Journal of Theoretical Biology 257 (2009) 627–641

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Predicting the phenotypic response of resource-competing communities to environmental change

Yoshinari Tanaka [a,*], Masafumi Yoshino [b]

[a] Research Center for Environmental Risk, National Institute for Environmental Studies, 16-2 Onogawa, Tsukuba, Ibaraki 306-8506, Japan
[b] Department of Mathematics, Graduate School of Science, Hiroshima University, 1-3-1 Kagamiyama, Higashi-Hiroshima, Hiroshima 739-8526, Japan

ARTICLE INFO

Article history:
Received 3 September 2008
Received in revised form
10 December 2008
Accepted 10 December 2008
Available online 30 December 2008

Keywords:
Community response
Ecosystem function
Functional trait
Phenotypic diversity
Resource competition

ABSTRACT

We formulated responses in functional traits by competitive communities to continual environmental changes, and examined the association of the trait dynamics with species richness and interspecific competition. As an aggregate measure for community properties we employed the mean community trait value as the species traits averaged over an entire community with weighting by relative species abundances. For three particular types of community, in which there was competition for abiotic resources, competition for biotic resources, or species packing on an environmental gradient, we analytically proved that the responses of the mean community trait to environmental change were determined by the total trait range in the community but were weakly associated with the strength of competition and the number of species. These results were provided with simplifying assumptions that the species trait determining the resource utility equally spaced along an univariate resource axis and the competition between species was symmetrical between pairs of competing species and within the entire community. Some numerical simulations based on stochastically-generated communities and randomly-sampled natural communities indicated that relaxation of the simplifying assumptions did not considerably violate the above conclusion. The suggested determinacy of trait dynamics with variable species richness and competition regime implies that aggregated description of communities in terms of trait distributions among composite species is relevant in predicting community responses, in terms of functional traits and ecosystem function, to environmental changes.

1. Introduction

Communities respond in terms of species composition or relative species abundances to continual changes in environment such as eutrophication (Cottingham and Carpenter, 1998; Cottingham, 1999), acidification (Frost et al., 1999; Fischer et al., 2001), chemical pollution (Blanck and Wängberg, 1988; Smith et al., 2001), and manipulation of predators (Cohen et al., 2003; Jonsson et al., 2005) or grazers (Bullock et al., 2001; Craine et al., 2002; Kahmen and Poschlod, 2004). One of the most important consequences of the community responses to environmental changes is the perturbation of ecosystem processes or functions, which in turn affects ecosystem services (Hooper et al., 2005; Millennium Ecosystem Assessment, 2005). To establish theories that are relevant to hazard prediction for ecosystems, many theoretical and empirical studies over the last decade have focused on the relationships between biodiversity and ecosystem functioning or stability under fluctuating environments (Petchey, 2000; Hughes and Roughgarden, 2000; Lehman and Tilman, 2000; Hughes et al., 2002; Ives and Hughes, 2002; Petchey and Gaston, 2002; Scheiner and Willig, 2005).

Meanwhile, communities may change in deterministic ways under directionally changing environments or continuous stresses. The proximate factors in community responses are associated with functional or adaptive species traits that decide species-specific resource use and environmental adaptability or tolerance. The consequent compositional changes in communities, in turn, affect ecosystem processes and functioning that are proximately attributed to species-specific properties or species' functional (effect) traits (Lavorel and Garnier, 2002; Eviner and Chapin, 2003; Mason et al., 2005).

Thus, an alternative approach to the analysis of communities based on species richness (the number of species) is to focus on species' functional traits rather than taxonomic species identities (Norberg et al., 2001; Petchey and Gaston, 2002, 2006; Naeem and Wright, 2003; McGill et al., 2006), and to construct predictable theories for community responses based on trait distribution as a state variable of communities. Although the trait-based approach has achieved success to some extent in identifying causal factors

* Corresponding author. Tel./fax: +81 29 850 2144.
E-mail addresses: ytanaka@nies.go.jp (Y. Tanaka), yoshinom@hiroshima-u.ac.jp (M. Yoshino).

0022-5193/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2008.12.017

for community disturbances (Frost et al., 1999; Bullock et al., 2001; Smith et al., 2001; Kahmen and Poschlod, 2004), revealing functional relationships between traits and ecosystem processes Craine et al., 2002; Eviner and Chapin, 2003), and decomposing biodiversity across different spatial scales (Ackerly, 2003; Cornwell et al., 2006), very few theoretical studies have explored trait dynamics in communities (e.g. Norberg et al., 2001; Pachepsky et al., 2001; Savage et al., 2007). And the possible influences of interspecific interaction to the trait dynamics in a community have not well examined. In the formulation of trait dynamics of a community, the concept of "guild character" is employed here to refer to a set of homologous characters among constituent species (see Garnier et al. (2004) and Violle et al. (2007) for other terminology with slightly different definition). These characters have equivalent ecological functions and, in theory, can be regarded as identical. The frequency distribution of a guild character is defined as the linear combination of phenotypic distributions of composite species weighted by their relative abundances or biomass (c.f. Norberg et al., 2001). Thus, the guild character distribution, which determines any community-level properties including those strongly influencing ecosystem processes and functioning, changes with relative species abundance or species replacement in response to environmental changes (Fig. 1).

This study, as a first step to incorporate interspecific interactions into community-level trait dynamics, focuses on a single functional trait that characterizes environmental demand or resource utilization for composite species. The environmental change is dealt with as affecting the frequency distribution of environmental factors or resources in the environmental gradient model or in the univariate resource competition model (Tilman, 1982; Grover, 1997). We analytically proved that the community response in mean guild character to an environmental change is proportional to the effective phenotypic range of the community but approximately independent of the species richness and the strength of competition. These analytical conclusions were derived with particular assumptions that the species trait determining the resource utility equally spaced along an univariate resource axis and the competition was both symmetrical

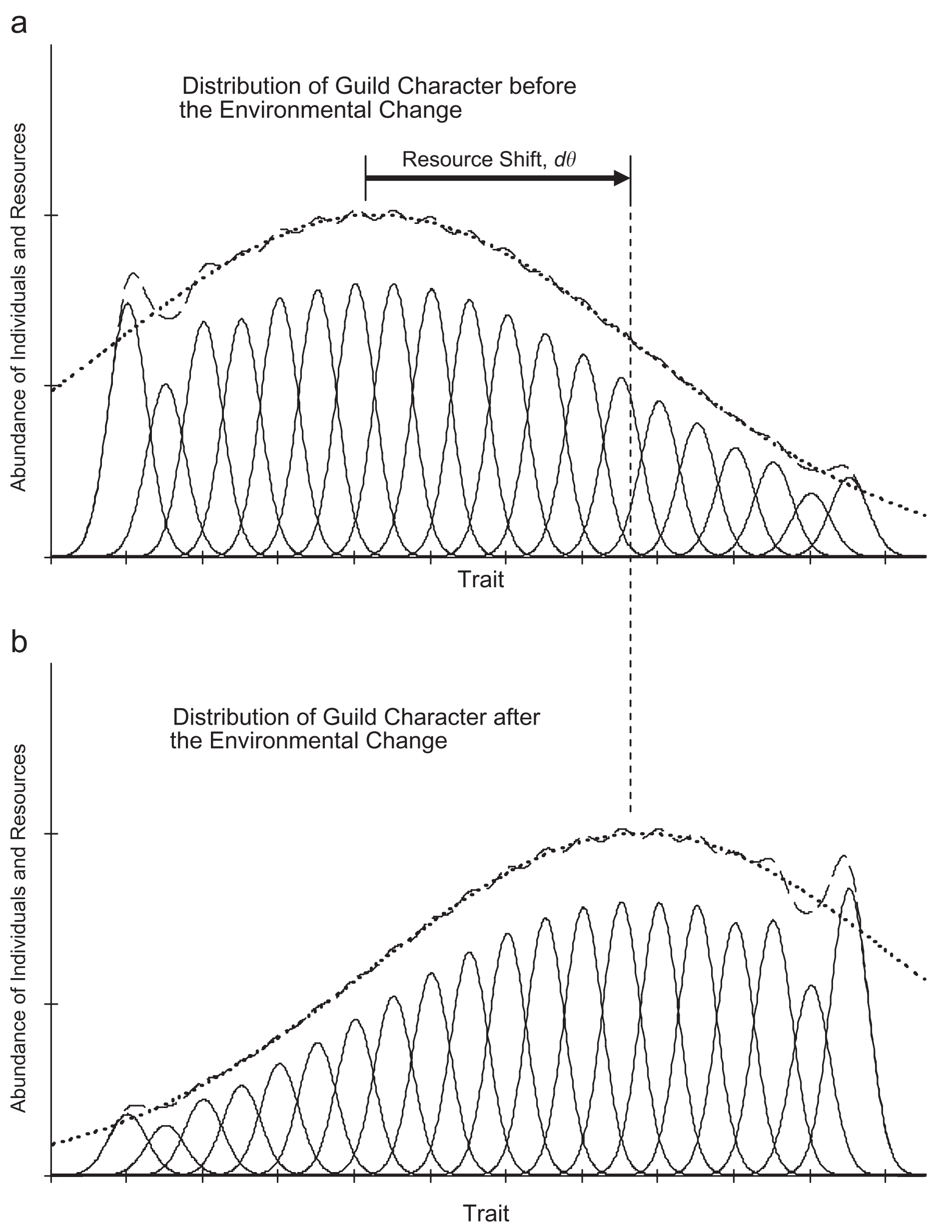

Fig. 1. Effect of environmental change in resource distribution upon trait distribution in an exploitatively competing community. See text for explanation.