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Impact of changing flood regime on a lakeshore plant community: Long-term observations and individual-based simulation

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ABSTRACT

Disturbance events shape plant communities depending on the disturbance regime as well as on the properties of the species constituting the community. We studied a lakeshore community at Lake Constance, a pre-alpine lake in Central Europe, where disturbance by flooding has a strong impact as the water level is almost not regulated by man. The lakeshore habitats are shaped by annual summer flooding during the vegetation period of plants, with seasonal course and magnitude of water-level fluctuations varying considerably between years. By a combination of field work and modelling we examined (1) whether flooding tolerance and interactions between individuals can explain zonation and species coexistence at lakeshore, (2) how strongly invasive species are affecting habitat specific species, and (3) whether changing flooding regimes due to potential climate changes will affect species composition.

The study was based on a long-term monitoring record (23 years; 1988–2005) of presence/absence of six species along two transects in a species-poor community at Lake Constance and on detailed records of annual flooding. We succeeded in parameterizing a spatially explicit individual-based life-cycle model of community dynamics on a pattern-oriented basis. This gave results on species demography, dispersal, and interactions. The parameterized model could be verified along additional data recorded in 2011.

The results of model parameterization showed that the habitat specialists (characteristic species for the studied lakeshore community) will be able to coexist with stable zonation over the coming decades, mainly due to a contrast between flood tolerance and strength of competitive interactions forming a variant of the competition–colonization trade-off model of coexistence. As a consequence, long-term shortening of the average flooding period, as predicted for the future, should negatively affect flood-tolerant but weakly competing habitat specialists. Here, an avoiding strategy, a shift of flood-tolerant plant species to lower parts of the lakeshore beyond transect boundary and hence beyond present model range, is to be expected.

The modelling results revealed that two native but invasive species will have an increasing impact on the community, and they are predicted to endanger habitat specialists on a long run. This was verified already by the re-examination in 2011. Following the parameter values, invasive species threatening the lakeshore community are both flood-tolerant and competitive. Their expected importance for the fate of the community even exceeds that of possible changes in flood duration.

The study demonstrates that an individual-based model can be developed on the basis of nonstationary, temporally and spatially changing local abundance data. Such a model goes beyond conventional matrix modelling by the inclusion of nonlinear features as a consequence of individual interactions, and such features turn out to be decisive factor for dealing with species coexistence and displacement in a plant community.

1. Introduction

It has long been aware that disturbances, i.e., pronounced external impacts resulting in strong reduction of biomass, will structure biodiversity and ecological functions (Connell, 1978; White and Jentsch, 2001; Johst and Huth, 2005; Turner, 2010). The spectrum of disturbances is manifold, and they can be found in a variety of ecosystems: e.g., tropical forests (Sheil and Burslem, 2003),

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Antarctic marine ecosystems (Johst et al., 2006), or riparian communities (Biswas and Mallik, 2010). Their impact on the structure and diversity of communities or ecosystems depends on attributes of both the disturbance regime and of the properties and dynamics of the community constituents: this interplay can in a general manner be studied by modelling (e.g., Winkler and Stöcklin, 2002; Banitz et al., 2008; Miller and Chesson, 2009; Dos Santos et al., 2011; Seifan et al., 2013).

Plant communities at lakeshore sites often depend on regular flooding leading to heavy impact on the physiology of plants but also to mechanical damage due to wave movement and sediment erosion (Keddy, 2010). The spatial extent and differentiation of such communities are governed (i) by the frequency as well as the intensity (flood duration, height of water layer) of flooding disturbance, and (ii) by the life history of the constituting species. In order to get detailed knowledge on the interaction of these two components in lakeshore communities, we studied, by interplay of long-term field monitoring and simulation modelling, an endangered lakeshore grassland community at Lake Constance (Central Europe). The selected community is phytosociologically described as Deschampsietum rhenanae (Lang, 1967). It consists of clonal plants, either small amphibious forbs or graminoid species, being characteristics of exposed and nutrient-poor shores with coarse-grained sediments. Communities at Lake Constance are exceptional examples for flooding-disturbance impact as the water level of this lake is almost non-regulated by man. The mean amplitude between low and high water levels is about 2 m. As a consequence, amphibious plants are flooded up to several months a year during the vegetation period in summer, and these water-level fluctuations decisively influence element cycles and biodiversity (Wantzen et al., 2008).

In the last decades a decrease in average water level has been observed (Jöhnk et al., 2004; Hoffmann et al., 2008). This decrease is probably an indication for climate-change processes that will lead to major changes in biodiversity. In the case of wetlands, extreme flooding events are expected to increase in number and extent in the course of climatic change (Beniston and Stephenson, 2004; Schär et al., 2004; Lehner et al., 2006). Since it was generally found that the water-depth gradient and water-level fluctuations directly influence lakeshore zonation and species diversity (Keddy, 2010; Strayer and Findlay, 2010), any changes in flood disturbance regime are likely to have dramatic effects on wetland plant communities, on their composition and zonation (Thompson et al., 2009). Moreover, wetlands are especially vulnerable to invasions, as disturbance events may facilitate invasive plants (Zedler and Kercher, 2004). In our context also native species must be considered as invasive if they have the ability to expand rapidly and to replace habitat specific species (Rahel and Olden, 2008; Keddy, 2010).

The impact of flooding on the dynamics of amphibious plants at Lake Constance was already the subject of earlier field work and of community modelling (Strang and Dienst, 2004; Peintinger et al., 1997, 2007, 2010; Peintinger, 2007; Winkler et al., 2011). The modelling approach was based on phenomenological transition models (nonlinear Markov-chain models), which directly referred to species abundances that were determined in the field by counting presence or absence of species in a cell grid (Peintinger et al., 1997; Winkler et al., 2011). These models were able to reproduce the habitat zonation perpendicular to lakeshore, as was found by long-term field monitoring. Simulations showed that habitat specialists will not heavily be affected by long-term changes in average flooding duration as long as these changes are small (<1 month). However, two widespread graminoid species originally not present in the ecosystem and hence at the study site, were found to invade the habitat, and modelling predicted that they may be competitively superior in the long run. The reasons for this invasion and its interfering with the possible impact of climatic change largely remained unclear.

To a large extent the phenomenological transition model of these studies neglected the demographic processes and individual-level interactions that were the basis for the observed abundance changes. However, a consideration of species dynamics only at this level is insufficient: populations consist of individuals with species-specific demography and dispersal; these individuals react locally and can adapt their behaviour to the current state of their biotic and abiotic environment. Simulation models that are spatially explicit and individual-based (SEIB models) are increasingly used for studying species dynamics in plant systems (Berger et al., 2008). In order to base ecological findings about flooding-dependent community dynamics on such a mechanistic level we now present a more complex model of our lakeshore community that technically includes two main aspects. First, it follows the fate of individuals in a spatially explicit manner with an inclusion of demographic details as clonal and sexual reproduction, death, and dispersal, and secondly, flooding as the disturbance process as well as species response is seasonally resolved. In this way a bridge is built to general biological knowledge and, at least potentially, to detailed demographic studies, with the aim to improve the reliability of mechanistic analyses and predictions.

The present study was performed under the methodical hypothesis that pattern-oriented (Grimm and Railsback, 2004) parameterization and validation of SEIB models is feasible on the basis of long-term data sets from simple monitoring species presence or absence in a spatially resolved manner, without counting or tracing individuals. Using the model that resulted in this way and that was verified by independent observations we simulated long-term community dynamics under the present as well as under changing flooding conditions and species composition. In order to get insight into the action of flooding as a community-shaping disturbance and of species invasion as an additional impact we addressed the following main questions:

(1) Can differences in flood tolerance as an important species trait in combination with interactions between individuals reproduce the observed zonation patterns and explain the coexistence of the habitat specialists?
(2) How strong invasive species will influence or even displace habitat specialists?
(3) To which degree will changes in flood disturbance (duration and timing) affect future species composition?

2. Methods

2.1. Study system and field study

Our study site is situated at Lake Constance, in the pre-Alpine region of Southern Germany. The seasonal course of water level at this lake is mainly determined by the weather in the high altitudinal Alpine catchment (Jöhnk et al., 2004). The lake level reaches its minimum at the end of February when precipitation in the catchment is mostly stored as snow and its maximum in June/July due to increased precipitation and snowmelt in spring. Despite basic seasonal regularity, the onset and duration of high water levels varies considerably from year to year. Within the last few decades Lake Constance experienced centennial floods in 1965, 1987, and 1999. Extremely low water levels were reached in 2003 and subsequent years (Jöhnk et al., 2004; Ostendorp et al., 2007). Decomposition of time series has shown that water levels have decreased since 1930 (Jöhnk et al., 2004).

The study was conducted on the peninsula Mettnau, at the lower part of Lake Constance (Untersee) near Radolfzell (south-western