 + \sum_{k \in \text{resources of species } i} h_{ik}a_{ik}X_k)$,

195 where a_{ij} is the consumption rate of species i by resource species j and h_{ij} is the handling time. $a_{ij} =$

196 $a_{0ij}c_i(t)$, where a_{0ij} is the basal consumption rate and $c_i(t)$ is a time-varying function that represents diel,

197 monthly, and/or annual cycles of foraging activity.

198 Each biological cycle is described by a sinusoidal function [44]:

199

200 $c_i(t) = 1 + \gamma_i \sin\{2\pi(t - u_i)/T\}, \qquad (2)$

201

202 where γ_i ($= 0$ or 1) is a parameter that determines the presence or absence of each rhythm (see main text)

203 and T and u_i are the cycle period and timing of activity peak, respectively. T is 1, 30, or 365 in a diel,

204 monthly, or annual cycle, respectively. Note that the time scale of a biological cycle has a day, whereas

205 that of a food web model is assumed to be normalized by a basal resource. In a diel cycle, u_i may be 0 or

206 1/2, which is defined as diurnal or nocturnal, respectively. In a monthly cycle, u_i may be 0 or 30/2,

207 which is defined as a full or new moon, respectively. In an annual cycle, u_i may be 0 or 365/2, which is

208 defined as summer or winter, respectively. The proportions of species active during bright times (i.e.,

209 diurnal, full moon, and summer) are defined as p_d, p_f, and p_s, respectively; those during night, a new

210 moon, and winter (cold season) are defined as $1 - p_d$, $1 - p_f$, and $1 - p_s$, respectively. The default setting

211 is $p_i = 1$ (all species are active during bright times), although relaxation of this assumption does not

212 affect the main result (Fig. S8). The models with either two or all cycles are given by the product of each

213 cycle function with different cycle periods (Eq. 2). For example, in a case with diel and monthly cycles,

214 $c_i(t) = [1 + \sin\{2\pi(t - u_i)\}][1 + \sin\{2\pi(t - u_i)/30\}]$, and in a case with all cycles, $c_i(t) = [1 + \sin\{2\pi(t - $

215 $u_i)\}][1 + \sin\{2\pi(t - u_i)/30\}][1 + \sin\{2\pi(t - u_i)/365\}]$. Note that each function with multiple periods has

216 the same mean value of 1, which allows for the appropriate comparisons with each model, including a

217 null model without a biological cycle.

218 In each iterated simulation, initial species abundance and parameters are randomly selected

219 from the uniform distribution ($X_i = 0.0$ to 1.0, $r_i = 0.05$ to 1.0, $a_{0ij} = 0$ to 0.05, $e_{ij} = 0.1$ to 0.5). The value

220 for s_i was set to a constant 1.0. A non-zero self-regulation term was used in all species to avoid a

221 confounding effect, in which an increase in interspecific links decreases the number of heterotrophic

222 species with no potential diet present in the web [45]. From a biological perspective, each species is either

223 autotrophic or uses external resources.

224   Community persistence [45] was then calculated by measuring the frequencies of all coexistent

225 species ($X_i > 10^{-3}$ for all i) after a sufficiently long time ($t = 2 \times 10^3$, which corresponded to the time

226 taken for community persistence to reach an asymptote) in 500 runs. Community persistence did not

227 show variance because it is only a probability.

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317

Supplementary material

319   Figures S1–S8, Code for Figures

320

Ethics

322   Not applicable.

323

Data accessibility

325   No new data was used. The source code for figures has been included in supplementary
326   material.

327

Competing interests

329   The author declares no competing interests.

330

339 aid to publish this article.
340

Author contributions

342 AM performed all research and wrote the manuscript.

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Figure legends

349 **Fig. 1**. Effects of foraging activity cycles on stability. Each circle represents a different
350 model with or without an activity cycle. D, M, and Y represent diel, monthly, and annual
351 cycles, respectively. DM, DY, MY, and DMY represent combinations of the cycles. A
352 random model was assumed. $N = 50$ and $C = 0.5$. $h_{ij} = 5$.

353

354 **Fig. 2**. Relationships between food web complexity and stability. (a) Effects of species
355 richness. $C = 0.5$. (b) Effects of connectance. $N = 50$. Red and blue represent cases with or
356 without activity cycles, respectively. $h_{ij} = 5$.

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