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Long-Term Effects of Predator Arrival Timing on Prey Community Succession

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ABSTRACT: The stochastic arrival of competing species and their subsequent interactions have been highlighted as principal forces underlying biotic historical effects in community assembly. However, despite the widely recognized effect of predation on prey communities, the effects that the stochastic arrival of predators may have on assembling communities are poorly understood. We used a microbial microcosm experiment to investigate whether the timing of predator arrival to a prey community undergoing naturalistic succession affected species abundances and community diversity. Predator arrival timing affected the long-term abundance of a prey species that was persistent throughout succession in the absence of predators. Our data indicate that this timing effect occurred indirectly via transient interactions between early-successional prey species and predators. Specifically, we suggest that transient early-successional prey species served as a springboard for early-arriving (but not late-arriving) predators, allowing the exploiting predators to increase their abundances and subsequently alter long-term community dynamics. These results show that the history of predator arrival can have lasting consequences for community structure in ecological succession.

Keywords: assembly history, historical contingency, predation, springboard species, succession, transient dynamics.

Introduction

The history of species arrival during community assembly and succession can have permeating effects on the structure of communities (Lewontin 1969; Drake 1990, 1991; Law and Morton 1996; Chase and Leibold 2003, pp. 123–143). In particular, the stochastic arrival of competing species and their subsequent competitive interactions have been highlighted as a principal force underlying these historical effects (e.g., Drake 1990, 1991; Lawler 1993; Ejrnaes et al. 2006; Fukami et al. 2007; Jiang and Patel 2008). In contrast, the effects that the stochastic arrival of predators may have on prey communities remain poorly understood. Predators have long been recognized as exerting strong effects on the structure of prey communities (e.g., Paine 1966; Lubchenco 1978; Power et al. 1985; Wilbur and Alford 1985; Croll et al. 2005; Jiang and Morin 2005; Borrvall and Ebenman 2006). Yet despite their importance, few empirical studies have conceptually included predators as dynamic members of the regional species pool. In many natural communities, not only prey but also predators are limited in their colonization ability, and stochastic forces can make their arrival time highly variable. However, we know little about the effect that such variation may have on community assembly.

Many theoretical investigations do include predators in the regional species pool from which communities assemble, but two limitations of these studies hinder a full understanding of the role species arrival timing plays in the context of succession. First, many studies do not consider transient population dynamics. For simplicity, theory assumes that species arrivals are sufficiently infrequent that the assembling community reaches a stable state between species arrivals. In other words, a separation in timescale is assumed between the frequency of species arrival from outside the community and the speed at which population dynamics occur within the community (e.g., Drake 1990; Law and Morton 1996; Steiner and Leibold 2004; but see Lockwood et al. 1997; Fukami 2004*b*, 2005). Although these studies have served as a framework for community assembly, models built on this assumption of timescale separation do not allow us to investigate the effect of transient population dynamics on the course of succession (Law and Morton 1996). This limitation prevents a full understanding of community assembly because transient population dynamics can play a key role in determining the fate of ecological succession (Hastings 2004; Fukami 2004*a*).

Second, most theoretical studies use a completely randomized regime in selecting species from a regional pool to attempt invasion into local communities (Law and Morton 1996; Fukami 2004*b*, 2005; Steiner and Leibold 2004).

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In reality, ecological succession is not entirely stochastic in terms of species arrivals: some species are categorized as early-successional because they disperse more rapidly and tend to arrive at newly disturbed sites earlier than other, late-successional species. Models that assume a completely random order of invasions have served as an important first step in understanding community assembly, but this assumption is clearly unrealistic in the context of natural succession.

In the meantime, empirical research has usually separated predators from assembly history and has either focused on how their presence affects the assembling prey community (Paine 1985; Berlow 1997; Petraitis and Dudgeon 1999; Shurin 2001; Louette and De Meester 2007) or paralleled theoretical studies in assuming separation of timescales (Warren et al. 2003). In doing so, most studies treat predators as a constant external pressure acting on the assembling prey community as it undergoes successional dynamics rather than as dynamic members of the assembling community (but see Drake 1991). Important progress has recently been made: both Price and Morin (2004) and Hoverman and Relyea (2008) manipulated the colonization history of predators to look for effects on prey species. However, neither experiment was performed in the larger context of succession involving multiple prey and predator species. Price and Morin (2004) used only a single prey species and focused on direct interactions and coexistence between two intraguild predators. While Hoverman and Relyea (2008) manipulated time of predator arrival, they did not manipulate the timing of predator arrival relative to that of the prey species (i.e., all prey species were already established before any predator introductions were made).

In this article, we use a laboratory microcosm experiment to test the hypothesis that predator arrival timing affects individual prey species abundances and the overall diversity of a prey community undergoing succession. For this purpose, we experimentally manipulated the timing of predator arrival while we introduced prey species to replicated microcosms according to their varying dispersal abilities in order to simulate natural succession. The experiment involved introduction of seven species of freshwater protists, of which five were prey species and two were predators. We paid particular attention to transient population dynamics, which we found to be pivotal for explaining the arrival-timing effect of predators on the succession of the prey community. Specifically, we suggest that a transient early-successional prey species serves as a springboard for early-arriving (but not for late-arriving) predators, allowing exploiting predators to increase their abundances and subsequently alter long-term community dynamics. To further evaluate this hypothesized mechanism, we present the results of a supplementary experiment in which we manipulated the presence/absence of the transient early-successional springboard species and determined whether population dynamics matched the outcome predicted by the hypothesized mechanism.

Methods

Testing for Effects of Predator Arrival Timing

The microcosms used in this experiment were sterile 250-mL glass jars. Sterilized lids were placed loosely over the mouth of each jar to minimize contamination and to allow for adequate gas exchange. The containers were filled with sterilized medium consisting of 0.55 g crushed protozoan pellet (Carolina Biological Supply, Burlington, NC) and 0.05 g Herpetivite powdered reptile vitamin supplement (Rep-Cal Research Labs, Los Gatos, CA) per liter of water filtered with a Milli-Q Biocel water filter (Millipore, Billerica, MA). This sterile medium was inoculated with four bacterial species (*Bacillus subtilis*, *Bacillus cereus*, *Proteus vulgaris*, and *Serratia marcescens*, from University of Hawaii Microbiology Department stock cultures). We distributed the media to microcosms 48 h after inoculation to allow bacterial species to reach carrying capacities. Bacteria provided a food source for protozoan species introduced later. The microcosms were semicontinuous cultures: we replaced nutrients once a week for the duration of the experiment by thoroughly mixing the medium and then removing and replacing 10% of the volume with sterile medium. Semicontinuous-culture techniques provided fresh nutrients for bacteria each week.

One challenge in designing this experiment was determining an assembly history of prey species that would adequately mimic colonization histories in natural systems undergoing succession. Using colonization ability rankings produced by Cadotte et al. (2006), we extrapolated a “natural” assembly history for five protist bacterivores (*Tetrahymena pyriformis*, *Colpidium striatum*, *Chilomonas* sp., *Paramecium aurelia*, and *Spirostomum* sp., purchased from Carolina Biological Supply; we refer to them hereafter by their genus names). Specifically, we introduced *Tetrahymena* and *Colpidium* on day 1, *Chilomonas* on day 3, *Paramecium* on day 14, and *Spirostomum* on day 19. Within this established prey assembly history, we tested for the effects of predator introduction timing by using a two-way factorial design with two different predator species and three introduction times. We had treatments in which each predator species was introduced individually at one of the three timings and treatments in which both predators were introduced together at one of the three timings. We replicated each treatment four times. The two predator species used were *Euplotes* sp. and *Blepharisma americanum* (purchased from Carolina Biological Supply; here-

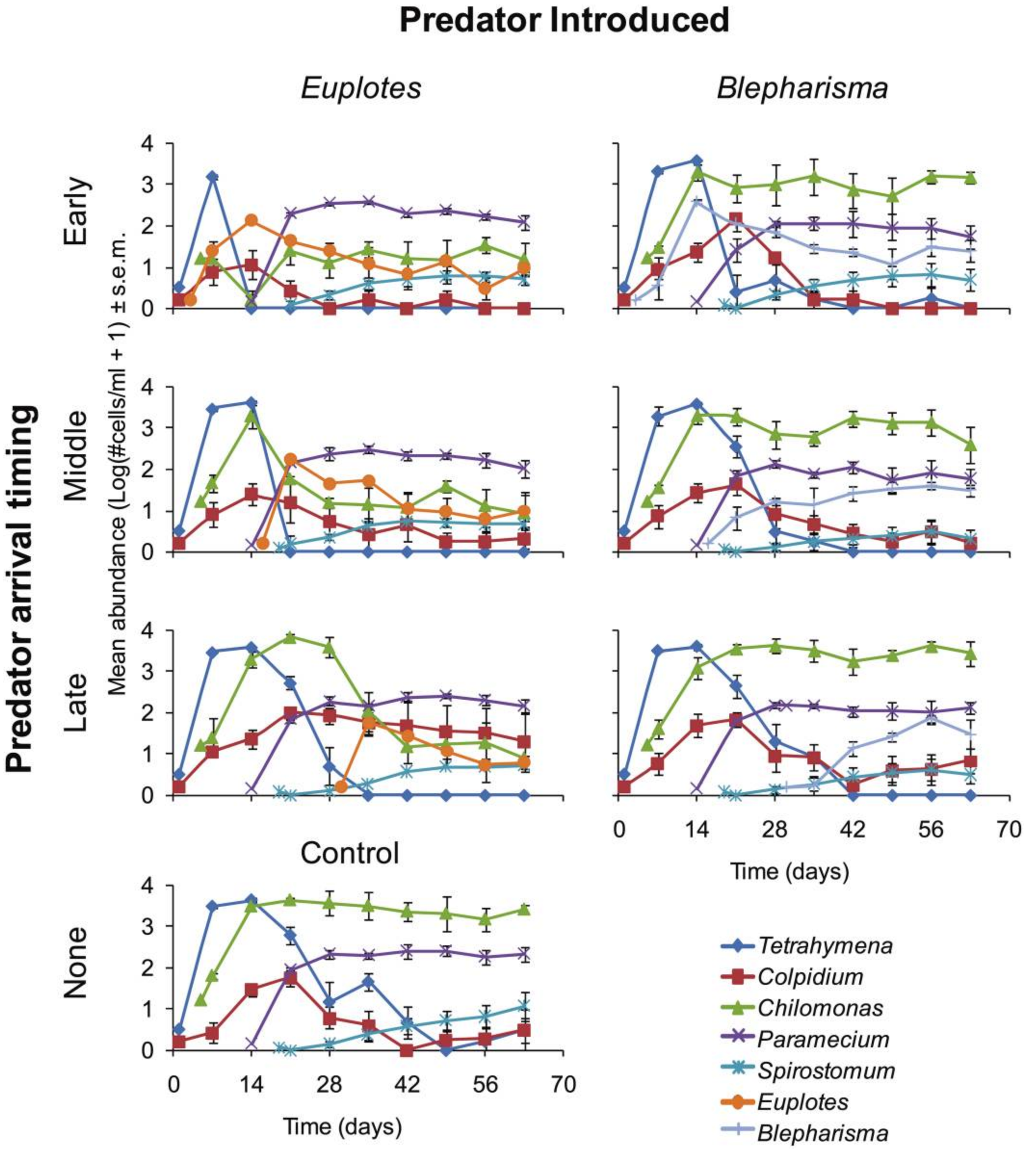

Figure 1: Temporal changes in species abundance (mean ± 1 SE) in single-predator introduction treatments and in the control treatment with no predators introduced (see app. C in the online edition of the *American Naturalist* for two-predator treatment data).

after referred to as *Euplotes* and *Blepharisma*, respectively). Both predators are omnivores, capable of preying on smaller prey, including *Tetrahymena*, *Chilomonas*, and *Colpidium*, but not on *Paramecium* or *Spirostomum*, because of their larger sizes. Predator introduction times were early, medium, and late, corresponding to days 3, 16, and 30.

A small number of individuals of each species were introduced in comparison to the abundances eventually attained through the course of the experiment (see app. A in the online edition of the *American Naturalist* for species-specific introduction densities). The initial abundance of each species was standardized across introduction events by estimating densities in stock cultures and transferring the appropriate volume to experimental microcosms. We standardized the age of stock cultures at the time of introduction to be 14 days, from the day of transfer from older cultures to the new stock cultures. Standardizing the age of cultures reduced variation in the condition of species between different introduction events.

Abundance of each protozoan species was measured weekly for a total of 63 days, 33 days past the final introduction. This length of time, corresponding to roughly

30–100+ generations of the protozoans used (see app. A), appeared sufficient for all assemblies to reach stable and persistent species compositions (fig. 1). To estimate densities for each replicate, we homogenized the media by mixing thoroughly the 10 mL of medium removed for nutrient replacement and counted live individuals in separate pipette drops of a 0.1–0.2-mL subsample, using a stereoscopic microscope.

Following the experimental design, we used two-way factorial repeated-measures ANOVAs to determine whether predator introduction timing and predator species identity had a significant effect on prey species abundance. Prey abundance measures for each species from the final three sampling days served as the repeated measures. To identify specific responses to predator introduction timing, we performed Tukey's pairwise comparisons with family $\alpha = 0.05$, using average densities across the final three sampling days. Density measures were $\log_{10}+1$ transformed to better meet the assumptions of normality and equal variances required in the ANOVAs (x^{-2} transformation of the raw abundance data gave better equality of variances for *Colpidium*; however, the ANOVA results were comparable, and we report only the results for $\log_{10}+1$-transformed data). We also performed two-way repeated-measures ANOVAs of predator abundances across the different introduction treatments for both predator species, again using abundance measures from the final three data points as the repeated measures.

In addition, we performed another pair of two-way repeated-measures ANOVAs to analyze effects of predator introduction timing and predator species identity on total prey community biomass and Simpson's diversity. Abundance values for each species were converted to biomass by using data from Fukami (2004*a*). The biomass values for each prey species were then summed to give the total community biomass. Again, data from the final three sampling days were used as repeated measures. We used two-way ANOVA to investigate differences in abundance of prey species at the time of predator arrival as well as the difference in predator abundance maxima across predator introduction timings.

Supplementary Experiment

The results of the above experiment indicated that an early-successional prey species, *Tetrahymena*, served as a springboard for early-arriving predators (as mentioned in "Introduction"; see "Results" for details). To evaluate the plausibility of this springboard mechanism, we conducted a supplementary experiment using the same methods as in the original experiment but with a different design. A factorial design, with the presence/absence of *Tetrahymena* (+/−T) as one factor and the presence/absence of potential competitors (+/−C) as a second, was used. In +C treatments, the potential competitors *Chilomonas* and *Paramecium* were included in the assembly (because of time constraints, we did not include *Spirostomum* in this experiment). In −C treatments, these competitors were not included in the assembly. When included in treatments, all species were introduced following the introduction schedule used in the *Euplotes* single-predator early-introduction treatment from the initial experiment. Each treatment was replicated six times, and microcosms were kept in a darkened incubator at 26°C. In this experiment, in addition to protist counts, total bacterial abundance was estimated on days 7, 21, and 49 with the methods of Jiang and Krumins (2006). We used plate counts to estimate bacterial abundance; estimations based on plate counts have been shown to approximate those of direct counts (Fox and Barreto 2006).

Results

Testing for Effects of Predator Arrival Timing

Two-way repeated-measures ANOVAs (rmANOVAs) indicated that one prey species had a significant response to predator introduction timing (see app. B in the online edition of the *American Naturalist*). *Colpidium* responded with progressively greater abundances as predator species were introduced later in the assembly history of the community ($F = 4.9$, $\text{df} = 2, 27$, $P = .015$; fig. 2*C*). Tukey's pairwise comparisons revealed that *Colpidium* abundance in the late-predator-introduction treatments was significantly higher than that in the early-introduction treatment but only marginally higher than that in the middle-introduction treatments ($P = .015$ and $.071$, respectively), and abundances in the early and middle treatments were not significantly different from each other ($P = .778$). Although the pattern was not clear in treatments with both predators introduced simultaneously (see app. C in the online edition of the *American Naturalist*), in the single-predator treatments the trend was obvious (fig. 1). In treatments with early single-predator introduction timing, *Colpidium* demonstrated stable abundance levels equivalent to extinction (no individuals observed in any replicate for two consecutive sampling days). In treatments with late predator introduction timing, *Colpidium* had stable abundance levels near 1.5/mL (abundances are $\log_{10} + 1$ transformed).

In contrast, *Chilomonas*, *Paramecium*, and *Spirostomum* converged in abundance across predator introduction treatments ($F = 0.1$, $\text{df} = 2, 27$, $P = .917$; $F = 1.0$, $\text{df} = 2, 27$, $P = .381$; and $F = 0.2$, $\text{df} = 2, 27$, $P = .787$, respectively). *Chilomonas* and *Paramecium* abundances showed a significant response to predator identity

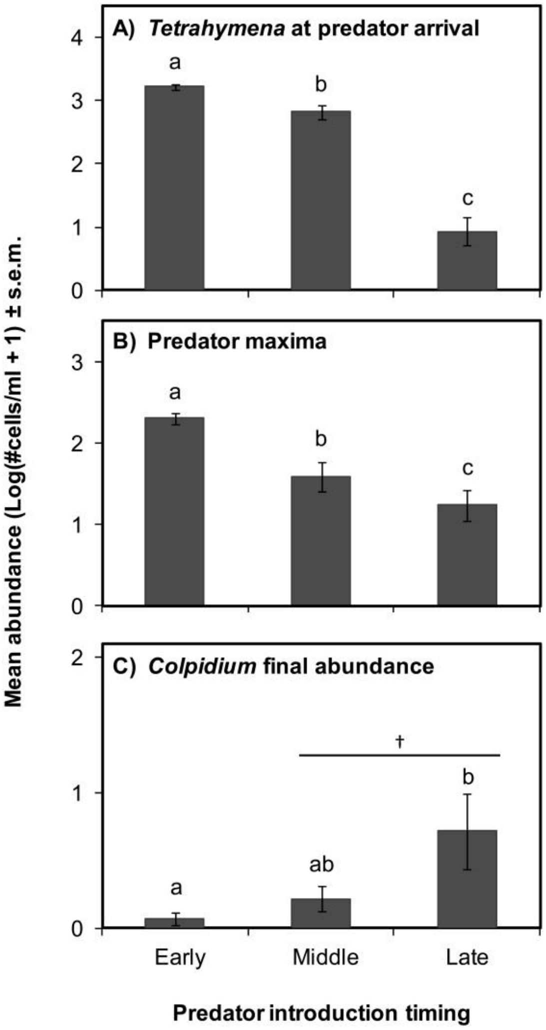

Figure 2: Species abundances (mean ± 1 SE) across predator introduction treatments. *A*, *Tetrahymena* abundance at the time of predator arrival. Note that for early treatments, we used *Tetrahymena* abundance values from day 7 because they represent *Tetrahymena* abundances after exponential population growth during the first 3 days of incubation better than the linear projected value shown in figure 1 (Lawler 1993; see also app. D in the online edition of the *American Naturalist*). *B*, Maximum predator abundances within 2 weeks of introduction. *C*, Final *Colpidium* abundance, averaged over the final three sampling days. In each plot, treatment groups sharing a letter do not differ significantly in a Tukey's test ($P > .05$). A dagger indicates a marginally significant difference between treatment groups ($P = .071$).

($F = 43.6$, df $= 2, 27$, $P = .000$; and $F = 3.4$, df $= 2, 27$, $P = .048$, respectively). A particularly strong interaction was present between *Chilomonas* and *Euplotes*. *Euplotes* depressed the abundance of *Chilomonas* by almost two orders of magnitude ($F = 184.2$, df $= 1, 106$, $P < .001$).

Tetrahymena was a transient member of the community and became extinct in almost all treatments before the final three sampling days (and could therefore not be included in the rmANOVA of the final three sampling days). However, the dynamics of *Tetrahymena* under different predator introduction treatments revealed a historically contingent predator-prey interaction. Specifically, the time to extinction for *Tetrahymena* was closely correlated with predator introduction timing (i.e., early predator introduction led to early extinction; $r^2 = 0.614$, $P \leq .001$). Furthermore, *Tetrahymena* abundances at the time of predator introduction were significantly lower in treatments in which predators were introduced later in the assembly history than in treatments in which predators were introduced earlier ($F = 133.39$, df $= 2, 27$, $P < .0001$; fig. 2*A*). Predator abundance maxima demonstrated a similar decline as they were introduced later in the assembly history ($F = 47.9$, df $= 2, 36$, $P < .001$; fig. 2*B*).

Prey abundance showed no significant differences over time across the final three sampling days in all but one species (*Colpidium*: $F = 0.8$, df $= 2, 54$, $P = .473$; *Chilomonas*: $F = 0.4$, df $= 2, 54$, $P = .647$; *Spirostomum*: $F = 2.4$, df $= 2, 54$, $P = .099$; *Paramecium*: $F = 7.0$, df $= 2, 54$, $P = .002$). Predator introduction timing did not significantly affect community diversity ($F = 0.1$, df $= 2, 27$, $P = .904$) or total prey community biomass ($F = 0.7$, df $= 2, 27$, $P = .527$). Predator identity, however, did have a significant effect on diversity ($F = 5.4$, df $= 2, 27$, $P = .01$) and a marginally significant effect on prey community biomass ($F = 2.8$, df $= 2, 27$, $P = .078$). Final predator abundances did not differ significantly across the introduction treatments ($F = 0.32$, df $= 2, 18$, $P = .489$ for *Euplotes*; $F = 0.38$, df $= 2, 18$, $P = .604$ for *Blepharisma*).

Supplementary Experiment

In the supplementary experiment (see app. D in the online edition of the *American Naturalist*), *Colpidium* was driven to extinction in all treatments in which *Tetrahymena* was also introduced, whereas it persisted for the duration of the experiment in treatments in which *Tetrahymena* was not introduced. Competitors had a significant positive effect on *Euplotes* maximum abundance ($F = 12.451$, df $= 1, 20$, $P = .002$), *Tetrahymena* had an insignificant effect ($F = 0.902$, df $= 1, 20$, $P = .353$), and the interaction term was significant ($F = 4.569$, df $= 1, 20$, $P = .045$). *Euplotes* maximum abundance was significantly higher in treatments with both competitors and *Tetrahymena* present (+C/+T) than in treatments with competitors only (+C/−T; $F = 5.824$, df $= 1, 20$, $P = .037$), but there was no significant difference between −C/+T and −C/−T treatments ($F = 0.597$, df $= 1, 20$, $P = .467$).

Discussion

Overall, our results support the hypothesis that predator arrival timing affects the abundance of prey species in the long term over the course of community succession. In what follows, we use our data to suggest that the mechanism of this historical contingency is indirect via an interaction between predators and a transient early-successional species. We then propose that the transient dynamics of this interaction had long-term effects on the community in the form of altered predation levels on a persistent prey species.

Patterns and Plausible Mechanisms

Predators had a historically contingent effect on the abundance of one prey species after assembly was complete and the communities had attained a relatively stable state. *Colpidium* was unable to persist when predators arrived early in the assembly history, and their final abundance significantly increased as predators arrived progressively later (figs. 1, 2*C*). Direct, as well as indirect, effects may explain the observed results.

The simplest potential explanation for the persistence of *Colpidium* in treatments with late-arriving predators is that it was an artifact of delayed extinction time directly associated with delayed predator arrival. However, time-to-extinction data show that this was not so. In early-predator-introduction treatments, *Colpidium* survived 25 and 39 days in *Euplotes* and *Blepharisma* treatments, respectively, after the predators were introduced. In contrast, when the predators were introduced later, *Colpidium* survived to the end of the experiment, a time corresponding to 47 days in the middle-predator-introduction treatments and 33 days in the late-introduction treatment (at a significantly higher abundance in the late-introduction treatment). Further, predator abundance over the final three sampling days was not statistically different across introduction timings, eliminating final predator abundance as an explanation for the variation in *Colpidium*'s persistence.

Direct effects of predators alone cannot explain our observed results. This is most obvious in early-predator-introduction treatments, in which predators and *Colpidium* arrive in the community within 2 days of each other. In these treatments, both predators and *Colpidium* increased in abundance, and predators attained maximum abundance either before or at the same time as *Colpidium* did (fig. 1). Ignoring, for the moment, any potential indirect effects in our explanation, this pattern is contrary to what is expected of a predator-prey interaction for two reasons. First, this would be an atypical predator-prey oscillation, as prey species usually reach maximum abundance before a subsequent peak in predator abundance. Second, both predators and *Colpidium* arrived in the community at very low density (see "Methods"), and the encounter rate between the two would be too small to explain the rapid establishment of predators.

Furthermore, three lines of evidence indicate that competitive effects alone also fail to explain the timing effect of predators on *Colpidium*. First, temporal changes in species abundances (fig. 1) and the rmANOVA results (app. B) show that the abundances of all prey species potentially competing with *Colpidium* eventually converged across predator introduction treatments. Second, in the early-introduction treatments, where *Colpidium* did not persist, we would expect competitors to have a strong effect on *Colpidium*; yet in these treatments, *Tetrahymena* was driven to extinction in the first 2 weeks and *Chilomonas* was kept at low densities for the duration of the experiment. Third, conversely, in the late-introduction treatments, where *Colpidium* persisted, we would expect competitive interaction to be weaker; however, in these treatments, *Tetrahymena* and *Chilomonas* sustained high densities for several weeks before *Tetrahymena* was driven to extinction and *Chilomonas* was reduced to lower densities.

We propose that indirect effects offer a better explanation. Specifically, the interaction between predators and the transient early-successional species *Tetrahymena* seems important in understanding the long-term response of *Colpidium* to predator arrival timing. *Tetrahymena* abundance fluctuations are characterized by rapid establishment of high abundance followed by an inevitable decline to extinction (fig. 1). When predators arrive early in the assembly, *Tetrahymena* serves as a highly abundant and easily exploitable species and seems to allow predators to rapidly establish high abundance levels of their own (fig. 2). It appears that *Tetrahymena*'s efficacy as a springboard for predator populations subsequently intensifies predation on *Colpidium*. In contrast, when predators arrive later in the assembly, *Tetrahymena* abundances have been reduced, presumably by competitive interactions with other prey species (fig. 2). As a consequence, exploiting predators appear unable to take advantage of a preferred prey species, and the springboard effect is lost. The persistent prey community, particularly *Colpidium*, would then be released from higher levels of predation.

The results from the supplementary experiment (see app. D) support this proposed mechanism: *Colpidium* persisted only in −T treatments, as expected. In addition, the results indicate that not only *Tetrahymena* but also *Chilomonas* contribute to the springboard effect. Specifically, inclusion of *Chilomonas* resulted in significant increases in *Euplotes* maximum abundances. Further, *Tetrahymena* boosted *Euplotes* abundance only when *Chilomonas* was also present. It appears that when *Euplotes* exploits both

Tetrahymena and *Chilomonas*, it crosses an abundance threshold above which *Colpidium* does not persist in the face of increased predation by *Euplotes*.

Euplotes may have responded to prey not only numerically but also morphologically. *Colpidium* persisted in −T/−C treatments and not in +T/−C, yet *Euplotes* maximum abundance was not significantly different between these treatments. Morphological, rather than numerical, responses of *Euplotes* to *Tetrahymena* may help to explain the results. For example, consumption of *Tetrahymena* may have increased the cell size of *Euplotes*, which allowed *Euplotes* to consume a wider size range of *Colpidium*, affecting their persistence despite the lack of a numerical response by *Euplotes*. We do not have the cell size data to test this hypothesis, however.

Long-Term Transient Dynamics and Historical Contingency

When predators arrived early in our experiment, the responses of both predators and the rest of the prey community persisted far longer than the actual predator-transient interaction. These responses persisted even after assembly was complete and the community had begun to stabilize. This result is relevant to recent interest regarding theoretical interpretations of long-term behavior in assembling communities. Historically, theoretical studies have focused on behaviors at equilibrium to describe long-term dynamics in assembling communities (May 1974; Law and Morton 1996; Steiner and Leibold 2004). However, theoretical models that use equilibrium-based criteria of species coexistence assume that local population dynamics within a community occur on a significantly faster timescale than colonization events by species external to the community (Law and Morton 1996). Under this assumed separation of timescales between local interactions and colonization events, the effects of transient species and interactions can be overlooked in the successional long term. Our results suggest that a short-lived, historically contingent dynamic between an early-successional prey species and arriving predators can have long-term effects on community dynamics.

Recent findings suggest that transient dynamics can have important effects on ecological systems (Hastings 2001; Noonburg and Abrams 2005) and that their effects can be on timescales that, while not asymptotic or "permanent," are of great ecological significance (Hastings 2004). In this theoretical framework, our results provide an empirical example of transient dynamics affecting behavior in an assembling community on a timescale that long exceeds the duration of the transient dynamic and is of ecological significance for the species involved. The exploitation of *Tetrahymena* by early-arriving predators lasted less than 2 weeks. Yet the effects of predator arrival timing on *Colpidium* lasted for 7 weeks, a period of time equivalent to roughly 100 generations of this species. Although *Colpidium* abundance may have eventually converged across treatments if the experiment had been run longer, 100 generations is certainly an ecologically significant time. Even with eventual community convergence, the long-term effects of transient dynamics make biotic historical contingency important in explaining community structure (Fukami 2004*a*).

More broadly, our results can be interpreted within the theoretical framework for interaction strengths and community stability. McCann et al. (1998) and Post et al. (2000) suggested the role of weak interaction strengths for stabilizing oscillations in simple food webs, including diamond-shaped food webs consisting of a predator, two prey species, and a resource. Their models indicate that these food webs destabilize as the relative interaction strength of a prey species with the predator is increased. Early in the assembly history of our experiment, predators, the prey species *Tetrahymena* and *Colpidium*, and bacteria formed a diamond-shaped food web. Predators interacted strongly with *Tetrahymena*, as evidenced by the high-amplitude but short-lived dynamics of predators and *Tetrahymena*. This strong interaction was unstable and led to food-web simplification via the extinction of *Tetrahymena*. The subsequent extinction of *Colpidium* in these treatments may have been caused by system instability as a historical legacy from the early predator-*Tetrahymena* dynamics. In contrast, when predators were introduced later, this strong interaction and the resulting food-web instability did not happen, because *Tetrahymena*, a weak competitor (Cadotte et al. 2006), was already at reduced abundance through competitive interaction with other prey species. Consequently, *Colpidium* persisted with predators.

Generality of Mechanisms

In this study, we used a microcosm experiment for its power in testing for historical effects. Two advantages are particularly relevant for our purpose: complete control over assembly history and long-term observations that span many generations of the species involved (Lawler 1993; Balciunas and Lawler 1995; Fukami 2001; Cadotte et al. 2006). Of course, results of microcosm experiments should be interpreted with caution because of their limited natural context (Carpenter 1996). Nevertheless, the transient dynamics underlying historical contingency of predator arrival time may be sufficiently general to help explain successional dynamics in a variety of natural communities. In our microcosms, the springboard mechanism rests largely on *Tetrahymena*'s characteristics as a fast-growing and highly palatable prey. These characteristics are not uncommon in early-successional species and have been demonstrated in a variety of systems (Amman 1977; Grootjans et al. 1998), indicating the potential generality of this mechanism. We suggest that the transient dynamics of early-successional species and their historically contingent interaction with predators are particularly important in determining long-term community dynamics in systems where generalist predators demonstrate a strong interaction with early-successional prey species. Possible examples include rocky intertidal communities (Connell and Slayter 1977; Sousa 1979; Barkai and McQuaid 1988), grassland communities grazed by invertebrate herbivores (Bishop 2002), coastal marsh communities in which geese demonstrate a preference for pioneer herbs (Olff et al. 1997), and temperate forest communities affected by introduced ungulate herbivores (Smale et al. 1995; Coomes et al. 2003).

Limitations and Future Directions

Our study has several limitations and should be viewed as only a first step in understanding long-term effects of transient dynamics in succession. First, most natural communities are more species-rich and more variable in their assembly than were our experimental communities. The degree to which our results can be extended to more diverse communities remains uncertain. Second, we focused on prey community succession, but predator arrival timing may also affect predators themselves. Further experiments are required to test more fully for this possibility. Finally, the absence of bacterial abundance data in our main experiment makes it impossible to rule out bottom-up effects due to aging media and declining bacterial abundances as possible explanations for the effect of predator arrival timing. However, we point out that bacterial abundance is unlikely to explain the results because (i) total bacterial abundances in the supplementary experiment showed little directional change over time, either positive or negative (app. E in the online edition of the *American Naturalist*) and (ii) total bacterial abundances sometimes show positive trends over time in protist microcosm experiments comparable to ours (e.g., Jiang and Krumins 2006). That said, interactive effects of top-down and bottom-up forces on historical contingency in community assembly merit further investigation.

Conclusion

Ecological succession has been viewed as a largely predictable process in the long term, albeit with an important stochastic component in the arrival timing of dispersing species. In particular, the role of early-colonizing species in determining long-term community dynamics has been largely overlooked because of their transient presence and inability to compete with later-successional species. However, our data suggest that transient, historically contingent interactions between predators and early-successional prey species can have long-term effects on community structure. In summary, this study has provided experimental evidence that predator arrival timing plays a key role in determining the long-term dynamics of a prey community and that this role manifests itself through transient dynamics occurring at early successional stages.

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