## Cyclic transitions in simulated food-web evolution Daisuke TAKAHASHI<sup>1</sup>, Åke BRÄNNSTRÖM<sup>2</sup>, Rupert MAZZUCCO<sup>2</sup>, Atsushi YAMAUCHI<sup>1,3</sup>, and Ulf DIECKMANN<sup>2</sup>

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## 9 Abstract

10 Eco-evolutionary food-web models help elucidate the processes responsible for the emergence and 11 maintenance of complex community structures. Using an individual-based model of evolving trophic 12 and competitive interactions, we highlight a pattern of community macroevolution involving two 13 meta-stable states, corresponding to a plant-herbivore community and a plant community, 14 respectively. On the evolutionary timescale, our model exhibits cyclic transitions between these 15 alternative community states. The model also helps understand the eco-evolutionary mechanisms 16 underlying these recurrent rapid transitions, which end intermittent periods of near-stasis or 17 punctuated equilibrium.

18 Keywords: prey-predator interactions, trophic traits, evolution, community ecology

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20 Interest is mounting in the evolutionary emergence of food-web structures. Understanding the 21 processes that maintain or alter community structure offers valuable insights into the functioning of 22 ecosystems, which may in turn facilitate the preservation of vulnerable natural systems. Several 23 models have been proposed for analyzing the coevolutionary dynamics of exploiter-victim 24 interactions (Drossel et al. 2001, 2004; Rossberg et al. 2006, 2008; see also models reviewed by 25 Yoshida 2006). However, most of the existing models assume that community evolution proceeds by 26 random speciation, and thus do not consider the gradual evolution of key functional traits. Ito and Ikegami (2006), Troost et al. (2008), and Ito et al. (2009) considered the gradual evolution of trait 27 28 distributions; however, their models do not include stochastic fluctuations. Rossberg et al. (2010a)

29 studied the gradual stochastic evolution and random speciation of trophic traits (Rossberg et al. 30 2010b) in predator-prey communities, but did not derive the examined evolutionary dynamics from 31 the underlying population dynamics. Here, we introduce and analyze an individual-based model in 32 which complex ecological communities emerge through the repeated evolutionary branching of 33 trophic traits driven by the underlying ecological interactions. In our model, individuals are 34 characterized by two quantitative traits that determine, respectively, predation ability and predation 35 vulnerability. The eco-evolutionary community dynamics unfold through the succession of 36 stochastic birth and death events (Gillespie 1976). Reproduction is asexual, and during each birth 37 event quantitative traits may undergo mutations of small effect with a small probability. The rates at 38 which birth and death events occur are determined by the intensity of interference competition and 39 predation among individuals.

40 Unexpectedly, we find that the structure of the evolving community does not settle toward an 41 equilibrium, but instead cyclically alternates between two meta-stable states (Figure 1). One state is 42 characterized by a diverse assembly of primary producers (plants), whereas the other state features a 43 collection of primary producers exploited by specialized consumers (herbivores). These two 44 meta-stable states are connected through unidirectional transitions: coevolutionary diversification of 45 producers and consumers, and cascading extinction of producers and consumers. In a meta-stable 46 community with diverse primary producers and matched consumers, the emergence of an additional 47 consumer species through evolutionary branching can destabilize the producer community and, thus, 48 trigger a cascade of extinctions. The implied sharp reduction in species richness is followed by the 49 coevolutionary diversification of producers and consumers, resulting in an increase in species 50 richness until the second meta-stable community state is reached, whence another evolutionary 51 community cycle starts.

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Figure 1. Changes in producer ratio (producer biomass per total biomass, measured across the entire community) caused by the modeled eco-evolutionary community dynamics. Two meta-stable states can be distinguished, corresponding to producer ratios of nearly 1 and approximately 0.8. In the latter case, producers coexist with consumers. Sharp increases and decreases of the producer ratio

88 indicate the rapid transitions between the two meta-stable community states.