Title
Toward a more temporally explicit framework for community ecology

Permalink
https://escholarship.org/uc/item/6gt9b0zt

Author
Yang, Louie H

Peer reviewed

1 **Towards a more temporally explicit framework for community ecology**

2 Louie H. Yang

3 Department of Entomology and Nematology, University of California, Davis, CA

4 95616, USA

5 lhyang@ucdavis.edu, 1-530-754-3261

6

7 **Abstract**

8 Although ecologists have long understood the fundamentally dynamic nature of

9 communities, ecology has until recently seemed to emphasize other aspects of

10 ecological complexity, such as diversity and spatial structure, ahead of temporal

11 variation. Climate change has made studies into the temporal dimensions of

12 community ecology more immediate and urgent, and has exposed the limits of our

13 general understanding about how species interactions change over time. Here, I

14 suggest four specific ways to continue building towards a more temporally explicit

15 understanding of community ecology: 1) by increasing the representation of

16 temporal change in interaction networks, 2) by developing both specific and general

17 insights into event-driven dynamics, 3) by developing and testing sequential

18 hypotheses to describe proposed explanations that unfold over time, and 4) by

19 characterizing seasonal windows of opportunity. A great deal about the temporal

20 dynamics of communities remains uncertain, but temporally explicit studies have

21 the potential to improve our fundamental understanding of how communities

22 function.

Introduction

In 1872, the English-American photographer Eadweard Muybridge was hired by
Leland Stanford, a former governor of California, railroad tycoon and horse
enthusiast, to do a photographic study of animal locomotion. At the time, the
precise way a horse moved while galloping was unknown, and the subject of
vigorous debate. Because the legs of a galloping horse move too quickly for
accurate observation with the unaided eye, previous hypotheses for the gait and
posture of a galloping horse were largely based on conjecture and imagination. In
order to observe how a horse gallops, Muybridge needed to develop new
photographic methods and tools. Prior to the completion of his photographic
studies, artists generally depicted galloping horses in a "flying gallop" posture (Fig.
1A), with their front legs extending in front of them, and their hind legs
simultaneously extended behind them. Muybridge's photographs showed horses
with a fundamentally different posture when galloping (Fig. 1B). With the first
publications of these images ("A horse's motion scientifically determined," 1878;
Muybridge, 1887), our understanding of animal movement was profoundly changed.
As *Scientific American* (1878) wrote at the time, *"Before these pictures were taken*
no artist would have dared to draw a horse as horse really is when in motion… yet
after a little study the conventional idea gives way to truth, and every posture
becomes instinct… Mr. Muybridge's ingenious and successful efforts to catch and fix
the fleeting attitudes of moving animals thus not only make a notable addition to
our stock of positive knowledge, but must also effect a radical change in the art of
depicting horses in motion."

49   As with galloping horses, our understanding of community ecology has historically

50   been influenced by static depictions of inherently dynamic processes. These static

51   representations of how species interact have become a principal part of our ability

52   to conceptualize complex natural systems, and have succeeded in conveying many

53   important insights about the structure of communities. However, like a painting of a

54   horse in motion, our static depictions of communities both reveal and shape our

55   assumptions about how communities work. While static representations of

56   communities have structured community ecology in many ways, ecologists have

57   always understood that the natural systems underlying these static representations

58   are highly dynamic. In his foundational book *Animal Ecology*, Charles Elton (1927)

59   established several concepts that have become central to ecology, including food

60   web diagrams, the biomass pyramid and the Eltonian niche concept. However, this

61   book also includes a chapter devoted to "time-communities", noting that *"animal*

62   *communities are organized into a series of smaller animal communities, each of*

63   *which is in action at a different time."* Elton's book makes it clear that the study of

64   temporal patterns in species interactions was central to community ecology from

65   the beginning, and this more temporally explicit perspective developed

66   concurrently with the first depictions of static food webs. These are not

67   contradictory or inconsistent perspectives; rather, they represent ways to examine

68   different aspects of ecological complexity in a more manageable way; emphasizing

69   the structure and spatial organization of species interactions on the one hand, and

70   emphasizing the dynamics and temporal organization of species interactions on the

71   other. Since the early days of ecology, these two perspectives have developed

72   along parallel but uneven paths; until recently, the study of important structural and

73   spatial issues in community ecology has seemed to outpace the development of a

74   more temporally explicit perspective.

75   The reality of ongoing climate change has made the study of temporal change in

76   community ecology more immediate and urgent, and has contributed to a

77   resurgence of interest in developing a better understanding of the temporal

78   dimension of species interactions on more fundamental level (Forrest & Miller-

79   Rushing, 2010; Parmesan & Yohe, 2003; Post, 2019; Visser, Caro, Oers, Schaper, &

80   Helm, 2010; Wolkovich, Cook, McLauchlan, & Davies, 2014b; Yang & Rudolf, 2010).

81   Climate change is causing widespread phenological shifts in the timing of life

82   histories (Hua et al., 2016; Parmesan, 2006), and phenological mis-matches have

83   the potential to disrupt species interactions in a community (Both, Van Asch,

84   Bijlsma, Van Den Burg, & Visser, 2009; Kharouba et al., 2018). Although there is a

85   general pattern of advancing phenologies in diverse taxa around the globe

86   consistent with expectations on a warming planet (Parmesan & Yohe, 2003), the

87   variability of phenological responses to climate change is large, complex and often

88   counterintuitive (Chmura et al., 2019; Cleland, Chiariello, Loarie, Mooney, & Field,

89   2006; Edwards & Yang, 2018; Forrest, 2016; Høye, Post, Schmidt, Trøjelsgaard, &

90   Forchhammer, 2013; Lane, Kruuk, Charmantier, Murie, & Dobson, 2012; Sherry et

91   al., 2007). While the study of phenology has traditionally focused on the timing of

92   life history events for single species, these changes in the timing of species

93   interactions are forcing us to grapple with the complexity of temporal dynamics in

94   community ecology more broadly; the reality of global climate change requires us

95   to consider phenology in a community context. Understanding phenology and the

96   timing of species interactions has never been more important, and the limits of our

97   current understanding are increasingly evident.

98   In response to this emerging reality, the study of phenology has advanced rapidly in

99   four specific ways. First, the study of phenology has progressed from the historical

100   study of single, annual life history events (such as the day of peak flowering, or the

101   first arrival of migratory birds) to examining phenological changes over multiple

102   stages in a seasonal trajectory or ontogeny (e.g., Inouye, Ehrlén, & Underwood,

103   2019; Yang & Rudolf, 2010). Second, the study of phenology is moving from pattern

104   to process; increasingly, studies are able to build upon previously documented

105   patterns of phenological change to ask questions about the causes or consequences

106   of those changes (e.g., Chmura et al., 2019; Forrest & Miller-Rushing, 2010; Inouye

107   et al., 2019; Pau et al., 2011; Visser et al., 2010). Third, ecologists are increasingly

108   investigating a wider range of phenological responses, including phenological

109   changes in the fall (e.g., Gallinat, Primack, & Wagner, 2015), phenological delays

110   (e.g., Lane et al., 2012), phenological responses to extreme events (e.g., Jentsch,

111   Kreyling, Boettcher-Treschkow, & Beierkuhnlein, 2009), changes in generation time

112   (e.g., Forrest, Cross, & CaraDonna, 2019), phenological variation in space (e.g.,

113   Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016), and individual variation

114   in phenological responses (e.g., Inouye et al., 2019). Finally, the study of phenology

115   is continuing to work towards putting single-species phenology into a multi-species

116   community context (e.g., Both et al., 2009; Nakazawa & Doi, 2012; Yang & Rudolf,

117   2010).

118   Along the way, these trends in the study of phenology are also building a more

119   temporally explicit perspective in community ecology. Fundamentally, a more

120   temporally explicit approach to ecology often requires examining smaller slices of

121   time; this is a recapitulation of Elton's "time-communities" concept in a modern

122   guise, and an ecological echo of Muybridge's photographic method. While

6

123   examining smaller slices of time is a quantitative change in the way we already do

124   community ecology, approaches that increase the temporal resolution of available

125   data could qualitatively improve our understanding of how communities work. In

126   many systems, these temporally explicit approaches will likely require the

127   application of new methods and technology, and there will certainly be many

128   questions in community ecology for which a temporally explicit approach will

129   remain unnecessary or impossible. Even as he was describing the richness of

130   temporal variation in communities, Elton wrote that temporal variation *"enormously*

131   *increase(s) the difficulty of studying (them)"*, and even comparatively regular

132   changes in communities *"make the study of this side of ecology excessively*

133   *complicated."* However, at its best, this approach allows us to see how nature works

134   more clearly than we could otherwise.

135   **Towards a more temporally explicit community ecology**

136   Here I suggest four ways to build towards a more temporally explicit understanding

137   of species interactions in community ecology: 1) by increasing the representation of

138   temporal change in interaction networks, 2) by developing both specific and general

139   insights into event-driven dynamics, 3) by developing and testing sequential

140   hypotheses to describe proposed explanations that unfold over time, and 4) by

141   characterizing seasonal windows of opportunity. These include both conceptual

142   frameworks and methodological tools that emphasize how species interactions

143   change over time.

144   *Temporally explicit interaction networks show changes in community structure*

145   In recent decades, the analysis of community structure in food webs has

146   emphasized taxonomically well-resolved summary datasets, generally compiled

147   over years of careful study in a given location (Dunne, 2006). These datasets have

148   undeniably shaped our current understanding of ecological communities (e.g.,

149   Gibert & DeLong, 2017; Williams & Martinez, 2000), and address many of the data

150   quality problems that arose from the analysis of less well-resolved datasets

151   previously (e.g., Hall & Raffaelli, 1997; Martinez, 1991; Paine, 1988; Polis, 1991).

152   However, the degree to which such static summary networks accurately represent

153   species interactions in nature remains unclear (Jordan & Osvath, 2009; Tavares-

154   Cromar & Williams, 1996). Because these networks are generally static, they are

155   unable to represent changes in community structure over time (Fig. 2; Akin &

156   Winemiller, 2006; Berlow et al., 2004; Tavares-Cromar & Williams, 1996; Warren,

157   1989). Moreover, because they are cumulative, they may reflect summary

158   community structures that have never existed at any point in time (Fig. 2; Close &

159   Lake, 1994; Jordan & Osvath, 2009; Schoenly & Cohen, 1991). These concerns are

160   not new (e.g., McMeans, McCann, Humphries, Rooney, & Fisk, 2015; Schoenly &

161   Cohen, 1991), and past studies have addressed them by examining time-specific

162   trophic networks in a range of systems (Akin & Winemiller, 2006; Baird & Ulanowicz,

163   1989; Ceneviva-Bastos, Casatti, & Uieda, 2012; Close & Lake, 1994; Hart, Stone, &

164   Berman, 2000; Kitching, 1987; Layer, Hildrew, Monteith, & Woodward, 2010;

165   Schoenly & Cohen, 1991; Tavares-Cromar & Williams, 1996; Thompson &

166   Townsend, 1999; Warren, 1989). Many of these studies documented substantial

167   temporal variation in specific food webs, with sometimes profound changes in

168   community composition and structure over time (Baird & Ulanowicz, 1989; Close &

169   Lake, 1994; Hart et al., 2000; Kitching, 1987; Schoenly & Cohen, 1991; Tavares-

8

170   Cromar & Williams, 1996; Thompson & Townsend, 1999; Warren, 1989; but see also

171   Akin & Winemiller, 2006; Ceneviva-Bastos et al., 2012). When compared directly,

172   the structural properties of temporally aggregated networks are often substantially

173   different from any of their time-specific constituents (Jordan & Osvath, 2009;

174   Schoenly & Cohen, 1991; Tavares-Cromar & Williams, 1996; Thompson &

175   Townsend, 1999; Warren, 1989). This suggests that our understanding of food web

176   structure is likely to be strongly dependent on the scale of temporal aggregation in

177   the underlying data in ways that parallel the unintended effects of species or

178   trophic species aggregation (Hall & Raffaelli, 1997; Martinez, 1991). If summary

179   descriptions create artifacts that substantially alter our understanding of food webs,

180   these quantitative differences between time-specific networks and cumulative

181   summary networks would be expected to increase as more data are gathered; in

182   the absence of a more explicit temporal dimension, the continued accumulation of

183   data could have the unintended effect of further obscuring how communities are

184   structured in time.

185   Despite the broad understanding that many real-world interaction networks change

186   substantially over time, and evidence that the structure of summary networks often

187   differs significantly from that of time-specific networks, relatively few temporally

188   explicit network datasets exist. This may reflect the fundamental challenge of

189   gathering temporally explicit and taxonomically well-resolved species interaction

190   data. While reconciling the widely recognized importance and ubiquity of

191   ontogenetic diet switching in nature and the observation that relatively few studies

192   that have attempted to incorporate them into food web studies, Tavares-Cromar

193   and Williams (1996) noted, *"...likely, the task of including different life stages has*

194   *proved intimidating."* Characterizing summary species interactions networks is

195   already notoriously difficult (Polis, 1991; Polis & Strong, 1996), and many past

196   efforts to develop time-specific food webs illustrate the uncommon combination of

197   sustained data gathering effort and the extraordinary breadth of taxonomic

198   familiarity that has traditionally been required to characterize interactions networks

199   over time. On top of this, it may be more difficult to generalize the insights afforded

200   by time-specific networks. By their nature, time-specific assessments of community

201   interactions are difficult to replicate, instead relying on the inherent value of their

202   larger temporal resolution and scope (Oksanen, 2001). However, past studies show

203   that temporally explicit network analyses are both possible and can offer unique

204   insights, despite the magnified challenge of characterizing species interactions at

205   multiple intervals of time. For their effort, these studies are often characterized by

206   an uncommonly detailed understanding of the dynamics and drivers behind specific

207   food webs, including informed insights about how environmental cycles and the

208   biology of key species affect community dynamics (e.g., Baird & Ulanowicz, 1989;

209   Closs & Lake, 1994; Warren, 1989). Similar insights have emerged from non-trophic

210   interaction networks, including plant-pollinator networks (e.g., Burkle, Marlin, &

211   Knight, 2013; CaraDonna et al., 2017; Olesen, Bascompte, Elberling, & Jordano,

212   2008), that been described with a more temporally explicit perspective. Studies

213   such as these inform our understanding of how species interactions change over

214   time.

215   A broader temporally explicit approach to interaction networks could yield new

216   general insights in community ecology. Attempts at generalization are limited in

217   part by the relatively small number of time-specific interaction networks currently

218   available, and the inherent difficulties of meaningfully comparing the dynamics of

219   species with different relevant timescales (Post, 2019; Rahel, 1990; Takimoto,

220   Iwata, & Murakami, 2009) and studies that use different sampling and analytical

221   methods (Closs & Lake, 1994; Jordan & Osvath, 2009; Schoenly & Cohen, 1991).

222   These are some of the same challenges that caused Lawton (1999) to conclude that

223   *"...community ecology is a mess, with so much contingency that useful*

224   *generalisations are hard to find."* New methods could help. For example, continuing

225   advances in the application of stable isotope analysis, molecular genetics and

226   remote sensing to community ecology may allow us to characterize time-specific

227   species interactions more rapidly and accurately in the future (Boecklen, Yarnes,

228   Cook, & James, 2011; Carreon-Martinez & Heath, 2010; Corse et al., 2010; Hardy,

229   Krull, Hartley, & Oliver, 2010; McMeans et al., 2015; Nielsen, Clare, Hayden, Brett, &

230   Kratina, 2018; Pompanon et al., 2012; Steenweg et al., 2017; Zellweger, De Frenne,

231   Lenoir, Rocchini, & Coomes, 2019). It seems possible that these new approaches

232   could increase the quality and availability of datasets in ways that substantially

233   improve our ability to generalize how communities change over time. For example,

234   the dynamic nature of species interactions may have implications for the stability

235   and persistence of communities. A growing number of models suggest that

236   consumer responses to spatially structured food webs can contribute to community

237   stability (McCann, Rasmussen, & Umbanhowar, 2005; Wolkovich et al., 2014a), and

238   that temporal structure may play a similar stabilizing role (Kondoh, 2003; McMeans

239   et al., 2015; Takimoto, 2003). The data required to create more temporally resolved

240   interaction networks could also potentially allow for more detailed analyses of

241   stage-structured phenological interaction paths (Yang & Rudolf, 2010) or the

242   geometric analysis of entire community trajectories in time (De Cáceres et al.,

243   2019). Moreover, by representing the dynamic nature of communities more

244   explicitly, time-specific representations help us to consider the effects of

245 phenological shifts and mismatches in a broader context, where both their direct

246 and indirect effects are more readily considered (e.g., Boggs & Inouye, 2012; Both

247 et al., 2009; Ogilvie et al., 2017). Thus, grappling with the dynamic nature of

248 species interaction networks may help to resolve persistent questions in ecology.

249 However, it may also be that the value of a temporally explicit approach to

250 interaction networks is less about the statistical analysis of common network

251 properties than it is about the ways we represent and conceptualize how

252 communities work. The ubiquity of static cumulative representations of

253 communities has shaped the way we think about species interactions, and more

254 dynamic representations of these networks have the potential to recast our

255 understanding of how communities change over time. Although an implicit

256 understanding of the dynamic nature of communities has been part of ecology from

257 the beginning of the field, explicitly depicting the dynamic nature of communities is

258 important. Ecologists view the natural world through a conceptual lens of

259 accumulated scientific knowledge and theory that we have built for ourselves. In

260 many ways, this lens allows us to see and understand the natural world with

261 increasing clarity as our field progresses. However, this lens can also distort the

262 complexity of nature as we make the simplifying assumptions that are sometimes

263 necessary to develop meaningful generality. As the conceptual lens of ecology is

264 refocusing on the dynamic nature of communities, continued efforts to document

265 and represent how species interactions change over time lay a foundation for

266 developing a more temporally explicit view of community ecology.

267 *Event-driven dynamics examine our climatic future*

268 Climate change includes trends in mean climatic conditions as well as changes in

269 the timing or magnitude of extreme climatic events (Easterling et al., 2000; Jentsch,

270 Kreyling, & Beierkuhnlein, 2007; Ummenhofer & Meehl, 2017; Wolkovich et al.,

271 2014b). These two aspects of climate change are closely connected; some changes

272 in climatic means are likely to be affected by changes in the frequency or intensity

273 of extreme events, and some changes in the magnitude of extreme events are

274 likely to be driven by the non-stationarity of climatic conditions over time (Bailey &

275 van de Pol, 2016; Easterling et al., 2000; Jentsch et al., 2007; Wolkovich et al.,

276 2014b). For example, increases in the frequency or intensity of heatwaves can

277 contribute to trends in mean annual temperature, while global warming trends may

278 increase the intensity of tropical storm disturbance events (Elsner, Kossin, & Jagger,

279 2008; Kossin, 2018). These challenges of characterizing the extreme values of

280 climatic distributions and the diversity of ways by which climate interacts with

281 biological systems makes it difficult to objectively define extreme climatic events

282 (Bailey & van de Pol, 2016; Wolkovich et al., 2014b). However, it is clear that

283 extreme climatic events are becoming a larger part of our climatic future (Beniston

284 et al., 2007; Easterling et al., 2000; Goswami, Venugopal, Sengupta,

285 Madhusoodanan, & Xavier, 2006; Groisman et al., 2005; IPCC, 2014), and that those

286 events can have strong effects on ecological communities (e.g., Jentsch et al., 2009;

287 Parmesan, Root, & Willig, 2000; Sergio, Blas, & Hiraldo, 2018).

288 The study of event-driven dynamics has accelerated as ecologists increasingly

289 recognize the potentially important impacts of extreme climatic events on

290 ecosystems. In 2007, Jentsch et al. advocated for new generation of climate-change

291 experiments focused specifically on the study of climatic events, not trends. Since

292 then, the number of studies focused on climatic events has continued to increase,

293   with recent studies focused on heat waves (e.g., McKechnie & Wolf, 2010; Siegle,

294   Taylor, & O'Connor, 2018), cold snaps (e.g, Bojorquez, Alvarez-Yepiz, Burquez, &

295   Martinez-Yrizar, 2019; Leriorato & Nakamura, 2019), drought (e.g, Jentsch et al.,

296   2009; Sankaran, 2019), flooding (e.g., Rivas, Spinola, Arrieta, & Faife-Cabrera, 2018;

297   Ujvari, Brown, Shine, & Madsen, 2016; Woodward, Bonada, Feeley, & Giller, 2015),

298   and wildfire events (e.g., Cooper et al., 2015; Hale et al., 2016), among many

299   others. However, while this emphasis has emerged recently in the context of

300   climate change, these questions have deep roots in the study of event-driven

301   dynamics more generally. Many ecosystems were strongly influenced by extreme

302   climatic events, such as El Niño precipitation events, prior to strong human-induced

303   rapid environmental changes (Gibbs & Grant, 1987; Grant & Grant, 1987; Grant,

304   Grant, Keller, & Petren, 2000; Holmgren, Scheffer, Ezcurra, Gutierrez, & Mohren,

305   2001; Holmgren et al., 2006; Polis, Hurd, Jackson, & Piñero, 1997). Moreover, the

306   contrast between climatic events and climatic trends has parallels with the

307   historical distinction between pulsed versus pressed perturbation experiments in

308   ecology (Bender, Case, & Gilpin, 1984), as well as the study of transient dynamics

309   following a broader range of experimental or natural perturbations (e.g., Hastings,

310   2004; Jensen, 1982; Jones, Ostfeld, Richard, Schauber, & Wolff, 1998; Piovia-Scott,

311   Yang, Wright, Spiller, & Schoener, 2019; Yang et al., 2010). More than three

312   decades ago, Roughgarden (1989) asked, *"How are ecosystem structure and*

313   *function influenced by the rare but important events that may occur every century*

314   *or so?"* This is a general ecological question with a long history, and though it has

315   re-emerged and become more urgent in the context of climate change, previous

316   studies may offer some relevant insights.

317 The detailed study of event-driven dynamics emerges readily from a broader

318 temporally explicit perspective in community ecology. However, because extreme

319 events are often unreplicated and unanticipated by their nature, identifying and

320 evaluating general hypotheses is a central challenge (Bailey & van de Pol, 2016). As

321 a result, the study of extreme events has initially and perhaps necessarily included

322 the accumulation of opportunistic, unique and descriptive studies. Although many of

323 these studies are focused on short-term community responses to singular

324 perturbations (Bailey & van de Pol, 2016), they nonetheless contribute to our

325 broader understanding of event-driven dynamics in nature. The variability of these

326 events, and of community responses to them, create rich opportunities to identify

327 general patterns through synthesis, meta-analysis and coordinated research

328 networks if we are able to characterize the fundamental, shared dynamic features

329 of seemingly disparate events in ways that allow for meaningful comparisons (e.g.,

330 Easterling et al., 2000; Holmgren et al., 2001; Yang et al., 2010). Short time-scale

331 descriptive studies of extreme events have also been followed by longer-timescale

332 studies (e.g., Grant & B.R. Grant, 1996; Meserve, Kelt, Milstead, & Gutierrez, 2003;

333 Stuble, Zefferman, Wolf, Vaughn, & Young, 2017b), manipulative experiments (e.g.,

334 Jentsch et al., 2009; Piovia-Scott et al., 2019; Yang & Karban, 2019), and theoretical

335 models (e.g., Collins et al., 2014; Davis, Grime, & Thompson, 2000; Holt, 2008). For

336 a wide range of episodic perturbations, explicitly examining how communities

337 respond over longer timescales allows us to track their direct and indirect effects

338 across a species interaction network (e.g., Jones et al., 1998; Piovia-Scott, Yang, &

339 Wright, 2017; Yang et al., 2010), and to consider the timing of perturbation events

340 in relation to seasonality and species life histories (Jentsch et al., 2007).

341 Experimental manipulations of extreme events create opportunities to simulate and

342   anticipate uncommon events, control the frequency and magnitude of events, and

343   infer the causes of community responses. However, such experimental

344   manipulations can be difficult to apply at relevant scales, and experimentally

345   pressed warming manipulations have been shown to underestimate the magnitude

346   of phenological responses relative to observational studies (Wolkovich et al., 2012).

347   Although a greater emphasis on the temporal dimension often seems to come at

348   some expense (e.g., of spatial or taxonomic resolution, or of conceptual generality),

349   the study of extreme climatic events provides a uniquely productive and relevant

350   context in which to explicitly examine the temporal dynamics of community

351   responses to perturbation. These studies, using a range of approaches, have the

352   potential to meaningfully advance our understanding of climate change specifically,

353   and inform our understanding of ecological stability and resilience more generally.

354   By their nature, events occur during a particular slice of time. Two temporally

355   explicit questions arise as a result: 1) To what extent does the specific timing of an

356   event matter? and 2) Under what conditions do events have persistent effects on

357   communities? Questions about the specific timing of events are relevant to both

358   transient and persistent effects, while questions about the persistence of effects

359   provide a converse perspective on questions about ecological resilience. The degree

360   to which differences in the seasonal or successional timing of events effects their

361   community responses remains unclear. Underlying temporal patterns in organismal

362   life history patterns, species interactions, or abiotic variability all provide the

363   context for strong perturbation events, with consequences in both natural and

364   experimental contexts (Jentsch et al., 2007). For example, the effects of both

365   hurricanes and seaweed subsidies on lizard populations depend on their seasonal

366   timing (Schoener, Spiller, & Losos, 2004; Wright et al., 2013). On a shorter

367   timescale, the effects of hurricanes on coastal and island communities tends to be

368   larger when the storm surge event coincides with high tide (Schoener, Spiller, &

369   Losos, 2001; Thomas et al., 2019). In general, extreme events during seasonal

370   windows of opportunity (e.g., Yang & Cenzer, 2020) may be more likely to have

371   strong effects on growth or reproduction, as windows of opportunity may also

372   represent important weak-link stages that are potentially vulnerable to

373   perturbation. On an inter-annual scale, many ecological experiments show strong

374   year-to-year variability in results (Stuble, Fick, & Young, 2017a; Stuble et al., 2017b;

375   Vaughn & Young, 2010); this environmental variability can both be caused by event-

376   driven dynamics (e.g., Stuble et al., 2017b), and affect the outcomes of event-

377   driven dynamics (Jentsch et al., 2007). By comparison, the potential for persistent

378   effects resulting from episodic events has been more clearly documented.

379   Numerous examples suggest that ecologically persistent effects could potentially

380   arise from both long timescale transient dynamics (Hastings, 2004) and changes in

381   equilibrium states (Beisner, Haydon, & Cuddington, 2003; Scheffer, Carpenter,

382   Foley, Folke, & Walker, 2001; Scheffer & Carpenter, 2003). While it can be difficult

383   to distinguish between these two mechanisms (Schroder, Persson, & De Roos,

384   2005), the persistence of effects on ecologically meaningful timescales can often be

385   observed directly. These include persistent changes in habitat (e.g., Brokaw &

386   Grear, 1991; del Arroyo & Silver, 2018; Lloren, Fahrig, Bennett, Contreras, &

387   McCune, 2019); organismal traits (e.g., Hunter & Forkner, 1999; Little, Fisher,

388   Schoener, & Pruitt, 2019; Siegle et al., 2018; Spiller & Agrawal, 2003); the

389   abundance or distribution of organisms (e.g., Spiller & Schoener, 2007; Wernberg et

390   al., 2013); community composition via invasion or extinction (e.g., Davis et al.,

391   2000; McKechnie & Wolf, 2010; Nowicki et al., 2019); and the frequency or intensity

17

392   of the perturbation regime itself (e.g., Crain, Tremblay, & Ferguson, 2019; Parmesan

393   et al., 2000). These are certainly not exclusive mechanisms, and many event-driven

394   dynamics reflect the combined effects of multiple dynamic processes. When

395   multiple dynamic processes take place on different timescales (e.g., Takimoto et al.,

396   2009), the study of event-driven dynamics may benefit from the development of

397   temporally explicit sequential hypotheses.

398   *Sequential hypotheses allow for different processes on different timescales*

399   Sequential hypotheses are proposed explanations that include multiple processes

400   that unfold over time. For example, sequential hypotheses allow for explanations

401   that explicitly describe how indirect effects are expected to ramify across networks,

402   or that describe how a community's response to perturbation can include multiple

403   processes that operate on different timescales. A sequential hypothesis avoids

404   necessarily treating processes on different timescales as strictly alternative

405   hypotheses, but instead recognizes that these multiple processes could all be part

406   of a single response dynamic. In the absence of sequential hypotheses, how we

407   interpret the results of an experiment could depend on its timing. For example, if

408   the relative importance of top-down and bottom-up processes changes over time, a

409   short-term experiment could yield different results and implicate different key

410   processes than an experiment conducted over a longer timescale. Thus, evaluating

411   a sequential hypothesis requires evaluating the component parts of each phase, as

412   well as any predictions that emerge from the coordination between them.

413   Sequential hypotheses have been implicit, or have emerged explicitly over time, in

414   many study systems (e.g., Ostfeld & Keesing, 2000; Yang, Bastow, Spence, &

415   Wright, 2008; Yang et al., 2010). Two specific examples illustrate some of the ways

416   sequential hypotheses can arise from the indirect effects of strong perturbations

417   and the overlay of multiple processes on multiple timescales. Community responses

418   to periodical cicadas (*Magicicada* spp.) in North American forests provide one

419   example (Fig. 3A). These insects spend 13- or 17-years feeding on the roots of host

420   plants before synchronously emerging as adults at high densities across large

421   geographic areas (Williams & Simon, 1995; Yang & Karban, 2009, 2019). The vast

422   majority of these cicadas will avoid predation, and fall to the ground as a pulse of

423   dead carcasses after reproducing (Whiles, Callaham, Meyer, Brock, & Charlton,

424   2001; Williams, Smith, & Stephen, 1993; Yang, 2004). This accumulated cicada

425   biomass fertilizes plant growth and reproduction (Yang, 2004, 2008; Yang & Karban,

426   2019), but also increases damage by mammalian and insect herbivores which

427   preferentially feed on rapidly growing, fertilized plant tissues (Yang, 2008; Yang &

428   Karban, 2019). Thus, the effects of periodical cicadas on their host plants are

429   initially dominated by a long-term, negative direct interaction (*chronic belowground*

430   *herbivory by cicadas*), followed by a positive, bottom-up, indirect interaction

431   mediated by detritivores and decomposers belowground (*fertilization by the detrital*

432   *resource pulse*), and a subsequent, negative, top-down indirect interaction

433   mediated by other consumers in the community (*increased consumption by*

434   *aboveground herbivores*). While community ecologists commonly ask questions

435   about the relative importance of top-down and bottom-up processes (Hunter &

436   Price, 1992; Power, 1992), this example illustrates how the relative importance of

437   top-down and bottom-up processes can change over time. Whereas a simple

438   alternative hypothesis-testing framework could ask *"What are the relative strengths*

439   *of bottom-up and top-down effects on plants from periodical cicadas?"*, a sequential

440   hypothesis-testing framework considers *"How do the relative strengths of these*

441   *bottom-up and top-down effects change over time?"*. Such temporal variability in

442   multi-trophic indirect effects may be common (Piovia-Scott et al., 2017). Developing

443   explicitly sequential hypotheses allows us to frame our explanations about how this

444   temporal variation is structured in time, and to propose and test general

445   expectations about changes in the nature of species interactions.

446   The effects of pulsed resource subsidies on small island communities provides

447   another example illustrating how sequential hypotheses allow us to consider

448   multiple processes operating on different timescales (Fig. 3B, Kenny et al., 2017;

449   Piovia-Scott et al., 2013; Piovia-Scott et al., 2019; Spiller et al., 2010; Wright et al.,

450   2013). In this system, rafts of seaweed occasionally wash up on small rocky islands.

451   This seaweed biomass represents marine primary productivity transported by ocean

452   currents and winds; when deposited on islands, this seaweed becomes a pulsed

453   subsidy to the terrestrial community (Piovia-Scott et al., 2019; Spiller et al., 2010;

454   Wright et al., 2013). This pulsed subsidy affects the interactions between terrestrial

455   plants and their herbivores via multiple processes operating on different timescales

456   (Fig. 3B). In experimental studies, lizards (*Anolis sagrei*) show behavioral responses

457   immediately following the additional of pulsed seaweed subsidies, including rapid

458   changes in foraging behavior and habitat use (Kenny et al., 2017). These changes in

459   lizard behavior correspond with rapid shifts in their diet towards marine-derived

460   arthropod prey (Spiller et al., 2010). This lizard diet shift creates a window of

461   opportunity for terrestrial herbivores, which may benefit from reduced predation as

462   lizards focus on a pulse of marine-derived prey (Piovia-Scott et al., 2019). This

463   *"lizard diet shift effect"* represents an indirect mechanism akin to apparent

464   mutualism (Abrams & Matsuda, 1996) by which pulsed seaweed subsidies can

465   reduce terrestrial herbivory in the short-term (Piovia-Scott et al., 2019). However,

20

466 these pulsed subsidies can also increase the density of lizards on islands, either by

467 increasing behavioral aggregation, reproduction or survival (Kenny et al., 2017;

468 Wright et al., 2013). As the availability of marine-derived prey declines and lizard

469 diets shift back towards terrestrial prey, these increased lizard densities can more

470 strongly suppress terrestrial herbivores, reducing herbivory (Piovia-Scott et al.,

471 2019). Thus, this *"lizard numerical response"* mechanism is an indirect pathway by

472 which pulsed subsidies of seaweed can increase terrestrial herbivory on

473 intermediate timescales, by a process akin to apparent competition (Holt, 1977).

474 On longer timescales, subsidies of seaweed biomass can also affect the interaction

475 between terrestrial plants and their herbivores via a third pathway, the "*fertilization*

476 *effect*". According to this hypothesized pathway, decomposing subsidies of

477 seaweed fertilize nutrient-limited terrestrial islands, enriching the belowground

478 component of these systems. In turn, this fertilization increases the growth and

479 quality of terrestrial plants, increasing rates of herbivory. This process is a strong

480 driver of observed herbivory rates in chronically subsidized locations (Piovia-Scott et

481 al., 2013), and may also play a role in responses to more strongly pulsed subsides.

482 Thus, this hypothesized community response includes three processes that occur on

483 different timescales. In this example, a simple alternative hypothesis framework

484 could ask *"What are the relative strengths of these three hypothesized indirect*

485 *pathways resulting from pulsed seaweed subsidies?"*, while a sequential hypothesis

486 framework considers *"How does the relative importance of these three*

487 *hypothesized indirect pathways change over time?"*. Developing a sequential

488 hypothesis requires a more detailed and specific explanation for the effects of a

489 perturbation over multiple timescales, including aspects that would be difficult to

490 explain without a temporally explicit, multi-stage hypothesis.

491   As with any hypothesis, sequential hypotheses should be evaluated relative to

492   alternatives, potentially including both alternative sequential hypotheses as well as

493   alternative simple (i.e., single-stage, nonsequential) hypotheses. Also, as with any

494   hypothesis, sequential hypotheses are likely to evolve over time with the addition of

495   new information or insight. The unique value of a sequential hypothesis is in its

496   temporal specificity; by encouraging researchers to propose explanations that

497   include multiple linked processes that unfold over time, sequential hypotheses

498   extend the temporal scope of studies to explicitly examine and evaluate our

499   expectations of how species interactions change.

500   Sequential hypotheses are narrative by their nature; they propose an explanation

501   that incorporates a series of connected events. Sequential hypotheses seek to

502   extend conventional hypotheses to allow for a more explicit consideration of time,

503   linking event-driven dynamics and dynamic interaction networks with a stronger

504   hypothesis-driven approach.

505   *Seasonal windows of opportunity put phenological shifts in context*

506   In 1957, G. Evelyn Hutchinson proposed a conceptual model of the ecological niche

507   as an *"n-dimensional hypervolume… every point of which corresponds to a state of*

508   *the environment which would permit the species S_1 to exist indefinitely."* This

509   formalization of the niche concept built upon the niche concepts of Grinnell (1917)

510   and Elton (1927), and established an explicit separation between the abstract

511   concept of a niche in environmental dimensions versus the mapping of that niche

512   onto the physical landscape (i.e., the "biotop", *sensu* Hutchinson 1957). This duality

513   between the conceptual niche and the physical instantiation of the niche, and the

514   ways in which those two realms are linked, continues to have relevance and

515   implications for ecology today (e.g, Colwell & Rangel, 2009). Considering how this

516   duality changes over time has emerged as one of the ways in which modern

517   ecologists are extending the utility of the Hutchinsonian niche concept. In a list of

518   the key limitations of this niche model, Hutchinson (1957) noted that, *"The model*

519   *refers to a single instant of time."* However, in much the same way that

520   Hutchinson's niche concept can be mapped onto specific locations in heterogeneous

521   space, the niche concept could also be mapped onto specific slices of time in

522   dynamic environments. In this sense, Hutchinson's duality becomes a *tri*ality as the

523   combination of factors that define the conceptual niche are mapped onto both

524   space and time. This niche concept could be further extended to represent both

525   temporal and spatial changes over ecological and evolutionary timescales. On an

526   ecological timescale, the physical locations where niches map onto the biotop can

527   change over time as a result of temporal variation in the environment. On an

528   evolutionary timescale, the fundamental niche itself can change over time, as a

529   result of organismal (i.e., evolutionary) change (Colwell & Rangel, 2009). These

530   changes are not exclusive, and reflect the dynamic nature of the niche concept.

531   Seasonal windows of opportunity are potentially relevant to the Hutchinsonian niche

532   concept, but approach this conceptual territory from a different direction. Seasonal

533   windows of opportunity are intervals of time in which an organism has improved

534   prospects for achieving key life history objectives such as growth or reproduction

535   (Fig. 4, Yang & Cenzer, 2020). Although windows of opportunity have been

536   described on daily to inter-decadal timescales, seasonal windows of opportunity

537   emphasize the timing of life history processes within a year. These seasonal

538   windows of opportunity provide moving temporal targets for phenological cueing

539   strategies with potential fitness payoffs (e.g., Farzan & Yang, 2018; Rafferty & Ives,

540   2011; Valdés & Ehrlén, 2017), similar to "phenological niches" (Post, 2019;

541   Wolkovich & Cleland, 2011, 2014). Identifying seasonal windows of opportunity for

542   specific organisms allows us to examine the potential consequences of phenological

543   shifts and mismatches, putting the fitness consequences associated with the timing

544   of key life history processes into a broader seasonal context (e.g, Fig. 4, see also

545   Yang & Rudolf, 2010). The studies required to identify seasonal windows of

546   opportunity may also suggest hypotheses about the specific combinations of biotic

547   and abiotic conditions that allow for successful development. Subsequent

548   experiments to identify the combination of conditions that limit seasonal windows of

549   opportunity could provide an entryway to better understand the mechanistic bases

550   of these windows.

551   Seasonal windows of opportunity and the Hutchinsonian niche concept both aim to

552   identify favorable combinations of conditions, and endeavor to map these

553   combinations of conditions in the real world. While the Hutchinsonian niche concept

554   has traditionally emphasized the spatial dimension, seasonal windows of

555   opportunity emphasize the temporal dimension. If we accept that the Hutchinsonian

556   niche concept could be extended to include a more explicit temporal aspect,

557   seasonal windows of opportunity represent a component of the Hutchinsonian niche

558   mapped onto specific slices of time. However, whereas the Hutchinsonian niche

559   concept is defined by the combination of conditions that allow a species to persist

560   indefinitely, seasonal windows of opportunity emphasize the transient nature of

561   favorable conditions in many systems. Where the Hutchinsonian niche concept

562   begins in the abstract realm of n-dimensional hyperspace and imagines mapping

563   this concept onto the physical world, seasonal windows of opportunity will more

564   commonly begin in the physical world, and seek some conceptual consequence

24

565   afterward. While it seems plausible that an organism's ability to consistently

566   capitalize on transient seasonal windows of opportunity could contribute to the

567   persistence of a species, more concrete links between these two related concepts

568   remain uncertain.

569   The experimental methods used to identify seasonal windows of opportunity can be

570   simultaneously straightforward and complex (Farzan & Yang, 2018; Yang & Cenzer,

571   2020; e.g., Yang & Rudolf, 2010). These studies are potentially straightforward in

572   the sense (and to the degree) that studies that assess the performance of an

573   organism at any given point in time can be conceptually simple to design and

574   execute. They are potentially complex in the sense that this experimental motif is

575   then repeated at intervals throughout the season, with each repetition of the core

576   assessment occurring under changed biotic and abiotic conditions. The dynamic

577   pattern describing how an organism's developmental prospects change over annual

578   time represents a seasonal performance landscape, with peaks and valleys

579   representing periods of improved or constrained performance, respectively. Much

580   like Eadweard Muybridge's photographic studies of animal locomotion, a series of

581   repeated ecological observations, each potentially unremarkable on its own, offers

582   the potential for emergent insights when structured in time and examined in series.

583   Studies that identify seasonal windows of opportunity can suggest at least three

584   kinds of follow-up studies. First, subsequent studies may ask about the *causes* of

585   observed seasonal windows of opportunity. What are the seasonally variable biotic

586   or abiotic factors that constrain and structure developmental potential in time?

587   What are the phenological cueing strategies that proximately determine the timing

588   of organismal life history events? A second kind of study asks about the *dynamics* of

589   seasonal windows of opportunity. How do seasonal windows of opportunity vary

590   across multiple years or across the range of a species? How is climate change

591   altering the timing of seasonal windows of opportunity across years? Finally, studies

592   could ask about the ecological and evolutionary *consequences* that emerge from

593   seasonal windows of opportunity. For a single species, how do seasonal windows of

594   opportunity for one life history stage interact with those of other stages (e.g.,

595   germination and flowering)? In a community context, how do seasonal windows of

596   opportunity for one species interact with those of other species (e.g., predators and

597   prey)? What are the fitness costs associated with phenological shifts and mis-

598   matches?

599   It is clear that phenology is a process that occurs across development (Chmura et

600   al., 2019; Inouye et al., 2019; Yang & Rudolf, 2010). The study of seasonal windows

601   of opportunity may further motivate the examination of phenology across entire life

602   history trajectories, and could offer a framework to examine both the causes and

603   consequences of phenological shifts in a community context.

604   **Conclusions**

605   The timing of species interactions matters in community ecology because ecological

606   communities are inherently dynamic. As careful observers of nature, ecologists

607   have always understood this at an intuitive level. Despite this (or perhaps because

608   of this), there is a great deal about the temporal dynamics of communities that

609   remains uncertain. As climate change continues, an increasing motivation to better

610   understand the temporal dimension of communities has intersected with advances

611   in the methods and technology to examine small slices of ecological time. At this

612   intersection, there is the potential to improve our fundamental understanding of

613   how communities function. By analogy, it could be that our understanding of

614   ecological communities today is akin to the way artists in the late 19th century

615   understood the galloping horse. In many cases, they likely understood the general

616   movement of horses quite well, intuitively and via direct experience, and were able

617   to successfully apply this general knowledge in useful ways. However, when

618   attempting to explicitly depict a galloping horse in mid-stride, even experienced

619   artists of the time were forced to rely on conventional wisdom to fill in the details.

620   Our modern understanding of how a horse gallops didn't emerge until a strong

621   motivation to better understand the movement of the galloping horse intersected

622   with the development of new methods and technology to explicitly examine small

623   slices of time. Prior to this, paintings of galloping horses represented the best

624   available understanding of the time, but poorly represented the dynamic aspect of

625   nature. Similarly, ecologists today understand the general dynamic nature of

626   communities quite well, both intuitively and via direct experience, and are often

627   able to successfully apply this general knowledge in useful ways. However,

628   relatively few studies have aimed to understand how species interactions change

629   over time in a detailed and temporally explicit way. As we fill in the details that

630   occupy smaller slices of time, we are progressing towards a more complete and

631   dynamic understanding of how ecological communities actually work.

632   **Acknowledgements**

645 **References**

646 A horse's motion scientifically determined. (1878, October 19). *Scientific American*,

647 　　　*39*(16), 241.

648 Abrams, P. A., & Matsuda, H. (1996). Positive indirect effects between prey species

649 　　　that share predators. *Ecology*, *77*(2), 610–616.

650 　　　https://doi.org/10.2307/2265634

651 Akin, S., & Winemiller, K. O. (2006). Seasonal variation in food web composition and

652 　　　structure in a temperate tidal estuary. *Estuaries and Coasts*, *29*(4), 552–567.

653 　　　https://doi.org/10.1007/BF02784282

654 Armstrong, J. B., Takimoto, G., Schindler, D. E., Hayes, M. M., & Kauffman, M. J.

655 　　　(2016). Resource waves: phenological diversity enhances foraging

656 　　　opportunities for mobile consumers. *Ecology*, *97*(5), 1099–1112.

657 　　　https://doi.org/10.1890/15-0554.1

658 Bailey, L. D., & van de Pol, M. (2016). Tackling extremes: challenges for ecological

659 　　　and evolutionary research on extreme climatic events. *Journal of Animal*

660 　　　*Ecology*, *85*(1), 85–96. https://doi.org/10.1111/1365-2656.12451

661 Baird, D., & Ulanowicz, R. E. (1989). The seasonal dynamics of the Chesapeake Bay

662 　　　ecosystem. *Ecological Monographs*, *59*(4), 329–364.

663 Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in

664 　　　ecology. *Frontiers in Ecology and the Environment*, *1*(7), 376–382.

665 Bender, E. A., Case, T. J., & Gilpin, M. E. (1984). Perturbation experiments in

666 　　　community ecology - theory and practice. *Ecology*, *65*(1), 1–13.

667 Beniston, M., Stephenson, D. B., Christensen, O. B., Ferro, C. A. T., Frei, C., Goyette,

668 　　　S., … Woth, K. (2007). Future extreme events in European climate: an

669   exploration of regional climate model projections. *Climatic Change*, *81*(S1),

670   71–95. https://doi.org/10.1007/s10584-006-9226-z

671 Berlow, E. L., Neutel, A. M., Cohen, J. E., De Ruiter, P. C., Ebenman, B., Emmerson,

672   M., … Petchey, O. (2004). Interaction strengths in food webs: issues and

673   opportunities. *Journal of Animal Ecology*, *73*(3), 585–598.

674 Boecklen, W. J., Yarnes, C. T., Cook, B. A., & James, A. C. (2011). On the use of

675   stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and*

676   *Systematics*, *42*(1), 411–440. https://doi.org/10.1146/annurev-ecolsys-

677   102209-144726

678 Boggs, C. L., & Inouye, D. W. (2012). A single climate driver has direct and indirect

679   effects on insect population dynamics. *Ecology Letters*, *15*(5), 502–508.

680   https://doi.org/10.1111/j.1461-0248.2012.01766.x

681 Bojorquez, A., Alvarez-Yepiz, J. C., Burquez, A., & Martinez-Yrizar, A. (2019).

682   Understanding and predicting frost-induced tropical tree mortality patterns.

683   *Global Change Biology*. https://doi.org/10.1111/gcb.14775

684 Both, C., Van Asch, M., Bijlsma, R. G., Van Den Burg, A. B., & Visser, M. E. (2009).

685   Climate change and unequal phenological changes across four trophic levels:

686   constraints or adaptations? *Journal of Animal Ecology*, *78*(1), 73–83.

687 Brokaw, N. V., & Grear, J. S. (1991). Forest structure before and after Hurricane

688   Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica*,

689   *23*(4 PART A).

690 Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over

691   120 years: loss of species, co-occurrence, and function. *Science*, *339*(6127),

692   1611–1615. https://doi.org/10.1126/science.1232728

693   CaraDonna, P. J., Petry, W. K., Brennan, R. M., Cunningham, J. L., Bronstein, J. L.,

694   Waser, N. M., & Sanders, N. J. (2017). Interaction rewiring and the rapid

695   turnover of plant–pollinator networks. *Ecology Letters*, *20*(3), 385–394.

696   https://doi.org/10.1111/ele.12740

697   Carreon-Martinez, L., & Heath, D. D. (2010). Revolution in food web analysis and

698   trophic ecology: diet analysis by DNA and stable isotope analysis. *Molecular*

699   *Ecology*, *19*(1), 25–27. https://doi.org/10.1111/j.1365-294X.2009.04412.x

700   Ceneviva-Bastos, M., Casatti, L., & Uieda, V. S. (2012). Can seasonal differences

701   influence food web structure on preserved habitats? Responses from two

702   Brazilian streams. *Community Ecology*, *13*(2), 243–252. Retrieved from

703   JSTOR.

704   Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L.

705   H. (2019). The mechanisms of phenology: the patterns and processes of

706   phenological shifts. *Ecological Monographs*, *89*(1), e01337.

707   https://doi.org/10.1002/ecm.1337

708   Cleland, E. E., Chiariello, N. R., Loarie, S. R., Mooney, H. A., & Field, C. B. (2006).

709   Diverse responses of phenology to global changes in a grassland ecosystem.

710   *Proceedings of the National Academy of Sciences*, *103*(37), 13740–13744.

711   https://doi.org/10.1073/pnas.0600815103

712   Closs, G. P., & Lake, P. S. (1994). Spatial and temporal variation in the structure of

713   an intermittent-stream food web. *Ecological Monographs*, *64*(1), 2–21. https://

714   doi.org/10.2307/2937053

715   Collins, S. L., Belnap, J., Grimm, N. B., Rudgers, J. A., Dahm, C. N., D'Odorico, P., …

716   Wolf, B. O. (2014). A multiscale, hierarchical model of pulse dynamics in arid-

717   land ecosystems. *Annual Review of Ecology, Evolution, and Systematics*,

718   *45*(1), 397–419. https://doi.org/10.1146/annurev-ecolsys-120213-091650

719 Colwell, R. K., & Rangel, T. F. (2009). Hutchinson's duality: the once and future

720   niche. *Proceedings of the National Academy of Sciences*, *106*(Supplement 2),

721   19651–19658.

722 Cooper, S. D., Page, H. M., Wiseman, S. W., Klose, K., Bennett, D., Even, T., …

723   Dudley, T. L. (2015). Physicochemical and biological responses of streams to

724   wildfire severity in riparian zones. *Freshwater Biology*, *60*(12), 2600–2619.

725   https://doi.org/10.1111/fwb.12523

726 Corse, E., Costedoat, C., Chappaz, R., Pech, N., Martin, J.-F., & Gilles, A. (2010). A

727   PCR-based method for diet analysis in freshwater organisms using 18S rDNA

728   barcoding on faeces. *Molecular Ecology Resources*, *10*(1), 96–108.

729   https://doi.org/10.1111/j.1755-0998.2009.02795.x

730 Crain, B. J., Tremblay, R. L., & Ferguson, J. M. (2019). Sheltered from the storm?

731   Population viability analysis of a rare endemic under periodic catastrophe

732   regimes. *Population Ecology*, *61*(1), 74–92. https://doi.org/10.1002/1438-

733   390X.1002

734 Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant

735   communities: a general theory of invasibility. *Journal of Ecology*, *88*(3), 528–

736   534.

737 De Cáceres, M., Coll, L., Legendre, P., Allen, R. B., Wiser, S. K., Fortin, M.-J., …

738   Hubbell, S. (2019). Trajectory analysis in community ecology. *Ecological*

739   *Monographs*, *89*(2), e01350. https://doi.org/10.1002/ecm.1350

740   del Arroyo, O. G., & Silver, W. L. (2018). Disentangling the long-term effects of

741   disturbance on soil biogeochemistry in a wet tropical forest ecosystem.

742   *Global Change Biology*, *24*(4), 1673–1684. https://doi.org/10.1111/gcb.14027

743   Dunne, J. A. (2006). The network structure of food webs. In M. Pascual & J. Dunne

744   (Eds.), *Ecological Networks: Linking Structure to Dynamics in Food Webs* (pp.

745   27–86). Oxford: Oxford University Press.

746   Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns,

747   L. O. (2000). Climate extremes: observations, modeling, and impacts.

748   *Science*, *289*(5487), 2068–2074.

749   Edwards, C. B., & Yang, L. (2018). Evolved phenological cueing strategies show

750   variable responses to climate change. *BioRxiv*, 436857.

751   https://doi.org/10.1101/436857

752   Elsner, J. B., Kossin, J. P., & Jagger, T. H. (2008). The increasing intensity of the

753   strongest tropical cyclones. *Nature*, *455*(7209), 92–95.

754   https://doi.org/10.1038/nature07234

755   Elton, C. S. (1927). *Animal Ecology*. London: Sidgwick and Jackson.

756   Farzan, S., & Yang, L. H. (2018). Experimental shifts in phenology affect fitness,

757   foraging, and parasitism in a native solitary bee. *Ecology*, *99*(10), 2187–2195.

758   https://doi.org/10.1002/ecy.2475

759   Forrest, J., & Miller-Rushing, A. J. (2010). Toward a synthetic understanding of the

760   role of phenology in ecology and evolution. *Philosophical Transactions of the*

761   *Royal Society B: Biological Sciences*, *365*(1555), 3101–3112.

762   https://doi.org/10.1098/rstb.2010.0145

763   Forrest, J. R. (2016). Complex responses of insect phenology to climate change.

764   *Current Opinion in Insect Science*, *17*, 49–54.

765   https://doi.org/10.1016/j.cois.2016.07.002

766   Forrest, J. R. K., Cross, R., & CaraDonna, P. J. (2019). Two-year bee, or not two-year

767   bee? How voltinism is affected by temperature and season length in a high-

768   elevation solitary bee. *The American Naturalist*, *193*(4), 560–574.

769   https://doi.org/10.1086/701826

770   Gallinat, A. S., Primack, R. B., & Wagner, D. L. (2015). Autumn, the neglected

771   season in climate change research. *Trends in Ecology & Evolution*, *30*(3),

772   169–176. https://doi.org/10.1016/j.tree.2015.01.004

773   Gibbs, H. L., & Grant, P. R. (1987). Ecological consequences of an exceptionally

774   strong El Niño event on Darwin's finches. *Ecology*, *68*(6).

775   Gibert, J. P., & DeLong, J. P. (2017). Phenotypic variation explains food web

776   structural patterns. *Proceedings of the National Academy of Sciences of the*

777   *United States of America*, *114*(42), 11187–11192.

778   https://doi.org/10.1073/pnas.1703864114

779   Goswami, B. N., Venugopal, V., Sengupta, D., Madhusoodanan, M. S., & Xavier, P. K.

780   (2006). Increasing trend of extreme rain events over India in a warming

781   environment. *Science*, *314*(5804), 1442–1445.

782   Grant, P. R., & B.R. Grant. (1996). Finch communities in a climatically fluctuating

783   environment. In M. L. Cody & J.A. Smallwood (Eds.), *Long-term studies of*

784   *vertebrate communities* (pp. 343–390). San Diego: Academic Press.

785   Grant, P. R., & Grant, B. R. (1987). The extraordinary El Niño event of 1982-1983:

786   effects on Darwin's finches on Isla Genovesa, Galapagos. *Oikos*, *49*(1), 55–66.

787   Grant, P. R., Grant, B. R., Keller, L. F., & Petren, K. (2000). Effects of El Niño events

788   on Darwin's finch productivity. *Ecology*, *81*(9), 2442–2457.

789   Grinnell, J. (1917). The niche-relationships of the California Thrasher. *The Auk*,

790   *34*(4), 427–433. https://doi.org/10.2307/4072271

791   Groisman, P. Y., Knight, R. W., Easterling, D. R., Karl, T. R., Hegerl, G. C., &

792   Razuvaev, V. A. N. (2005). Trends in intense precipitation in the climate

793   record. *Journal of Climate*, *18*(9), 1326–1350.

794   Hale, S., Nimmo, D. G., Cooke, R., Holland, G., James, S., Stevens, M., … White, J. G.

795   (2016). Fire and climatic extremes shape mammal distributions in a fire-

796   prone landscape. *Diversity and Distributions*, *22*(11), 1127–1138.

797   https://doi.org/10.1111/ddi.12471

798   Hall, S. J., & Raffaelli, D. (1997). Food-web patterns: What do we really know? In A.

799   C. Gange & V. K. Brown (Eds.), *Multitrophic Interactions in Terrestrial*

800   *Systems*. Cambridge University Press.

801   Hardy, C. M., Krull, E. S., Hartley, D. M., & Oliver, R. L. (2010). Carbon source

802   accounting for fish using combined DNA and stable isotope analyses in a

803   regulated lowland river weir pool. *Molecular Ecology*, *19*(1), 197–212. https://

804   doi.org/10.1111/j.1365-294X.2009.04411.x

805   Hart, D. R., Stone, L., & Berman, T. (2000). Seasonal dynamics of the Lake Kinneret

806   food web: The importance of the microbial loop. *Limnology and*

807   *Oceanography*, *45*(2), 350–361. https://doi.org/10.4319/lo.2000.45.2.0350

808   Hastings, A. (2004). Transients: the key to long-term ecological understanding?

809   *Trends in Ecology & Evolution*, *19*(1), 39–45.

810   Holmgren, M., Scheffer, M., Ezcurra, E., Gutierrez, J. R., & Mohren, G. M. J. (2001). El

811   Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology &*

812   *Evolution*, *16*(2), 89–94.

813   Holmgren, M., Stapp, P., Dickman, C. R., Gracia, C., Grahams, S., Gutierrez, J. R., …

814   Squeo, F. A. (2006). Extreme climatic events shape arid and semiarid

815   ecosystems. *Frontiers in Ecology and the Environment*, *4*(2), 87–95.

816   Holt, R. D. (1977). Predation, apparent competition, and the structure of prey

817   communities. *Theoretical Population Biology*, *12*(2), 197–229. https://doi.org/

818   doi: DOI: 10.1016/0040-5809(77)90042-9

819   Holt, R. D. (2008). Theoretical perspectives on resource pulses. *Ecology*, *89*(3), 671–

820   681.

821   Høye, T. T., Post, E., Schmidt, N. M., Trøjelsgaard, K., & Forchhammer, M. C. (2013).

822   Shorter flowering seasons and declining abundance of flower visitors in a

823   warmer Arctic. *Nature Climate Change*, *3*(8), 759–763.

824   https://doi.org/10.1038/nclimate1909

825   Hua, F., Hu, J., Liu, Y., Giam, X., Lee, T. M., Luo, H., … Zhu, J. (2016). Community-

826   wide changes in intertaxonomic temporal co-occurrence resulting from

827   phenological shifts. *Global Change Biology*, *22*(5), 1746–1754. https://doi.org/

828   10.1111/gcb.13199

829   Hunter, M. D., & Forkner, R. E. (1999). Hurricane damage influences foliar

830   polyphenolics and subsequent herbivory on surviving trees. *Ecology*, *80*(8),

831   2676–2682.

832   Hunter, M. D., & Price, P. W. (1992). Playing chutes and ladders: heterogeneity and

833   the relative roles of bottom-up and top-down forces in natural communities.

834   *Ecology*, *73*(3), 724–732. https://doi.org/10.2307/1940152

835   Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on*

836   *Quantitative Biology*, *22*, 415–427.

837   https://doi.org/10.1101/SQB.1957.022.01.039

838   Inouye, B. D., Ehrlén, J., & Underwood, N. (2019). Phenology as a process rather

839   than an event: from individual reaction norms to community metrics.

840   *Ecological Monographs*, *89*(2), e01352. https://doi.org/10.1002/ecm.1352

841   IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working*

842   *Groups I, II and III to the Fifth Assessment Report of the Intergovernmental*

843   *Panel on Climate Change* (p. 151 pp). Geneva, Switzerland: IPCC.

844   Jensen, T. (1982). Seed production and outbreaks of non-cyclic rodent populations

845   in deciduous forests. *Oecologia*, *54*, 184–192.

846   Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-

847   change experiments: events, not trends. *Frontiers in Ecology and the*

848   *Environment*, *5*(7), 365–374.

849   Jentsch, A., Kreyling, J., Boettcher-Treschkow, J., & Beierkuhnlein, C. (2009). Beyond

850   gradual warming: extreme weather events alter flower phenology of

851   European grassland and heath species. *Global Change Biology*, *15*(4), 837–

852   849.

853   Jones, C. G., Ostfeld, R. S., Richard, M. P., Schauber, E. M., & Wolff, J. O. (1998).

854   Chain reactions linking acorns to gypsy moth outbreaks and lyme disease

855   risk. *Science*, *279*, 1023–1026.

856   Jordan, F., & Osvath, G. (2009). The sensitivity of food web topology to temporal

857   data aggregation. *Ecological Modelling*, *220*(22), 3141–3146.

858   https://doi.org/10.1016/j.ecolmodel.2009.05.002

859   Kenny, H. V., Wright, A. N., Piovia-Scott, J., Yang, L. H., Spiller, D. A., & Schoener, T.

860   W. (2017). Marine subsidies change short-term foraging activity and habitat

861   utilization of terrestrial lizards. *Ecology and Evolution*, *7*(24), 10701–10709.

862   https://doi.org/10.1002/ece3.3560

863   Kharouba, H. M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J. M., Travers, S. E., &

864   Wolkovich, E. M. (2018). Global shifts in the phenological synchrony of

865   species interactions over recent decades. *Proceedings of the National*

866   *Academy of Sciences*, 201714511. https://doi.org/10.1073/pnas.1714511115

867   Kitching, R. L. (1987). Spatial and temporal variation in food webs in water-filled

868   treeholes. *Oikos*, *48*(3), 280–288. https://doi.org/10.2307/3565515

869   Kondoh, M. (2003). Foraging adaptation and the relationship between food-web

870   complexity and stability. *Science*, *299*(5611), 1388–1391.

871   https://doi.org/10.1126/science.1079154

872   Kossin, J. P. (2018). A global slowdown of tropical-cyclone translation speed. *Nature*,

873   *558*(7708), 104–107. https://doi.org/10.1038/s41586-018-0158-3

874   Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O., & Dobson, F. S. (2012).

875   Delayed phenology and reduced fitness associated with climate change in a

876   wild hibernator. *Nature*, *489*(7417), 554–557.

877   https://doi.org/10.1038/nature11335

878   Lawton, J. H. (1999). Are There General Laws in Ecology? *Oikos*, *84*(2), 177–192.

879   Layer, K., Hildrew, A., Monteith, D., & Woodward, G. (2010). Long-term variation in

880   the littoral food web of an acidified mountain lake. *Global Change Biology*,

881   *16*(11), 3133–3143. https://doi.org/10.1111/j.1365-2486.2010.02195.x

882 Leriorato, J. C., & Nakamura, Y. (2019). Unpredictable extreme cold events: a threat

883   to range-shifting tropical reef fishes in temperate waters. *Marine Biology*,

884   *166*(8), 110. https://doi.org/10.1007/s00227-019-3557-6

885 Little, A. G., Fisher, D. N., Schoener, T. W., & Pruitt, J. N. (2019). Population

886   differences in aggression are shaped by tropical cyclone-induced selection.

887   *Nature Ecology & Evolution*, *3*(9), 1294–1297. https://doi.org/10.1038/s41559-

888   019-0951-x

889 Lloren, J. I., Fahrig, L., Bennett, J. R., Contreras, T. A., & McCune, J. L. (2019). The

890   influence of landscape context on short- and long-term forest change

891   following a severe ice storm. *Journal of Ecology*. https://doi.org/10.1111/1365-

892   2745.13255

893 Martinez, N. D. (1991). Artifacts or attributes - effects of resolution on the Little Rock

894   Lake food web. *Ecological Monographs*, *61*(4), 367–392.

895 McCann, K. S., Rasmussen, J. B., & Umbanhowar, J. (2005). The dynamics of spatially

896   coupled food webs. *Ecology Letters*, *8*(5), 513–523.

897   https://doi.org/10.1111/j.1461-0248.2005.00742.x

898 McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of

899   catastrophic avian mortality events during extreme heat waves. *Biology

900   Letters*, *6*(2), 253–256. https://doi.org/10.1098/rsbl.2009.0702

901 McMeans, B. C., McCann, K. S., Humphries, M., Rooney, N., & Fisk, A. T. (2015). Food

902   web structure in temporally-forced ecosystems. *Trends in Ecology &

903   Evolution*, *30*(11), 662–672. https://doi.org/10.1016/j.tree.2015.09.001

904 Meserve, P. L., Kelt, D. A., Milstead, W. B., & Gutierrez, J. R. (2003). Thirteen years of

905   shifting top-down and bottom-up control. *Bioscience*, *53*(7), 633–646.

906   Muybridge, E. (1887). *Animal Locomotion: An Electro-Photographic Investigation of*

907   *Consecutive Phases of Animal Movements: Prospectus and Catalogue of*

908   *Plates*. Philadelphia: J.B. Lippincott Co.

909   Nakazawa, T., & Doi, H. (2012). A perspective on match/mismatch of phenology in

910   community contexts. *Oikos*, *121*(4), 489–495. https://doi.org/10.1111/j.1600-

911   0706.2011.20171.x

912   Nielsen, J. M., Clare, E. L., Hayden, B., Brett, M. T., & Kratina, P. (2018). Diet tracing

913   in ecology: Method comparison and selection. *Methods in Ecology and*

914   *Evolution*, *9*(2), 278–291. https://doi.org/10.1111/2041-210X.12869

915   Nowicki, R., Heithaus, M., Thomson, J., Burkholder, D., Gastrich, K., & Wirsing, A.

916   (2019). Indirect legacy effects of an extreme climatic event on a marine

917   megafaunal community. *Ecological Monographs*, *89*(3), UNSP e01365. https://

918   doi.org/10.1002/ecm.1365

919   Ogilvie, J. E., Griffin, S. R., Gezon, Z. J., Inouye, B. D., Underwood, N., Inouye, D. W.,

920   & Irwin, R. E. (2017). Interannual bumble bee abundance is driven by indirect

921   climate effects on floral resource phenology. *Ecology Letters*, *20*(12), 1507–

922   1515. https://doi.org/10.1111/ele.12854

923   Oksanen, L. (2001). Logic of experiments in ecology: Is pseudoreplication a

924   pseudoissue? *Oikos*, *94*(1), 27–38.

925   Olesen, J. M., Bascompte, J., Elberling, H., & Jordano, P. (2008). Temporal dynamics

926   in a pollination network. *Ecology*, *89*(6), 1573–1582.

927   https://doi.org/10.1890/07-0451.1

928   Ostfeld, R. S., & Keesing, F. (2000). Pulsed resources and community dynamics of

929   consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, *15*(6),

930   232–237.

931 Paine, R. T. (1988). Road maps of interactions or grist for theoretical development?

932   *Ecology*, *69*(6), 1648–1654. https://doi.org/10.2307/1941141

933 Parmesan, C. (2006). Ecological and evolutionary responses to recent climate

934   change. *Annual Review of Ecology Evolution and Systematics*, *37*, 637–669.

935 Parmesan, C., Root, T. L., & Willig, M. R. (2000). Impacts of extreme weather and

936   climate on terrestrial biota. *Bulletin of the American Meteorological Society*,

937   *81*(3), 443–450.

938 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change

939   impacts across natural systems. *Nature*, *421*(6918), 37–42.

940 Pau, S., Wolkovich, E. M., Cook, B. I., Davies, T. J., Kraft, N. J. B., Bolmgren, K., …

941   Cleland, E. E. (2011). Predicting phenology by integrating ecology, evolution

942   and climate science. *Global Change Biology*, *17*(12), 3633–3643.

943   https://doi.org/10.1111/j.1365-2486.2011.02515.x

944 Piovia-Scott, J., Spiller, D. A., Takimoto, G., Yang, L. H., Wright, A. N., & Schoener, T.

945   W. (2013). The effect of chronic seaweed subsidies on herbivory: plant-

946   mediated fertilization pathway overshadows lizard-mediated predator

947   pathways. *Oecologia*, *172*(4), 1129–1135.

948 Piovia-Scott, J., Yang, L. H., & Wright, A. N. (2017). Temporal variation in trophic

949   cascades. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 281–

950   300. https://doi.org/10.1146/annurev-ecolsys-121415-032246

951 Piovia-Scott, J., Yang, L. H., Wright, A. N., Spiller, D. A., & Schoener, T. W. (2019).

952   Pulsed seaweed subsidies drive sequential shifts in the effects of lizard

953   predators on island food webs. *Ecology Letters*.

954   https://doi.org/10.1111/ele.13377

955 Polis, G. A. (1991). Complex trophic interactions in deserts: an empirical critique of

956   food-web theory. *American Naturalist*, *138*(1), 123–155.

957 Polis, G. A., Hurd, S. D., Jackson, C. T., & Piñero, F. S. (1997). El Niño effects on the

958   dynamics and control of an island ecosystem in the Gulf of California.

959   *Ecology*, *78*(6), 1184–1897.

960 Polis, G. A., & Strong, D. R. (1996). Food web complexity and community dynamics.

961   *American Naturalist*, *147*(5), 813-846.

962 Pompanon, F., Deagle, B. E., Symondson, W. O., Brown, D. S., Jarman, S. N., &

963   Taberlet, P. (2012). Who is eating what: diet assessment using next

964   generation sequencing. *Molecular Ecology*, *21*(8), 1931–1950.

965 Post, E. (2019). *Time in Ecology: A Theoretical Framework*. Retrieved from

966   www.jstor.org/stable/j.ctv3s8sns

967 Power, M. E. (1992). Top-down and bottom-up forces in food webs: do plants have

968   primacy? *Ecology*, *73*, 733–746.

969 Rafferty, N. E., & Ives, A. R. (2011). Effects of experimental shifts in flowering

970   phenology on plant–pollinator interactions. *Ecology Letters*, *14*(1), 69–74.

971   https://doi.org/10.1111/j.1461-0248.2010.01557.x

972 Rahel, F. J. (1990). The hierarchical nature of community persistence: a problem of

973   scale. *The American Naturalist*, *136*(3), 328–344.

974   https://doi.org/10.1086/285101

975 Rivas, M. L., Spinola, M., Arrieta, H., & Faife-Cabrera, M. (2018). Effect of extreme

976   climatic events resulting in prolonged precipitation on the reproductive

977   output of sea turtles. *Animal Conservation*, *21*(5), 387–395.

978   https://doi.org/10.1111/acv.12404

979 Roughgarden, J., May, R., & Levin, S. (1989). Introduction. In J. Roughgarden, R.

980   May, & S. Levin (Eds.), *Perspectives in Ecological Theory* (pp. 3–10). Retrieved

981   from http://www.jstor.org/stable/j.ctt7zv1xs.3

982 Sankaran, M. (2019). Droughts and the ecological future of tropical savanna

983   vegetation. *Journal of Ecology*, *107*(4), 1531–1549.

984   https://doi.org/10.1111/1365-2745.13195

985 Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic

986   shifts in ecosystems. *Nature*, *413*(6856), 591–596.

987 Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems:

988   linking theory to observation. *Trends in Ecology & Evolution*, *18*(12), 648–

989   656.

990 Schoener, T. W., Spiller, D. A., & Losos, J. B. (2001). Natural restoration of the

991   species-area relation for a lizard after a hurricane. *Science*, *294*(5546), 1525–

992   1528.

993 Schoener, T. W., Spiller, D. A., & Losos, J. B. (2004). Variable ecological effects of

994   hurricanes: The importance of seasonal timing for survival of lizards on

995   Bahamian islands. *Proceedings of the National Academy of Sciences of the*

996   *United States of America*, *101*(1), 177–181.

997   https://doi.org/10.1073/pnas.0306887101

998 Schoenly, K., & Cohen, J. E. (1991). Temporal variation in food web structure - 16

999   empirical cases. *Ecological Monographs*, *61*(3), 267–298.

1000 Schroder, A., Persson, L., & De Roos, A. (2005). Direct experimental evidence for

1001   alternative stable states: a review. *Oikos*, *110*, 3–19.

1002   Sergio, F., Blas, J., & Hiraldo, F. (2018). Animal responses to natural disturbance and

1003   climate extremes: a review. *Global and Planetary Change*, *161*, 28–40.

1004   https://doi.org/10.1016/j.gloplacha.2017.10.009

1005   Sherry, R. A., Zhou, X., Gu, S., Arnone, J. A., Schimel, D. S., Verburg, P. S., … Luo, Y.

1006   (2007). Divergence of reproductive phenology under climate warming.

1007   *Proceedings of the National Academy of Sciences*, *104*(1), 198–202.

1008   https://doi.org/10.1073/pnas.0605642104

1009   Siegle, M. R., Taylor, E. B., & O'Connor, M. I. (2018). Prior heat accumulation

1010   reduces survival during subsequent experimental heat waves. *Journal of*

1011   *Experimental Marine Biology and Ecology*, *501*, 109–117.

1012   https://doi.org/10.1016/j.jembe.2018.012

1013   Spiller, D. A., & Agrawal, A. (2003). Intense disturbance enhances plant

1014   susceptibility to herbivory: natural and experimental evidence. *Ecology*,

1015   *84*(4), 890–897.

1016   Spiller, D. A., Piovia-Scott, J., Wright, A. N., Yang, L. H., Takimoto, G., Schoener, T.

1017   W., & Iwata, T. (2010). Marine subsidies have multiple effects on coastal food

1018   webs. *Ecology*, *91*(5), 1424–1434. https://doi.org/10.1890/09-0715.1

1019   Spiller, D. A., & Schoener, T. W. (2007). Alteration of island food-web dynamics

1020   following major disturbance by hurricanes. *Ecology*, *88*(1), 37–41.

1021   Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., …

1022   Rich, L. N. (2017). Scaling-up camera traps: monitoring the planet's

1023   biodiversity with networks of remote sensors. *Frontiers in Ecology and the*

1024   *Environment*, *15*(1), 26–34. https://doi.org/10.1002/fee.1448

1025   Stuble, K. L., Fick, S. E., & Young, T. P. (2017a). Every restoration is unique: testing

1026   year effects and site effects as drivers of initial restoration trajectories.

1027   *Journal of Applied Ecology*, *54*(4), 1051–1057. https://doi.org/10.1111/1365-

1028   2664.12861

1029   Stuble, K. L., Zefferman, E. P., Wolf, K. M., Vaughn, K. J., & Young, T. P. (2017b).

1030   Outside the envelope: rare events disrupt the relationship between climate

1031   factors and species interactions. *Ecology*, *98*(6), 1623–1630.

1032   https://doi.org/10.1002/ecy.1820

1033   Takimoto, G. (2003). Adaptive plasticity in ontogenetic niche shifts stabilizes

1034   consumer-resource dynamics. *The American Naturalist*, *162*(1), 93–109.

1035   Takimoto, G., Iwata, T., & Murakami, M. (2009). Timescale hierarchy determines the

1036   indirect effects of fluctuating subsidy inputs on in situ resources. *American*

1037   *Naturalist*, *173*(2), 200–211.

1038   Tavares-Cromar, A. F., & Williams, D. D. (1996). The importance of temporal

1039   resolution in food web analysis: Evidence from a detritus-based stream.

1040   *Ecological Monographs*, *66*(1), 91–113. https://doi.org/10.2307/2963482

1041   Thomas, A., Dietrich, J. C., Asher, T. G., Bell, M., Blanton, B. O., Copeland, J. H., …

1042   Luettich, R. A. (2019). Influence of storm timing and forward speed on tides

1043   and storm surge during Hurricane Matthew. *Ocean Modelling*, *137*, 1–19.

1044   https://doi.org/10.1016/j.ocemod.2019.03.004

1045   Thompson, R. M., & Townsend, C. R. (1999). The effect of seasonal variation on the

1046   community structure and food-web attributes of two streams: implications for

1047   food-web science. *Oikos*, *87*(1), 75–88.

1048   Ujvari, B., Brown, G., Shine, R., & Madsen, T. (2016). Floods and famine: climate-

1049   induced collapse of a tropical predator-prey community. *Functional Ecology*,

1050   *30*(3), 453–458. https://doi.org/10.1111/1365-2435.12505

1051   Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events

1052   with ecological relevance: a review. *Philosophical Transactions of the Royal*

1053   *Society B-Biological Sciences*, *372*(1723), 20160135.

1054   https://doi.org/10.1098/rstb.2016.0135

1055   Valdés, A., & Ehrlén, J. (2017). Caterpillar seed predators mediate shifts in selection

1056   on flowering phenology in their host plant. *Ecology*, *98*(1), 228–238.

1057   https://doi.org/10.1002/ecy.1633

1058   Vaughn, K. J., & Young, T. P. (2010). Contingent conclusions: year of initiation

1059   influences ecological field experiments, but temporal replication is rare.

1060   *Restoration Ecology*, *18*(s1), 59–64.

1061   Visser, M. E., Caro, S. P., Oers, K. van, Schaper, S. V., & Helm, B. (2010). Phenology,

1062   seasonal timing and circannual rhythms: towards a unified framework.

1063   *Philosophical Transactions of the Royal Society B: Biological Sciences*,

1064   *365*(1555), 3113–3127. https://doi.org/10.1098/rstb.2010.0111

1065   Warren, P. H. (1989). Spatial and temporal variation in the structure of a freshwater

1066   food web. *Oikos*, *55*(3), 299–311.

1067   Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies,

1068   T., … Rousseaux, C. S. (2013). An extreme climatic event alters marine

1069   ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*,

1070   *3*(1), 78–82. https://doi.org/10.1038/NCLIMATE1627

1071   Whiles, M. R., Callaham, M. A., Meyer, C. K., Brock, B. L., & Charlton, R. E. (2001).

1072   Emergence of periodical cicadas (*Magicicada cassini*) from a Kansas riparian

1073   forest: densities, biomass and nitrogen flux. *American Midland Naturalist*,

1074   *145*(1), 176–187.

1075 Williams, K. S., & Simon, C. (1995). The ecology, behavior, and evolution of

1076   periodical cicadas. *Annual Review of Entomology*, *40*, 269–295.

1077 Williams, K. S., Smith, K. G., & Stephen, F. M. (1993). Emergence of 13-yr periodical

1078   cicadas (Cicadidae, *Magicicada*) - phenology, mortality, and predator

1079   satiation. *Ecology*, *74*(4), 1143–1152.

1080 Williams, R. J., & Martinez, N. D. (2000). Simple rules yield complex food webs.

1081   *Nature (London)*, *404*(6774).

1082 Wolkovich, E. M., Allesina, S., Cottingham, K. L., Moore, J. C., Sandin, S. A., & de

1083   Mazancourt, C. (2014a). Linking the green and brown worlds: the prevalence

1084   and effect of multichannel feeding in food webs. *Ecology*, *95*(12), 3376–3386.

1085   https://doi.org/10.1890/13-1721.1

1086 Wolkovich, E. M., & Cleland, E. E. (2011). The phenology of plant invasions: a

1087   community ecology perspective. *Frontiers in Ecology and the Environment*,

1088   *9*(5), 287–294. https://doi.org/10.1890/100033

1089 Wolkovich, E. M., & Cleland, E. E. (2014). Phenological niches and the future of

1090   invaded ecosystems with climate change. *AoB PLANTS*, *6*.

1091   https://doi.org/10.1093/aobpla/plu013

1092 Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers,

1093   S. E., … Cleland, E. E. (2012). Warming experiments underpredict plant

1094   phenological responses to climate change. *Nature*.

1095   https://doi.org/10.1038/nature11014

1096 Wolkovich, E. M., Cook, B. I., McLauchlan, K. K., & Davies, T. J. (2014b). Temporal

1097   ecology in the Anthropocene. *Ecology Letters*, *17*(11), 1365–1379.

1098   https://doi.org/10.1111/ele.12353

1099   Woodward, G., Bonada, N., Feeley, H. B., & Giller, P. S. (2015). Resilience of a

1100   stream community to extreme climatic events and long-term recovery from a

1101   catastrophic flood. *Freshwater Biology*, *60*(12), 2497–2510.

1102   https://doi.org/10.1111/fwb.12592

1103   Wright, A. N., Piovia-Scott, J., Spiller, D. A., Takimoto, G., Yang, L. H., & Schoener, T.

1104   W. (2013). Pulses of marine subsidies amplify reproductive potential of lizards

1105   by increasing individual growth rate. *Oikos*, *122*(10), 1496–1504.

1106   https://doi.org/10.1111/j.1600-0706.2013.00379.x

1107   Yang, L. H. (2004). Periodical cicadas as resource pulses in North American forests.

1108   *Science*, *306*(5701), 1565–1567.

1109   Yang, L. H. (2008). Pulses of dead periodical cicadas increase herbivory of American

1110   bellflowers. *Ecology*, *89*(6), 1497–1502.

1111   Yang, L. H. (2013). Resource pulses of dead periodical cicadas increase the growth

1112   of American bellflower rosettes under competitive and non-competitive

1113   conditions. *Arthropod-Plant Interactions*, *7*(1), 1–6.

1114   https://doi.org/10.1007/s11829-012-9223-2

1115   Yang, L. H., Bastow, J. L., Spence, K. O., & Wright, A. N. (2008). What can we learn

1116   from resource pulses? *Ecology*, *89*(3), 621–634.

1117   Yang, L. H., & Cenzer, M. L. (2020). Seasonal windows of opportunity in milkweed-

1118   monarch interactions. *Ecology*, *101*(1). Retrieved from

1119   https://doi.org/10.1002/ecy.2880

1120   Yang, L. H., Edwards, K., Byrnes, J. E., Bastow, J. L., Wright, A. N., & Spence, K. O.

1121   (2010). A meta-analysis of resource pulse-consumer interactions. *Ecological*

1122   *Monographs*, *80*(1), 125–151.

1123   Yang, L. H., & Karban, R. (2009). Long-term habitat selection and chronic root

1124   herbivory: explaining the relationship between periodical cicada density and

1125   tree growth. *American Naturalist*, *173*(1), 105–112.

1126   Yang, L. H., & Karban, R. (2019). The effects of pulsed fertilization and chronic

1127   herbivory by periodical cicadas on tree growth. *Ecology*, *100*(6), e02705.

1128   https://doi.org/10.1002/ecy.2705

1129   Yang, L. H., & Rudolf, V. (2010). Phenology, ontogeny and the timing of species

1130   interactions. *Ecology Letters*, *13*(1), 1–10.

1131   Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., & Coomes, D. (2019). Advances

1132   in microclimate ecology arising from remote sensing. *Trends in Ecology &*

1133   *Evolution*, *34*(4), 327–341. https://doi.org/10.1016/j.tree.2018.12.012

1134

1135 **Figure 1.** (a) Pre-1872 paintings illustrating the "flying gallop" posture (row-wise

1136 from the top left): *A Grey Horse Galloping in a Field* by George Stubbs; *Baronet with*

1137 *Samuel Chifney up* by George Stubbs; *A Grey Arab Stallion Galloping with Dogs* by

1138 Alfred de Dreux; *Galloping Horse* by Alfred de Dreux; *Foxhunting, Encouraging*

1139 *Hounds* by John Frederick Herring, Sr.; *The Baron with Bumpy Up at Newmarket* by

1140 John Frederick Herring, Sr,; *Yoi Yoi! At Him Hannibal* by Henry Thomas Alken, Sr.; *On*

1141 *the Scent Foxhunting* by Samuel Henry Alken; *Wild Dayrell, Winner of the Epsom*

1142 *Derby, 1855* by Samuel Henry Alken; *Thomas Mellish on Saucebox* by Benjamin

1143 Marshall; *Le Derby de 1821 à Epsom* by Theodore Gericault; *Mameluke Horse* by

1144 Carle Vernet. (b) *The Horse in Motion* by Eadweard Muybridge.

1145 **Figure 2.** (a) A hypothetical species interaction network. Because taxonomically

1146 well-resolved datasets often reflect compiled observations of species interactions

1147 accumulated over many years of detailed study, the resulting network structure

1148 may not accurately represent the realized structure of species interactions at any

1149 single point in time. (b) A diagram of phenology in a community context. One way

1150 to add an explicit temporal dimension to interaction networks would be to examine

1151 the changing structure of interaction networks during specific slices of time. The

1152 data requirements for this kind of analysis are high; here we show hypothetical

1153 patterns of development for six species in a community (shown on the vertical axis)

1154 over twelve time points (shown on the horizontal axis). Here, we interpret this figure

1155 on an annual scale, with time steps corresponding to months in a year, in order to

1156 examine seasonal changes in the structure of species interactions. However, this

1157 approach could also be applied to other timescales; for example, these time points

1158 could represent intervals in a daily cycle if examining diel changes in community

1159   composition or larger timescales (e.g., years or decades) if examining changes in

1160   the structure of species interactions over an inter-annual timescale. Each species is

1161   represented by a hue; within each species, developmental stages are represented

1162   by differences in saturation. The absence of a species at particular time point

1163   corresponds to periods of relatively low interactivity in the community; on different

1164   timescales, these periods of low interactivity could be caused by dormancy,

1165   diapause, seasonal migration or local extinction, for example. (c) A temporally

1166   explicit network representation of stage-structured species interactions over time

1167   (see also Yang & Rudolf, 2010). The graph in each frame represents the structure of

1168   species interactions in the community at a single time point; the set of graphs

1169   together represents the temporal dynamics of species interactions in the

1170   community. Point size corresponds to the developmental stage of each interacting

1171   species. (d) An alternative diagram of phenology in a community context, with

1172   phenological shifts from the diagram shown in panel *b*. These phenological shifts

1173   are consistent with the range of observed phenological responses to climate

1174   change. In this alternative diagram, species 1 and 6 show unchanged phenological

1175   trajectories. Species 2 shows an advancement of one time step, while species 3

1176   shows a phenological delay of one time step. Species 4 shows a change from one

1177   generation to two generations per year, while species 5 shows an accelerated,

1178   temporally compressed developmental phenology. (e) A temporally explicit

1179   network representation of stage-structured species interactions over time

1180   corresponding to the alternative dataset shown in panel *d*. In this figure, the

1181   structure and dynamics of species interactions have changed in multiple ways; in

1182   nature, the effects of these changes would be likely to reciprocally influence the

1183   evolution and ecology of phenological responses to climate change.

1184   **Figure 3.** Applying sequential, as opposed to strictly alternative, hypotheses to

1185   examine the timing of species interactions in communities in two systems. The

1186   diagrams in each panel represent hypothesized interaction networks. From a

1187   conventional perspective, these could each represent strictly alternative hypotheses

1188   on their own (labeled as H_1, H_2, and H_3). Conversely, from a more temporally explicit

1189   perspective, they could represent time-points in an integrated sequential

1190   hypothesis (labeled as t_1, t_2, and t_3). (a) The dead bodies of 13- and 17-year

1191   periodical cicadas fall to the ground each generation, creating a detrital pulse. As

1192   their collective biomass decomposes, a pulse of nutrients becomes available to

1193   plants, fertilizing the soil and increasing plant growth (Yang, 2004, 2013; Yang &

1194   Karban, 2019). However, these fertilized plants were preferentially consumed by

1195   mammalian and invertebrate herbivores (Yang, 2008; Yang & Karban, 2019). Solid

1196   arrows indicate the direction of mass or energy flow from resource to consumer,

1197   dashed arrows indicate the hypothesized relative strength of top-down and bottom-

1198   up effects under each hypothesized scenario. Red arrows indicate the direct

1199   bottom-up fertilization effects of the detrital pulse on plants; blue arrows indicate

1200   the consumption of plants by herbivores. The first diagram (labeled H_1 or t_1) shows

1201   chronic belowground root herbivory by periodical cicadas, while the second diagram

1202   (labeled H_2 or t_2) shows detrital fertilization-driven bottom-up effects, and the third

1203   diagram (labeled H_3 or t_3) shows stronger top-down effects mediated by other

1204   herbivores. (b) Pulsed subsidies of seaweed can have multiple effects on small

1205   island communities (Kenny et al., 2017; Piovia-Scott et al., 2013; Piovia-Scott et al.,

1206   2019; Spiller et al., 2010; Wright et al., 2013). In particular, pulsed seaweed

1207   subsidies could affect plant-herbivore interactions in at least three ways. First,

1208   under the *"lizard diet shift"* hypothesis labeled "H_1 or t_1", lizards respond the
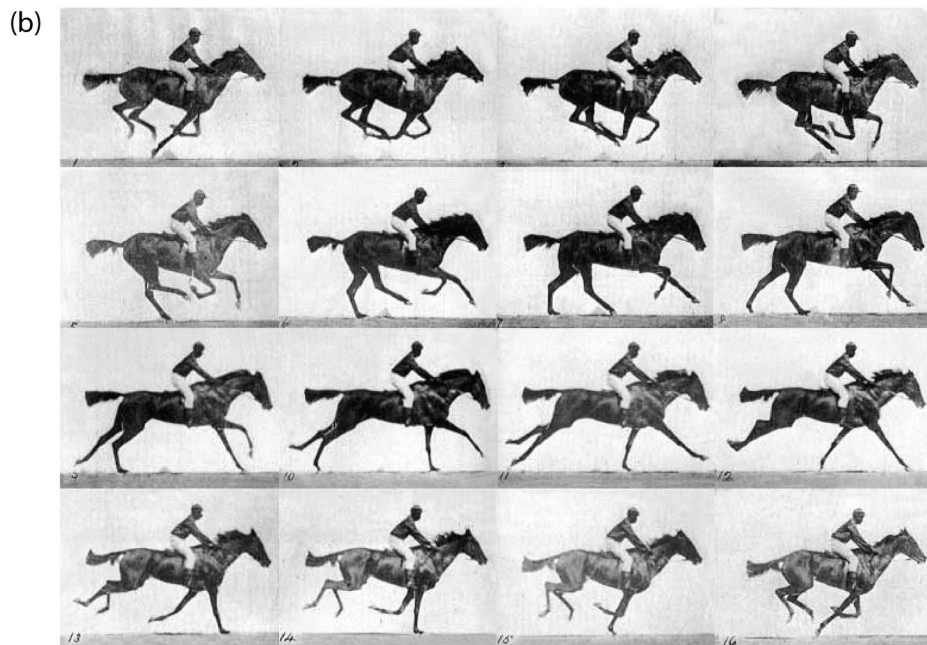
1209 seaweed subsidy with a behavioral diet shift towards increasingly marine-derived

1210 prey, thus reducing their consumption of terrestrial herbivores, and indirectly

1211 increasing measures of herbivory. Second, under the *"lizard numerical response"*

1212 hypothesis labeled "H_2 or t_2", local lizard densities increase due to increased

1213 survival or reproduction in the presence of a pulsed seaweed subsidy, ultimately

1214 increasing the consumption of terrestrial herbivores and decreasing measures of

1215 herbivory. Third, in the *"fertilization"* hypothesis labeled "H_3 or t_3", the

1216 decomposition of seaweed subsidies fertilizes the soil, increasing plant quality and

1217 measures of herbivory. In these diagrams, solid arrows represent the direction of

1218 mass or energy flow from resource to consumer, while dashed arrows indicate the

1219 hypothesized indirect effect of the seaweed subsidy on herbivores under each

1220 scenario. Red arrows indicate resource-consumer interactions related to the indirect

1221 bottom-up effects of the detrital pulse on herbivores, while blue arrows indicate

1222 resource-consumer interactions associated with the indirect top-down effect of

1223 lizards on herbivores.

1224 **Figure 4.** Seasonal windows of opportunity represent intervals in time when

1225 organisms experience improved prospects for advancing their life history objectives,

1226 constrained by the combined effects of seasonally variable biotic and abiotic

1227 conditions acting independently or in combination (Yang & Cenzer, 2020). In the

1228 sense that they are limited by the combined effects of multiple factors, these

1229 seasonal windows are a temporally explicit analog of the *n*-dimensional

1230 Hutchinsonian niche concept. Here we illustrate the seasonal windows of

1231 opportunity associated with a simplified, hypothetical organism whose expected

1232 fitness prospects are determined by the combined effects of seasonally variable (a)

1233 temperature and (b) precipitation. The seasonal pattern of temperature and

1234 precipitation presented here are based on actual monthly means for Davis,

1235 California, USA. Here, the fitness effects of temperature and precipitation are

1236 modeled with a Gaussian distribution centered on an arbitrary optimum

1237 temperature and precipitation value. Favorable abiotic conditions for this

1238 hypothetical species are shown in green; unfavorable conditions are shown in

1239 yellow or blue. (c) The resulting seasonal fitness landscape (shown in red)

1240 represents the combined fitness effects of temperature and precipitation scaled as

1241 the product of the two fitness dimensions. The two periods in the year when

1242 favorable climatic conditions overlap define the seasonal windows of opportunity in

1243 this example. Although this example shows two seasonally variable abiotic

1244 dimensions for simplicity, seasonal windows of opportunity are likely to be

1245 structured by *n*-dimensions more generally, including both biotic and abiotic factors.
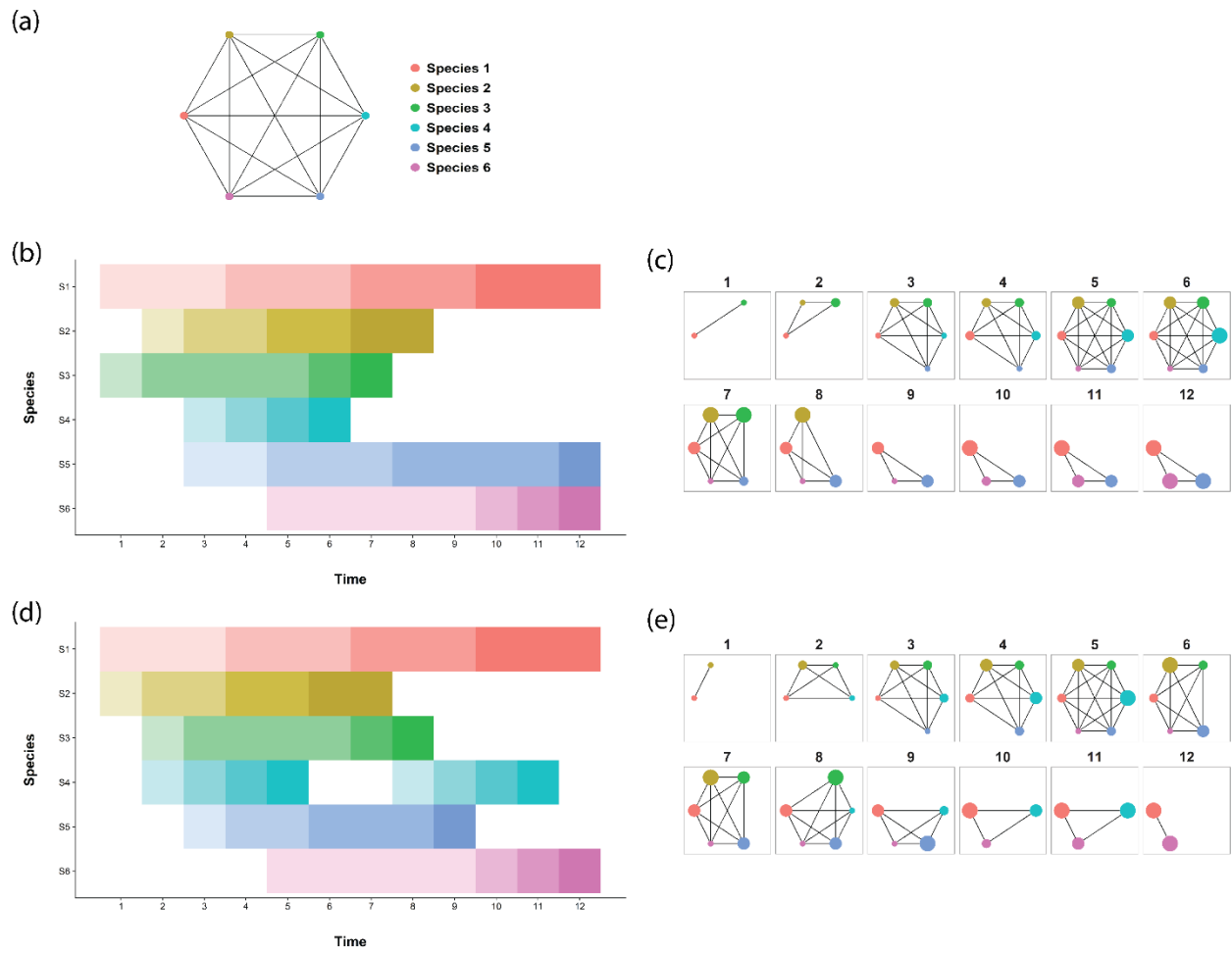

1246

1247   **Figure 1.**
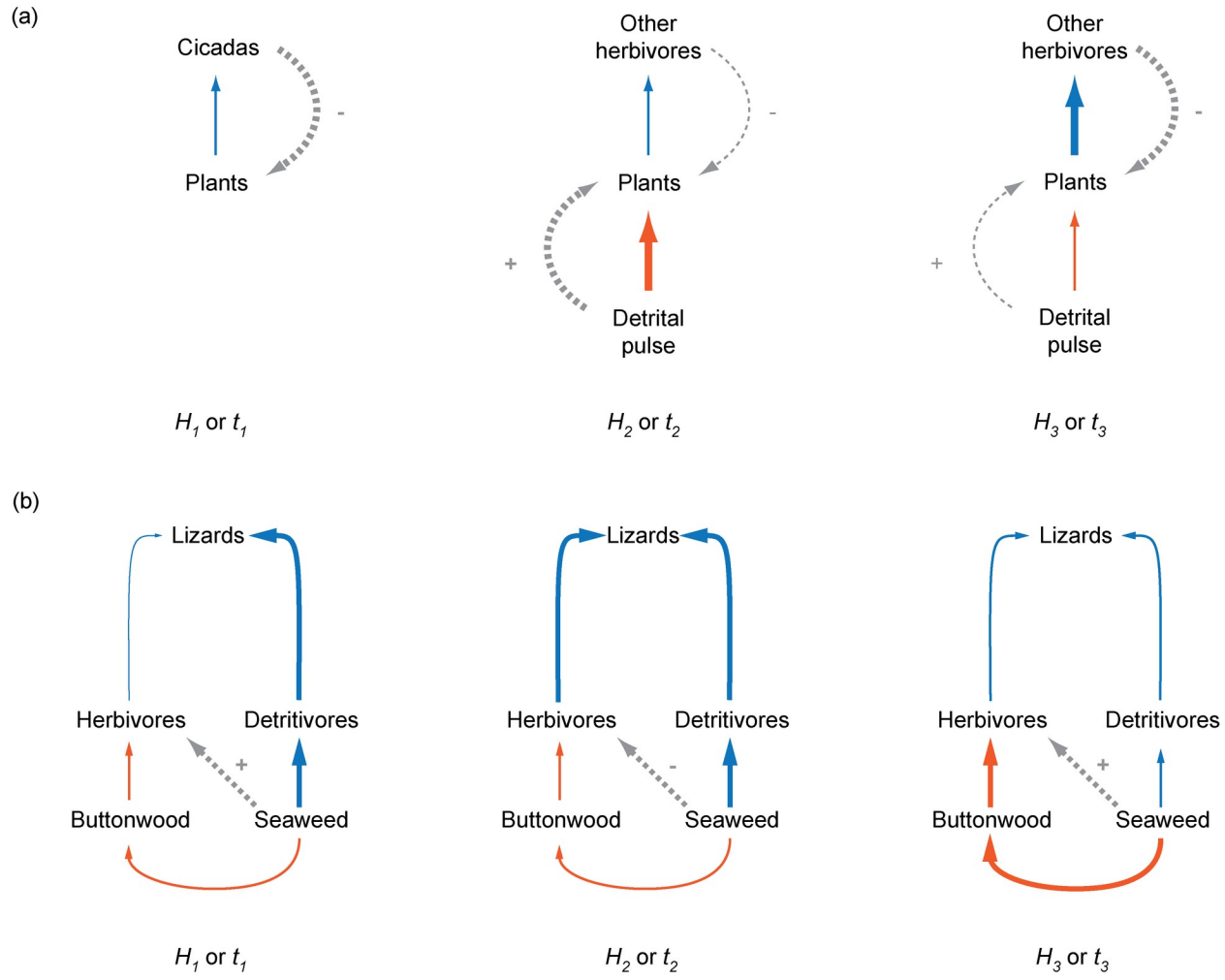
(a)

(b)

1248

55

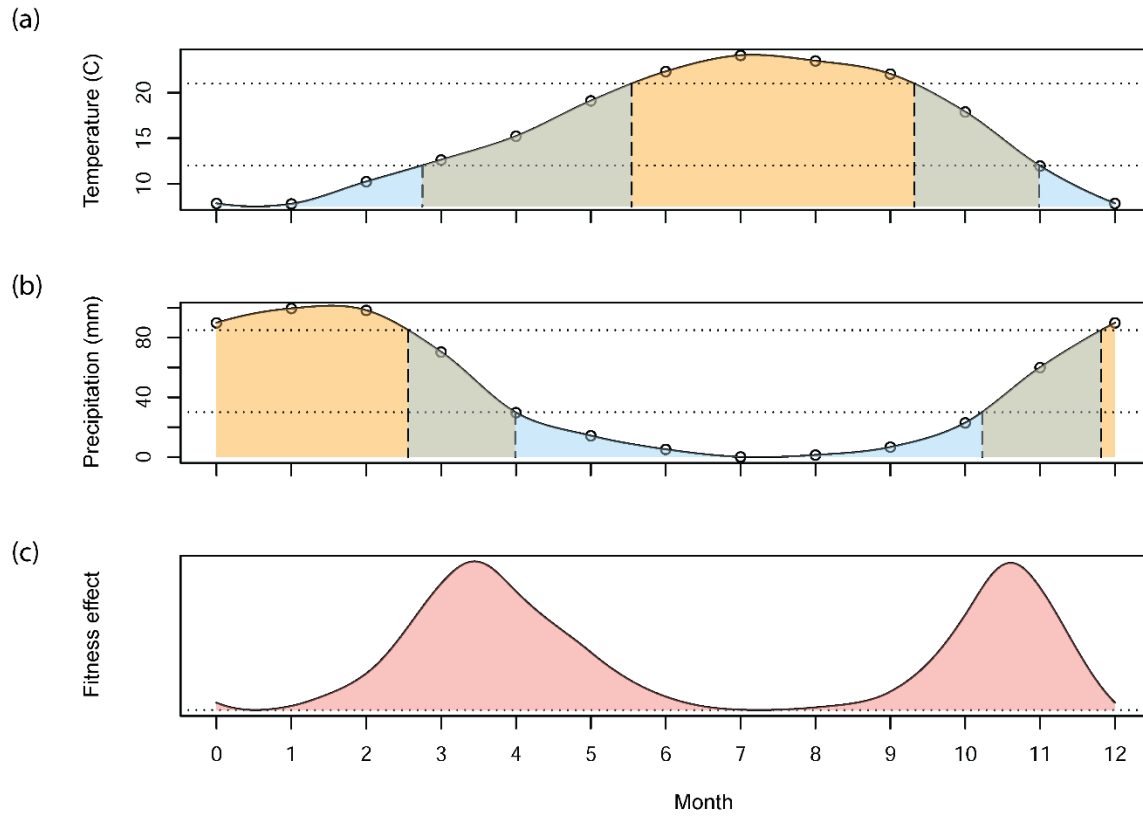1249 **Figure 2.**

1250

1251

1252

1253 **Figure 3.**

1254

(a)

H_1 or t_1 H_2 or t_2 H_3 or t_3

(b)

H_1 or t_1 H_2 or t_2 H_3 or t_3

1255

1256

1257 **Figure 4.**

1258

(a)

(b)

(c)

1259

1260

1261

58