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Functional traits mediated cascading effects of water depth and light availability on temporal stability of a macrophyte species

Hui Fu[a,b,*], Guixiang Yuan[a,b], Qian Lou[b], Taotao Dai[b], Jun Xu[c], Te Cao[c,*], Leyi Ni[c], Jiayou Zhong[b], Shaowen Fang[d]

[a] Ecology Department, College of Bioscience Biotechnology, Institute of Ecology, Hunan Agricultural University, Changsha 410128, PR China
[b] Jiangxi Institute of Water Sciences, Nanchang 330029, China
[c] Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, The Chinese Academy of Sciences, Donghu South Road 7, Wuhan 430072, PR China
[d] Hydrological Bureau of Jiangxi Province, Nanchang 330099, China

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ABSTRACT

Interspecific trait variability (e.g., functional diversity) is often correlated with community productivity and thus promotes ecosystem stability. However, we know little about how intraspecific trait variability mediated the effects of environmental gradients on population stability. We applied generalized multilevel path models to investigate multivariate causal hypotheses that environmental effects on population stability of a macrophyte species - *Potamogeton maackianus* - are mediated by physiological and morphological traits variability. Using a hierarchical nested design, we measured quarterly nine physiological traits, and monthly ten morphological traits from 9720 individuals at 27 plots along water depth gradients in Lake Erhai, China. Results showed that changes in water depth and light availability caused significant shifts in intraspecific trait variability, with cascading direct and indirect effects on temporal stability of *P. maackianus*. Water depth exerted major control over population stability, both directly and indirectly via shifts in morphological and physiological traits. Light availability affected population stability indirectly by altering morphological traits. Size traits (shoot morphology and root/shoot ratio) and metabolic traits captured the effect of water depth and light availability on population stability with a relative high accuracy. Our study provide a strong support to the hypothesis that intraspecific trait variability mediate the combined effects of variations on water depth and light conditions on the temporal stability of a dominant macrophtye species in Lake Erhai. Maintaining and enhancing trait variability within plant populations may help to buffer negative effects of anthropogenic environmental changes on population stability.

1. Introduction

Scientists have long been interested in whether diversity mediated environmental effects on stability (Hooper et al., 2002; Tilman et al., 2005; Isbell et al., 2009; Loreau and Mazancourt, 2013; Wang and Loreau, 2016). A body of recent research on this topic has focused on the diversity-stability relationship at community or ecosystem level (Tilman et al., 2006; Grman et al., 2010; Mazancourt et al., 2013; Xu et al., 2015; de la Riva et al., 2016; Zhang et al., 2016). However, how environmental factors influence temporal stability of individual populations remains largely unexplored despite that population dynamic has potential effects on ecosystem stability (Emery and Gross, 2006; Hector et al., 2010; Jucker et al., 2014; Majeková et al., 2014).

To date, the trait-based approach has been increasingly applied to understand the mechanisms governing the effects of environmental gradients on ecosystem functioning (e.g., stability) (Díaz et al., 2007; Laughlin and Laughlin, 2013; Valencia et al., 2015; de la Riva et al., 2016; Strecker et al., 2016). This approach mainly focus on individual functional traits, morpho-physio-phenological attributes which have an indirect impact on fitness via their effects on growth, reproduction and survival (Violle et al., 2007), which can greatly link the processes across ecological scales spanning from individual to ecosystem (McGill et al., 2006). A well excepted response–effect framework based on plant functional traits has been proposed to scale-up from species to

* Corresponding authors at: Ecology Department, College of Bioscience Biotechnology, Institute of Ecology, Hunan Agricultural University, Changsha 410128, PR China (H. Fu). Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, The Chinese Academy of Sciences, Donghu South Road 7, Wuhan 430072, PR China (T. Cao).
E-mail addresses: huifu367@163.com (H. Fu), caote@ihb.ac.cn (T. Cao).

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community level in response to environmental gradients (Shipley et al., 2006; Valencia et al., 2015; de la Riva et al., 2016), which states that changes in the functional structure of communities can partly affect stability. Most of these studies have indicated interspecific trait variability (functional diversity) mediated the environmental effects on stability at community or ecosystem scale, highlighting the role of trait variability in determining the community/ecosystem responses to environmental gradients (Valencia et al., 2015; Fischer et al., 2016; Strecker et al., 2016). However, much less is known about how intraspecific trait variability mediated the effects of environmental gradients on population stability (Crutsinger et al., 2008; Majeková et al., 2014). More insights will be thus gained from approaches including intraspecific trait variability in determining population dynamics (Prasad et al., 2003; Albert et al., 2010).

In freshwater habitats, strong environmental filters such as water depth and light availability are expected to constrain the range and variance of certain key functional traits of macrophyte community (Fu et al., 2014b, 2015), selecting those species from the regional pool harbouring a set of traits that enable them to persist in a particular site. To date, broad morphological, physiological and life history traits of submersed macrophytes have been generally understood and can be associated with effects on ecological, biogeochemical and physical processes (Fu et al., 2014a,b, 2015). Combining ammonium dosing tests and field surveying, our studies have suggested an important link between physiologic traits related to carbon and nitrogen metabolism and depth distribution of macrophyte species (Yuan et al., 2013). Our recent studies have also indicated that there are significant functional responses of macrophyte species along environmental gradients, and higher functional diversity consequently promote productivity of local macrophytes community (Fu et al., 2014a). We found significant effects of environmental filtering and niche differentiation on most of tested morphological traits, and suggested that there were strongly interspecific competition among macrophyte species at local scale (Fu et al., 2014b). The typically strong competition among macrophyte species often result in local dominance of one or a few species and obvious zonation patterns along environmental gradients. However, how individual population of macrophyte species keep itself dominant and stable as response to varying environment has yet to be identified. Notably, macrophyte species showed remarkably high trait variations within species (Santamaría, 2002), and including intraspecific trait variability would greatly improve the detection of biotic interaction among species (Fu et al., 2014b). Thus, the highly intraspecific trait variability may contribute strongly to population-level trait variation and species' response to environmental gradients, which could be used to predict the effects of environmental changes on temporal stability of individual population.

In this study, our main objective was to discern what the causal mechanisms govern the processes of temporal stability in macrophyte population - *Potamogeton maackianus* - along broad environmental gradients (e.g., water depth and light availability), and related to the effects of intraspecific trait variability in a freshwater lake of south China. *P. maackianus* is a submerged macrophyte widely distributed in East Asia (Sun, 1995). It is one of dominate species and mostly forms mono-specific mats in many shallow lakes near the middle reaches of Yangtze River and some plateau lakes in Yunnan Province, China (Sun, 1995). The habitats of this species span across a broad range of ecological scale, involving different environmental gradients (i.e., nutrients, water depth, latitude and altitude). Furthermore, this species show a highly phenotypic plasticity and comparable high genetic diversity as adaptive responses to freshwater habitats (Ni, 2001; Fu et al., 2013). However, it is mysterious that why this species can dominate and keep stable since 1960s and why the macrophyte communities are hardly restored after this species disappeared during eutrophication and dramatic water level fluctuation (Fu et al., 2013). So the stabilizing mechanism of this species should have important ecological significance for the management, restoration of freshwater ecosystem in this region. In this study, we employed a trait based response-effect framework quantifying a broad range of plant morphological and physiological traits associated to resource acquisition, plant structure and metabolism. We used generalized multilevel path models applying a directional separation approach (Shipley, 2009) to test multivariate causal hypotheses that the cascading effects of water depth and light availability on population stability are mediated by intraspecific traits variability.

2. Methods

2.1. Field sampling designs

Present study was carried out in Erhai Lake (25°52′N, 100°06′E) in Yunnan Province, China. It is the second biggest lake of Yunnan Province, with a water surface area of 250 km^2, an average water depth of 11 m (maximum depth of 21 m), and altitude of 1972 m (Fu et al., 2014b). Submersed macrophytes covered more than 60% area of the lake in the 1970 s but reduced to less than 8% in 2009 because of eutrophication and water level fluctuation (Dai, 1984, Li et al., 2008). The macrophyte community compositions in this lake has experienced dramatic changes, with *Potamogeton pectinatus* Linn., *Najas marina* Linn. and *Ottelia acuminata* (Lévl. et Vant.) Dandy dominated during 1960s, *Vallisneria natans*, *Hydrilla verticillatta* and *Potamogeton maackianus* dominated during 1980s, and *P. maackianus* dominated since the late 1990s. Surprisingly, more than 50 km^2 of macrophyte community dominated by *P. maackianus* in the center of south lake (with an average depth of 6.0 m) has been disappeared since 2003–2004, which may be largely attributed to anthropogenic rising of water level.

P. maackianus was sampled monthly from the Haichao (HC, 25°57′N, 100°08′E), Xifeng (XF, 25°36′N, 100°13′E), and Shaping (SP, 25°55′N, 100°06′E) sites from June in 2009 to May in 2010. The samples were obtained from plots with 0.5 m water depth intervals along transects from the shore to the pelagic regions of the lake where the plants are present. Figures of the study sites in Lake Erhai can be viewed in our previous study (Fu et al., 2015). The three sites were selected to represent the full range of the water depth gradient and macrophyte community variation along this gradient. At each site, a series of 5 m × 5 m plots were located along the water depth gradient in each 0.5 m interval as a depth stratum. These surveys extended from the marginal to pelagic regions, where the water depth varied from 0.5 m to 6 m and depended on the maximum colonization depth of macrophyte at specific sites of the lakes. There were a total of 10 plots in HC, 9 plots in XF and 8 plots in SP. The plots were randomly assigned to the water depth gradients in areas dominated by macrophyte species. Locations that were disturbed by recent human activity (e.g., mowing and fishing) were excluded from sampling. Three 0.2 m^2 quadrats of macrophytes were sampled within each 25 m^2 plot by a rotatable reaping hook (diameter = 0.5 m, area = 0.2 m^2). The plants were subsequently weighed to determine the fresh weight of this species in each quadrat. The population biomass was assessed with the average values of four to eight quadrats within a plot. For each plot, the longitude and latitude were recorded by GPS for subsequent revisit sampling, and the water depth was measured by a sounding cone. The photosynthetic available radiation was measured in each plot just beneath the water surface and at 0.5 m depths by a radiation sensor (UW-192) connected to a data logger (Li-1400; Li-cor Company, Lincoln, NE, USA). The light attenuation coefficient (K) in the water column for each plot was calculated as $K = -(1/Z) * \text{Ln}(I_z/I_o)$, where Z is water depth, Iz is irradiance in the depth of Z, and I_o is irradiance in the water surface (Duarte et al., 1986).

2.2. Physiological traits measurements

We measured three physiologic traits – soluble carbohydrate (SC), free amino acid (FAA) and starch - related to carbon (C) and nitrogen