Plant trait composition as an indicator for the ecological memory of rehabilitated floodplains

Marjolein Sterk[a,b,*], Gerrit Gort[c], Hendrika De Lange[d], Wim Ozinga[d],
Marlies Sanders[d], Kris Van Looy[e], Astrid Van Teeffelen[f]

[a]*Wageningen University, Environmental Systems Analysis Group, P.O. Box 47, 6700 AA Wageningen, The Netherlands*
[b]*Open University, Faculty of Management, Science and Technology, P.O. Box 2960, 6401 DL Heerlen, The Netherlands*
[c]*Wageningen University, Biometris, P.O. Box 100, 6700 AC Wageningen, The Netherlands*
[d]*Wageningen University, Alterra, P.O. Box 47, 6700 AA Wageningen, The Netherlands*
[e]*National Research Institute of Science and Technology for Environment and Agriculture IRSTEA Lyon, UR MALY, River Hydro-Ecology Unit ONEMA IRSTEA, 5 rue de la Doua, 69626 Villeurbanne, Lyon, France*
[f]*VU University Amsterdam, Faculty of Earth and Life Sciences, P.O. Box 1087, 1081 HV Amsterdam, The Netherlands*

Abstract

Maintaining ecosystem functioning under global change requires resilient ecosystems to absorb disturbances, reorganize and maintain the adaptive capacity. Maintaining resilience is therefore a common objective for ecosystem management, but how this objective may be achieved remains largely unclear. The concept of ecological memory provides a perspective on how the adaptive capacity of ecosystems can be enhanced through management. It specifies how ecological processes in space and time assist in the reorganization of communities after disturbances. We present a trait-based approach that links environmental variables at site and patch level to plant traits. With a generalized linear mixed-effects model we test how environmental variation in management and floodplain dynamics, within and between sites, relates to plant traits that are considered relevant for ecological memory. The results show different mechanisms that intervene in ecological memory. Grazing enhances recruitment opportunities, both for internal reorganization and for colonization between sites. Dense vegetation structure selects for species survival via resprouting after disturbance and competitive species. Hydrodynamics interact with seed dispersal mechanisms and seed persistence. We show that at different spatial levels, plant trait composition can act as an indicator of ecological processes contributing to the ecological memory of a floodplain ecosystem. For ecosystem management to maintain and use as much of this memory as possible it should incorporate management measures at various levels of scale to enhance ecosystem resilience.

Zusammenfassung

Der Erhalt von Ökosystemfunktionen bei globalen Umweltveränderungen erfordert elastische Ökosysteme, um Störungen zu absorbieren, sich zu reorganisieren und die Anpassungsfähigkeit zu erhalten. Die Resilienz zu erhalten, ist daher ein allgemeines Ziel des Ökosystemmanagements, aber wie dieses Ziel erreicht werden kann, ist weitgehend unklar. Das Konzept des

*Corresponding author at: Open University, Faculty of Management, Science and Technology, P.O. Box 2960, 6401 DL Heerlen, The Netherlands.
Tel.: +31 620449292; fax: +31 317 419000.
E-mail address: marjosterk@gmail.com (M. Sterk).

ökologischen Gedächtnisses bietet einen Ansatz, wie die Anpassungsfähigkeit von Ökosystemen durch Management gestärkt werden kann. Es beschreibt, wie ökologische Prozesse in Raum und Zeit die Reorganisation von Gemeinschaften nach Störungen unterstützen. Wir stellen einen Merkmal-basierten Ansatz vor, der Umweltvariablen auf der Standort- und patch-Ebene mit Pflanzenmerkmalen verbindet. Mit einem verallgemeinerten linearen gemischtem Modell *t*esteten wir, wie sich Unterschiede im Management und bei der Flussauendynamik, innerhalb und zwischen Standorten, zu Pflanzenmerkmalen verhielten, die als bedeutsam für das ökologische Gedächtnis angesehen wurden. Die Ergebnisse zeigten, dass unterschiedliche Mechanismen in das ökologische Gedächtnis eingriffen: Beweidung stärkte die Gelegenheiten für Rekrutierungen sowohl für die interne Reorganisation als auch für Kolonisierungen zwischen Standorten. Dichte Vegetationsstruktur selektiert Arten, die durch Wiederaustrieb nach Störung überleben, und konkurrenzstarke Arten. Die Hydrodynamik interagiert mit Samenausbreitungsmechanismen und Samenpersistenz. Wir zeigen, dass auf unterschiedlichen räumlichen Ebenen die Zusammensetzung der Pflanzenmerkmale als ein Indikator für das ökologische Gedächtnis eines Flussauensystems fungieren kann. Damit das Ökosystemmanagement dieses Gedächtnis erhalten und so viel wie möglich davon nutzen kann, sollte es auf verschiedenen Skalenebenen Maßnahmen einschließen, die die Resilienz des Ökosystems stärken.

Introduction

Ecosystem conservation objectives are increasingly aimed at enhancing ecosystem resilience, particularly in the context of climate adaptation (Heller & Zavaleta 2009; Van Teeffelen, Vos, & Opdam, 2012). Ecosystems are dynamic entities, subject to variation in biotic and abiotic properties which are induced by natural and anthropogenic processes and disturbances over time (Seifan, Seifan, Schiffers, Jeltsch, & Tielbörger 2013). The reorganization of ecosystems after disturbance is referred to as resilience (Holling 1992). In the context of dynamic ecosystems, resilience is the magnitude of disturbance that an ecosystem can absorb before the variables and processes that control its functioning change, and move the system into another stability domain (Holling 1992). The system's resilience is partially determined by 'ecological memory', defined as the capacity of an ecosystem to maintain its structure and function after a disturbance, e.g. through reorganization of the plant community (Bengtsson et al. 2003). Ecological memory is considered to have an internal as well as an external component. The internal component supports reorganization in the area subject to disturbance, for example through survival and seed bank regeneration (e.g., Temperton & Hobbs, 2004; Bischoff, Warthemann, & Klotz, 2009). The external component refers to a species' capacity to recolonize from surrounding areas, through dispersal (Fig. 1; Jeltsch et al. 2013). The extent to which ecological memory can facilitate resilience, is determined by (i) community processes (like competition and survival), (ii) landscape structure (like heterogeneity and patch size), and (iii) changes in (i) and (ii) over time and space (Bengtsson et al. 2003; Sun et al. 2013). The relative importance of internal and external memory will vary depending on disturbance regime and landscape structure (Bengtsson et al. 2003).

Insight in the mechanisms that influence ecological memory is fundamental to identify planning and management strategies with the aim of increasing resilience. This is of particular relevance in human-dominated landscapes, where ecosystem sites are typically small and isolated (DeAngelis & Waterhouse, 1987; Standish et al. 2014). Although several studies have examined how ecological memory is encoded in site history and biological legacies, for example through seed-banks, bud banks, stem fragments and dispersal agents (Sun et al. 2013; Ortmann-Ajkai, Lóczy, Gyenizse, & Pirkhoffer, 2014), the degree to which these mechanisms underlying ecological memory are influenced by the relative role of internal and external memory is poorly understood. A trait-based approach can link environmental variables to plant species' traits. With the growing number of trait-based descriptions of plant strategies, we should be able to gain understanding of how communities respond to disturbances and discern which traits are important for internal and which ones for external memory (Schweiger et al. 2005; Violle et al. 2011). The advantage of using traits over species is that results are applicable beyond biogeographic borders, since species with homologous traits are expected to respond similarly to environmental filters (Keddy, 1992; Sun et al. 2013; Purschke et al. 2014).

In river floodplain systems, variation in flood frequency and duration induces environmental heterogeneity (Southwood 1988; Ortmann-Ajkai et al., 2014) by destroying and generating habitats and controlling connectivity (Sedell, Reeves, Hauer, Stanford, & Hawkins 1990; Ward & Tockner 2001; Leyer 2006). Because river floodplain systems are characterized by high patch turnover, studying such systems allows to identify changes in plant trait composition, in response to discrete flood events over considerable time frames (Wiens 2000). This makes river floodplain systems highly suitable for investigating the relative roles of internal and external memory for ecosystem resilience. This paper focuses on riparian ecosystem sites along the river Meuse in the Netherlands. We study the relation between the
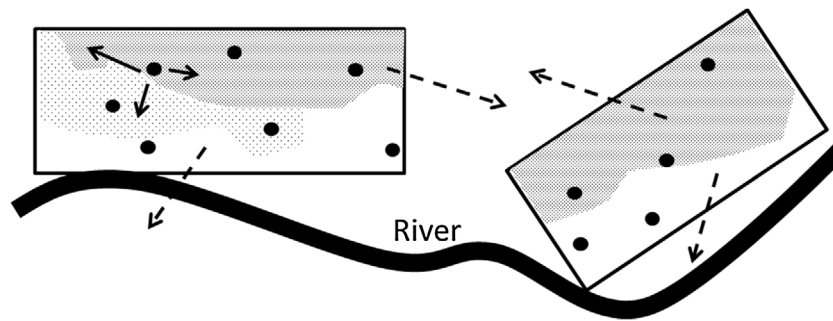
Fig. 1. Schematic representation of rehabilitation sites (rectangles), riparian plant species monitoring sites (black circles) situated along the river (black line). The different background shadings in the rehabilitation sites indicate patches that differ in suitability for plant species as measured by the environmental variables. The solid arrows indicate the scale at which internal memory is considered to operate (within sites). The dashed arrows indicate the scale at which external memory is considered to operate (beyond sites).

spatio-temporal ecosystem dynamics as captured by environmental variables, and plant traits that we hypothesized to be representative of internal and external memory. Two different spatial scales are used, the site and the patch level, where patches represent homogenous areas within sites (Fig. 1). Patch- and site-level variables relate to disturbances at different scales. Objectives of our study are:

1. To identify mechanisms contributing to community reorganization based on the analysis of species traits that reflect riparian plant distribution patterns along disturbance gradients.
2. To discern what factors drive the internal and external memory at different spatial scales.

Materials and methods

Study area

The River Meuse is one of Europe's large rain-fed rivers located in North-western Europe. The floodplain's soil and hydromorphological characteristics are specified in Van Looy, Honnay, Pedroli, and Muller (2006). The Meuse is divided into six reaches based on geomorphological and hydrological characteristics. This study focuses on the section between Eijsden, at the border between Belgium and the Netherlands, and Ammerzoden in the Netherlands covering three reaches: Common Meuse, Peelhorst Meuse and Sand Meuse. This section has a total length of circa 550 km.

From 1990 onward floodplain rehabilitation measures like river widening and dyke relocation have actively been pursued in several areas in the Netherlands. Floodplain rehabilitation aims at creating natural river landscapes including ecological processes, such as erosion, sedimentation, and natural grazing (Geerling et al. 2008). Our study area comprises 38 floodplain rehabilitation sites, covering 1514 ha of floodplain habitats, each with a minimum area of 5.0 ha. From these sites both riparian plant species abundance data and environmental data about abiotic conditions and management were available (described below). We consider two levels of

scale in our analysis, following the hierarchical structure and related processes of floodplain systems. The upper hierarchical level is the level of the rehabilitated floodplain sites. These sites are designated as natural areas by the Dutch government with nature conservation as the main objective. Measures like natural grazing and gravel extraction apply to the sites. The lower hierarchical level is the level of the habitat patches within the rehabilitated floodplains (*sensu* Tansley, 1939; Fig. 1). The number of patches per site fluctuates.

Vegetation data

Across the 38 rehabilitation sites, point abundance data were available for 125 riverine plant species that are considered indicators for a natural river system. The data were recorded once from 15,000 monitoring locations (GPS localized), in the period 2007–2009, and collected in the context of the MaasinBeeld programme (Peters & Kurstjens, 2008; http://www.maasinbeeld.nl).

From the 125 recorded species we excluded aquatic species, as they are related to different environmental factors than terrestrial species (Ozinga et al. 2005), and species for which trait values were not available (trait values are described in section 'plant traits'). The final data set comprised 118 riparian plant species (Appendix A: Table S1). Abundance data were converted into presence-absence records to make the records comparable for statistical analyses.

Environmental data

For each rehabilitation site, two sets of environmental variables were used. The first group comprised five variables at site level (hereafter called site variables) associated with large scale ecological processes: site area in hectares excluding open water (*AreaS*), years since the start of rehabilitation (*Years*), hydromorphological processes (*Hydro*), gravel extraction (*Dist*), and grazing intensity by free roaming semi-wild large herbivores (*Grazing*) (Lejeune, Limpens, & Van der Veen 2002). *Hydro* is an indicator for the rehabilitation

measures taken to improve hydromorphological conditions in the sites (Lejeune et al. 2002; Pedroli, De Blust, Van Looy, & van Rooij 2002) and is classified from no measurements taken, measures that are only affected with extreme floodings, to measures that are based on the morphological characteristics of a particular site (Van Looy, Meire, & Wasson 2008). *Dist* indicates if gravel mining was done (1) or not (0) to lower the bank and floodplain to restore the river contact (Pedroli et al. 2002). *Grazing* indicates the grazing intensity and is divided in classes from no grazing, grazing by one species, grazing by more than one species, to grazing by several species during the whole year (Lejeune et al. 2002). The latter three variables were estimated using expert knowledge (Peters & Kurstjens 2008; http://www.maasinbeeld.nl). The second group of environmental variables comprised three variables at the patch level (hereafter called patch variables) associated with small scale (hydrodynamic) processes in the landscape: patch area (*AreaP*), vegetation structure (*Veg*) and hydrodynamics (*Zone*). *Veg* is an indicator of the effect of water quantity on the patch and is classified in vertical vegetation structures ranging from waterbodies, grassland without/with structures, helophytes, rush, bushes, to trees. *Zone* combines physiological and chemical effects of flood events, like duration, depth, frequency, time of flooding, and salinity. Variables *AreaS* and *AreaP* were log transformed. Patch variables were calculated using the two-dimensional hydrodynamic river model WAQUA (Middelkoop & Perk, 1998; Warmink, Straatsma, Huthoff, Booij, & Hulscher 2013; version 2008). WAQUA is calibrated and validated at the level of the vegetation patches used in this study, providing water level and flow velocities both for static and dynamic flow events. It was applied to a schematic representation of the river Meuse in the period 2004–2008 with corresponding input parameters. See Middelkoop and Perk (1998) for a detailed description.

Plant traits

The five traits that reflect a plant's capacity to locally reorganize after disturbance (internal memory) are growth form (*grform*), specific leaf area (*SLA*), seed mass (*SeedMass*) and seed bank persistence (*SeedPers*). *grform* is a classification of the way plants are morphologically adapted to unfavourable conditions (Raunkiaer 1934). *SLA* is described to relate to plants' ability to tolerate submersion due to flooding (e.g., Clevering 1997; Voesenek, Colmer, Pierik, Millenaar, & Peeters 2006; Violle et al. 2011). Low seed mass is inherent to high seed production, contributes to the chance of successfully colonizing a habitat patch (e.g. Westoby, Leishman, Lord, Poorter, & Schoen 1996; Dupré & Ehrlén 2002; Violle et al. 2011) and can contribute to seed bank persistence (e.g. Nathan 2006; Ozinga et al. 2009). The traits that reflect the capacity to reorganize through spatial processes (external memory) are seed mass, as described above and via long distance dispersal, and seed dispersal by water, wind, fur, dung and birds. We consider the following dispersal vectors with a high efficiency for long-distance dispersal: water (hydrochory), wind (anemochory) and birds (endozoochory and epizoochory) (e.g., Westoby et al. 1996; Dupré & Ehrlén 2002; Ozinga et al. 2009).

Quantitative information on the traits was compiled from the trait database LEDA (Kleyer et al. 2008). To avoid categories with very few species, the ordinal trait *grform* with eleven classes was reduced to two categories: (1) above-ground perennating buds, and (2) and below-ground perennating buds. For *SeedPers*, we classified each species according to its seed bank persistence: (1) not persistent, or (2) persistent. The quantitative traits *SLA* and *SeedMass* were log-transformed. To quantify dispersal mechanisms we classified each species into one or more dispersal agents. When a species showed memberships in multiple categories of dispersal agents, the number of trait categories was added up into the variable polychory (*poly*) and log-transformed (Ozinga et al. 2009). Resulting in *poly low* when species do not score on any of the dispersal agents. *Poly mid* if a species scores one category. And *poly high* if a species score 2 categories (Appendix B Table S2).

Data analysis

The data to be analyzed consist of three tables: a **R** table with location * environmental data, connected by a **L** table with location * species occurrence to a **Q** table with species * trait data. For such data, the typical statistical method to use is the RLQ method (for an application see Sterk et al. 2013). However, in the present study the location * environmental data table has an hierarchical structure of sites and patches within sites, which cannot be handled in ordinary RLQ analysis. An alternative approach is the generalized linear mixed model (GLMM), as described by Jamil, Ozinga, Kleyer, and ter Braak (2013). In this approach the species occurrence is explained by traits of the species and environmental variables of the locations. It handles binary data by assuming a binomial distribution, using a logit link function to link the probability of a species' occurrence to plant traits, environmental data, and their interaction. In the interaction of plant traits and environmental variables the ecological message is hidden: which plant traits modify the regression coefficients of which environmental variables? The GLMM handles pseudo-replication, both for location (multiple species per location), and species (multiple locations per species) by inclusion of random effects for location and species. The GLMM is an example of a random coefficient model, because in the random part of the model random slopes of environmental variables over species are specified. We extended the GLMM, described by Jamil et al. (2013), by inclusion of random effects not only for sites, but also for patches within sites, thereby accommodating the hierarchical structure of the location data. We used the lme4 package in R (R Development Core Team 2010) to fit the GLMM to the data. All explanatory variables were standardized, with the exception of the binary variables *grform*, *SeedPers*, and *Dist*.

In the model building phase, we applied a tiered model selection approach, modified from Jamil, Opdekamp, van Diggelen, and ter Braak (2012). In tier 1 we started with a null model containing only random effects for species, sites, and patches within sites, handling the pseudo-replication. Next, we added, one-by-one, species-dependent random coefficients for environmental variables to the null model, selecting variables which showed the largest improvement of Akaike's Information Criterion (AIC) first. In this tier we selected candidate environmental variables with effects that showed random variation over species, so that potentially they interact with species traits. In tier 2, a new null model was defined as the model from tier 1 with added fixed effects for all selected environmental variables and all five plant traits. This null model served as a starting point for selection of interactions of plant traits with selected environmental variables. Next we added, one-by-one, sets of interactions of each selected environmental variable with all plant traits, selecting first the set which improved the AIC most. In tier 3, individual interactions and main effects, not involved in remaining interactions, labelled as unimportant according to AIC, were removed from the model, yielding the most parsimonious final model.

Results

In the model selection process, all eight environmental variables were included in the first tier with random effects for species, sites and patches within sites. The fact that all environmental variables were selected means that plant species showed different responses (occurrences) to all environmental variables, indicating the relevance of the environmental variables for the set of species in question. The order of variable selection was *Hydro*, *Zone*, *Grazing*, *AreaS*, *Dist*, *Years*, *Veg*, *AreaP*. The second tier – with starting model containing main effects of selected environmental variables and all species traits – selected the sets of interactions of site variable *Grazing*, and patch variables *Zone* and *Veg*. In the final model, the following interactions between variables were significant ($p < 0.05$): *SeedMass:Grazing*, *SeedPers:Zone*, *poly:Zone*, *grform:Veg* and *SLA:Veg* (Table 1). Of these, the interactions between *SeedMass* and *Grazing*, *grform* and *Veg*, and between *SLA* and *Veg* had a positive sign (Table 1). The interactions between *SeedPers* and *Zone* and between *poly* and *Zone* had a negative sign. A positive interaction parameter indicates that at higher values of the plant trait (e.g. *SeedMass*) the change in occurrence probability for a unit change in environmental variable (e.g. *Grazing*) becomes larger (more positive). These relationships are visualized in Fig. 2. Note that the occurrence probability of plant species is low due to a high amount of absence records. Because the GLMM analyses used the median occurrence of species per patch. The median patch occurrence fraction of plant species was 0.0063 (5 occurrences in 797 patches; range 1–235). This median is calculated with the species fraction of

Table 1. Effects of site and patch variables on plant traits in floodplains along the Dutch Meuse using GLMM. Parameter estimates are taken from the fixed effects of the final model based on tiered forward selection. Bolded *p*-values reflect statistical significance at the 0.05 level. See Table S2 for key to variable names.

Explanatory variables	Parameter estimate	Standard Error	*p*-Value
SeedPers:Zone	−0.21131	−2.5310	**<0.05**
grform:Veg	0.18456	0.07677	**<0.05**
SeedMass:Grazing	0.18186	0.04355	**<0.001**
poly:Zone	−0.08795	0.03632	**<0.05**
SLA:Veg	0.08003	0.03630	**<0.05**
poly:Grazing	−0.07502	0.03961	0.06
SeedMass:Zone	0.07099	0.04004	0.08

occurrence for all 797 patches, resulting in a minimum occurrence of 0.001254 (species is present in only one patch) and a maximum occurrence of 0.2949 (species is present in 235 patches), Fig. 2 shows for each significant interaction, how species' probabilities of occurrence change over the values of the environmental variable, predicted from the GLMM analyses. Each interaction is split for species with low, medium, or high trait values (for *SeedMass*, *poly*, and *SLA*) or binary values (for *SeedPers* and *grform*), keeping all other explanatory variables at their average values. The interactions quantitatively show how species are selected through environmental variables based on their traits. For example, species with a high seed mass show a positive response (higher occurrence probability) to increased grazing intensity, whereas species with a low seed mass respond negatively to increased grazing. In other words: in sites with high grazing intensity relatively more species with high seed mass are found, whereas in low grazing sites species with low seed mass dominate. For all other interactions the probability of species occurrence increases with increasing environmental value (*Zone* and *Veg*), but the rate of change differs. Plant species with a low number of dispersal mechanisms (low values of *poly*) and no seed bank persistence (low values of *SeedPers*) showed higher sensitivity to changes in the hydromorphology at the patch level (*Zone*) compared to plant species with high values of *poly* and *SeedPers*. Plant species with high *SLA* and below ground growth form showed to be more sensitive to changes in *Veg* compared to plant species with low *SLA* and above ground growth form.

Discussion

The external (spatial) component of ecological memory is considered to be sensitive to landscape configuration and composition, factors that can be partially changed through landscape management (Peterson, Allen, & Holling 1998). Therefore, it is important to mechanistically understand the link between spatial landscape characteristics, ecological memory and system responses to disturbances. By studying
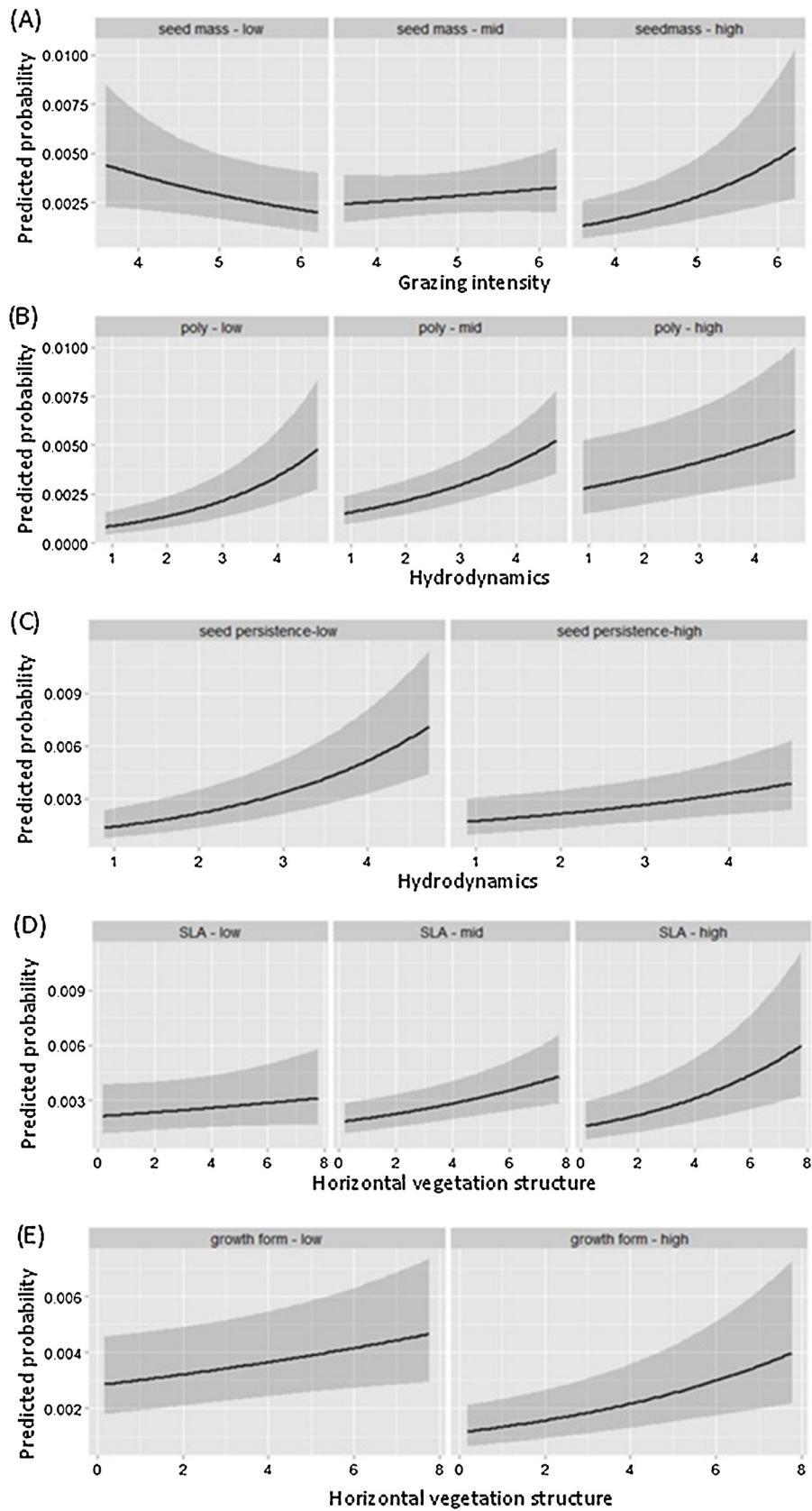
Fig. 2. Predicted probability of plant species occurrence (solid lines) for different classes of traits with a 95% confidence band, in relation to site or patch variables. Interactions between (A) seed mass and grazing (site variable), (B) polychory and hydrodynamic zone (patch variable), (C) seed persistence and hydrodynamic zone (patch variable), (D) specific leaf area and vegetation structure (patch variable), and (E) growth form and vegetation structure (patch variable). Based on data from floodplains along the Dutch Meuse using GLMM.

for real systems how disturbance shapes community composition, measured through plant traits, it is possible to identify mechanisms behind ecological memory and their relation to management measures. The advantage of using traits over species is that the results can be extrapolated to other ecosystems, since species with homologous traits are expected to respond similarly to environmental filters.

Interactions contributing to internal and external memory

The approach applied in this study allowed to extract the most relevant interactions between environmental variables and plant traits which are considered important for internal and external ecological memory in floodplains. As the patch occurrence probabilities of plant species are small (median 0.0063; range 0.001–0.295), the probabilities predicted by the GLMM as shown in Fig. 2 are very low too. Quite a large number of species (25 out of 118) were present in only a single patch. Such isolated populations that are not part of a may indicate vulnerability of particular species. Although the probability of species occurrence is low, an increase in the occurrence probability from 0.001 to 0.005 is a fivefold increase of the chance to find a species in a patch with specific environmental conditions. We think this is valuable information for ecologists who are concerned about environmental impacts on ecosystems. Moreover trait-based approaches to ecology offer several powerful advantages over approaches relying on species identity alone. First, traits are more directly connected to and influenced by the environment (Cornelissen et al. 2003; Kleyer et al. 2008). Second, species come and go, but certain traits may remain and be influenced similarly by environment regardless of which species carries the trait. Thus, if we want to understand how disturbances influence species over long time scales, focusing on their traits is a powerful way of gaining insight. We discuss the significant interactions here, starting with the interaction with the highest parameter value (see Table 1).

We found higher occurrence probability of plant species with low seed persistence in patches with high hydrodynamics. This contradicts earlier studies indicating that most species living in disturbed habitats have persistent seeds (Ackerly 2004). Though, work on large datasets showed that a collection of variables, including seed shape, ease of burial and physiological traits, influences seed persistence. Our results seem in accordance with studies showing that pioneer plant species are adapted to high dynamic environments and do not invest in seed persistence (Amoros & Bornette 2002; Ozinga et al. 2009; Casanova 2015). In contrast, species adapted to low dynamic environments have to invest in seed persistence to survive on the long term, thus relying on internal memory. Taken together, internal memory is the major driver in less dynamic floodplain zones, whereas external memory dominates highly dynamic floodplains.

The higher occurrence probability of species with an aboveground budbank in dense vegetation indicates the abundance of endurers. Endurers are one of the adaptation strategies to flooding described by Naiman and Décamps (1997). Endurers resprout after breakage or burial of either the stem or roots from floods. High occurrence of endurers can promote short distance dispersal with flooding as above-ground connections are easily able to spread in the water through adventitious roots, which are characteristic of flood-tolerant plant species (Boedeltje, Bakker, Bekker, Van Groenendael, & Soesbergen 2003). Therefore, functional adaptation of these species indicates a positive contribution of the aboveground budbank to the internal memory of the ecosystem.

Our results show a positive interaction between seed mass and grazing of the sites. Seed mass is probably the most important characteristic of a plant species with regard to seedling recruitment (Leishman, Westoby, & Jurado, 1995; Coomes & Grubb, 2003; Turnbull, Coomes, Hector, & Rees 2004). Large seeds are better sustained by nutrients and more buoyant in water favouring long-distance dispersal (Römermann, Tackenberg, & Poschlod, 2005; Leyer 2006). The relationship between seed mass and grazing by free roaming 'semi-wild' herbivores is relatively poorly studied though. One study including low-intensity permanent grazing with free-ranging cattle, sheep and ponies, showed that large seeds germinated better in the presence of herbivores then in abandoned areas compared to small seeds (Kahmen & Poschlod, 2007). Since the herbivores in our study are free-ranging in a site, some areas are intensively grazed and others are barely grazed. Grazed areas are characterized by gradients of bare soil through trampling, regenerating vegetation and mature vegetation and the positive effects of gaps in enhancing seedling recruitment is widely acknowledged (e.g., Leemans 1991; Zobel, Otsus, Liira, Moora, & Möls 2000). In this way grazing promotes the internal and external memory of floodplain plant species by creating suitable habitats for internal reorganization and contributing to colonization of previously disturbed sites.

Plant species with few dispersal vectors (low polychory) showed to be more sensitive to changes in hydrodynamics compared to plant species with high polychory. Hydrodynamics is a combination of physiological and chemical water influences, like duration, depth, frequency and time of flooding, and salinity. The variable hydrodynamics is often used as an indicator of river-floodplain connectivity. The studies of Boedeltje et al. (2003) and Leyer (2006) also show high numbers of water-dispersed seeds in frequently disturbed habitats, and low importance of wind and animal dispersal in these areas. Their results suggest increased importance of investment in colonization of new patches (external memory) relative to short-distance dispersal and local persistence. However, in this study dispersal vectors are not analyzed separately because the amount of data that can be processed with a GLMM is limited.

The significant relation between dense vegetation structure and high specific leaf area of plant species at patch level is consistent with the hypothesis that species in less disturbed floodplain habitats invest more in their potential relative growth rate. These species are also known for their shade-tolerance and resource-rich environments (Cornelissen et al. 2003). As disturbance frequency decreases, biological interactions increase (e.g. competition and herbivory), favouring competitive species. Disturbances by floods no longer dominate plant communities at this end of the gradient. This shows that species living in dense vegetation structures rely on internal memory of the ecosystem for reorganization.

Importance of scale for ecosystem management

Our study showed that species traits can be explained by an extended GLMM that incorporates environmental gradients of disturbances at site and patch level. Scale is essential to the analysis of ecological processes (Holling 1992). The relationship between two variables in a natural system can be obscured by other variables at other scales and the interferences drawn from an observed relationship can be distorted or even reversed depending on the scale at which that relationship is measured. Van Looy et al. (2006) found that the taxonomic and functional structure of floodplain meadow communities was distinct among ecoregions and that clustering of species by ecoregion reflected different species' affinities for environmental variables. Relationships between species traits and environmental gradients provide information about environmental filtering, particularly when the traits suggest an advantage in the associated environment (e.g., Keddy 1992; Schweiger et al. 2005). Our results show how different mechanisms intervene in ecological memory. The variability in ecological mechanisms found at different spatial scales, represent a memory that enables ecosystems to adapt to changes in the environment. For ecosystem management to maintain and use as much of this memory as possible it should incorporate measures at various levels of scale. While it is often possible for a manager to intervene at the level of a site, managing to maintain ecological memory over larger spatial scales becomes increasingly more difficult. Managers will face constraints in jurisdiction over larger spatial scales, trade-offs with other land use types such as agriculture and other management goals such as flood prevention, and financial constraints on the amount of restoration measures. Therefore, only few management plans explicitly consider the spatio-temporal dynamics to which ecosystems are subjected.

Conclusions

We found that environmental variables associated with floodplain disturbances were significantly related to plant traits at two spatial scale levels. At site level grazing pressure is significantly related to seed mass. At patch level hydrodynamics is significantly related to polychory and seed persistence, and vegetation structure to specific leaf area and growth form. We linked these significant relationships to ecological processes that allow ecosystems to reorganize following disturbances: internal and external ecological memory. By better understanding how the environment filters species and shape communities based on traits, the capacity of these systems to reorganize after disturbances can be better managed, in favour of ecological resilience. GLMM's are useful tools in this respect, allowing to obtain a better understanding of the relative role of ecological factors at different spatial scales and ultimately reinforcing management strategies to support ecological resilience. Our trait-based approach contributes to understand phenomena that can be used to predict vegetation responses to disturbances.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2016.05.002.

References

Ackerly, D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs, 74*, 25–44.

Amoros, C., & Bornette, G. (2002). Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology, 47*, 761–776.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., et al. (2003). Reserves, resilience and dynamic landscapes. *AMBIO: A Journal of the Human Environment, 32*, 389–396.

Bischoff, A., Warthemann, G., & Klotz, S. (2009). Succession of floodplain grasslands following reduction in land use intensity: The importance of environmental conditions, management and dispersal. *Journal of Applied Ecology, 46*, 241–249.

Boedeltje, G., Bakker, J. P., Bekker, R. M., Van Groenendael, J. M., & Soesbergen, M. (2003). Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *Journal of Ecology, 91*, 855–866.

Casanova, M. T. (2015). The seed bank as a mechanism for resilience and connectivity in a seasonal unregulated river. *Aquatic Botany, 124*, 63–69.

Clevering, O. A. (1997). Effects of litter accumulation and water table on morphology and productivity of *Phragmites australis*. *Wetlands Ecology and Management, 5*, 275–287.

Coomes, D. A., & Grubb, P. J. (2003). Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology and Evolution, 18,* 283–291.

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., et al. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany, 51,* 335–380.

DeAngelis, D. L., & Waterhouse, J. C. (1987). Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs,* 1–21.

Dupré, C., & Ehrlén, J. (2002). Habitat configuration, species traits and plant distributions. *Journal of Ecology, 90,* 796–805.

Geerling, G., Kater, E., Van den Brink, C., Baptist, M., Ragas, A., & Smits, A. (2008). Nature rehabilitation by floodplain excavation: The hydraulic effect of 16 years of sedimentation and vegetation succession along the Waal River, NL. *Geomorphology, 99,* 317–328.

Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation, 142,* 14–32.

Holling, C. S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological Monographs, 62,* 447–502.

Jamil, T., Opdekamp, W., van Diggelen, R., & ter Braak, C. J. (2012). Trait-environment relationships and tiered forward model selection in linear mixed models. *International Journal of Ecology, 2012*

Jamil, T., Ozinga, W. A., Kleyer, M., & ter Braak, C. J. (2013). Selecting traits that explain species–environment relationships: A generalized linear mixed model approach. *Journal of Vegetation Science, 24,* 988–1000.

Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., et al. (2013). Integrating movement ecology with biodiversity research-exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology, 1,* 1–13.

Kahmen, S., & Poschlod, P. (2007). Does germination success differ with respect to seed mass and germination season? Experimental testing of plant functional trait responses to grassland management. *Annals of Botany, 101,* 541–548.

Keddy, P. A. (1992). Assembly and response rules – 2 goals for predictive community ecology. *Journal of Vegetation Science, 3,* 157–164.

Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., et al. (2008). The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology, 96,* 1266–1274.

Leemans, R. (1991). Canopy gaps and establishment patterns of spruce (*Picea abies* (L.) Karst.) in two old-growth coniferous forest in central Sweden. *Vegetatio, 93,* 157–165.

Leishman, M. R., Westoby, M., & Jurado, E. (1995). Correlates of seed size variation: A comparison among five temperate floras. *Journal of Ecology, 83,* 517–530.

Lejeune, M., Limpens, H., & Van der Veen, J. (2002). The Border Meuse Nature Development Project Where water meets gravel meets nature . . .. In B. Redecker, W. Härdtle, P. Finck, U. Riecken, & E. Schröder (Eds.), *Pasture landscapes and nature conservation* (p. 346). Springer.

Leyer, I. (2006). Dispersal, diversity and distribution patterns in pioneer vegetation: The role of river-floodplain connectivity. *Journal of Vegetation Science, 17,* 407–416.

Middelkoop, H., & Van Der Perk, M. (1998). Modelling spatial patterns of overbank sedimentation on embanked floodplains. *Geografiska Annaler: Series A, Physical Geography, 80,* 95–109.

Naiman, R. J., & Décamps, H. (1997). The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics,* 621–658.

Nathan, R. (2006). Long-distance dispersal of plants. *Science, 313,* 786–788.

Ortmann-Ajkai, A., Lóczy, D., Gyenizse, P., & Pirkhoffer, E. (2014). Wetland habitat patches as ecological components of landscape memory in a highly modified floodplain. *River Research and Applications, 30,* 874–886.

Ozinga, W. A., Schaminée, J. H., Bekker, R. M., Bonn, S., Poschlod, P., Tackenberg, O., et al. (2005). Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos, 108,* 555–561.

Ozinga, W. A., Römermann, C., Bekker, R. M., Prinzing, A., Tamis, W. L., Schaminée, J. H., et al. (2009). Dispersal failure contributes to plant losses in NW Europe. *Ecology Letters, 12,* 66–74.

Pedroli, B., De Blust, G., Van Looy, K., & van Rooij, S. (2002). Setting targets in strategies for river restoration. *Landscape Ecology, 17,* 5–18.

Peters, B., & Kurstjens, G. (2008). *Maas in Beeld: Succesfactoren voor een natuurlijke rivier. Projectgroep Maas in Beeld.* pp. 99. Bureau Drift/Kurstjens ecologisch adviesbureau, Berg en Dal/Ubbergen (in Dutch).

Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems, 1,* 6–18.

Purschke, O., Sykes, M. T., Poschlod, P., Michalski, S. G., Römermann, C., Durka, W., et al. (2014). Interactive effects of landscape history and current management on dispersal trait diversity in grassland plant communities. *Journal of Ecology, 102,* 437–446.

Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography.* Oxford: Clarendon.

Römermann, C., Tackenberg, O., & Poschlod, P. (2005). How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. *Oikos, 110,* 219–230.

Schweiger, O., Maelfait, J. P., van Wingerden, W., Hendrickx, F., Billeter, R., Speelmans, M., et al. (2005). Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *Journal of Applied Ecology, 42,* 1129–1139.

Sedell, J. R., Reeves, G. H., Hauer, F. R., Stanford, J. A., & Hawkins, C. P. (1990). Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems. *Environmental Management, 14,* 711–724.

Seifan, M., Seifan, T., Schiffers, K., Jeltsch, F., & Tielbörger, K. (2013). Beyond the competition-colonization trade-off: Linking multiple trait response to disturbance characteristics. *The American Naturalist, 181,* 151–160.

Southwood, T. R. E. (1988). Tactics, strategies and templates. *Oikos,* 3–18.

Standish, R. J., Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T., Suding, K. N., Battaglia, L. L., et al. (2014). Resilience in ecology: Abstraction, distraction, or where the action is? *Biological Conservation, 177,* 43–51.

Sterk, M., Gort, G., Klimkowska, A., Van Ruijven, J., Van Teeffelen, A. J. A., & Wamelink, G. W. W. (2013). Assess ecosystem

resilience: Linking response and effect traits to environmental variability. *Ecological Indicators*, *30*, 21–27.

Sun, Z., Ren, H., Schaefer, V., Lu, H., Wang, J., Li, L., et al. (2013). Quantifying ecological memory during forest succession: A case study from lower subtropical forest ecosystems in South China. *Ecological Indicators*, *34*, 192–203.

Tansley, A. G. (1939). . *The British islands and their vegetation* (vol. 1 of 2) United Kingdom: Cambridge University Press., 484 pp.

Temperton, V. M., & Hobbs, R. J. (2004). The search for ecological assembly rules and its relevance to restoration ecology. In *Assembly rules and restoration ecology: Bridging the gap between theory and practice* (pp. 34–54). Washington: Island Press.

Turnbull, L. A., Coomes, D., Hector, A., & Rees, M. (2004). Seed mass and the competition/colonization trade-off: Competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology*, *92*, 97–109.

Van Looy, K. V., Honnay, O., Pedroli, B., & Muller, S. (2006). Order and disorder in the river continuum: The contribution of continuity and connectivity to floodplain meadow biodiversity. *Journal of Biogeography*, *33*, 1615–1627.

Van Looy, K. V., Meire, P., & Wasson, J.-G. (2008). Including riparian vegetation in the definition of morphologic reference conditions for large rivers: A case study for Europe's Western Plains. *Environmental Management*, *41*, 625–639.

Van Teeffelen, A. J. A., Vos, C. C., & Opdam, P. (2012). Species in a dynamic world: Consequences of habitat network dynamics on conservation planning. *Biological Conservation*, *153*, 239–253.

Violle, C., Bonis, A., Plantegenest, M., Cudennec, C., Damgaard, C., Marion, B., et al. (2011). Plant functional traits capture species richness variations along a flooding gradient. *Oikos*, *120*, 389–398.

Voesenek, L. A. C. J., Colmer, T. D., Pierik, R., Millenaar, F. F., & Peeters, A. J. M. (2006). How plants cope with complete submergence. *New Phytologist*, *170*, 213–226.

Ward, J. V., & Tockner, K. (2001). Biodiversity: Towards a unifying theme for river ecology. *Freshwater Biology*, *46*, 807–820.

Warmink, J. J., Straatsma, M. W., Huthoff, F., Booij, M. J., & Hulscher, S. J. M. H. (2013). Uncertainty of design water levels due to combined bed form and vegetation roughness in the Dutch River Waal. *Journal of Flood Risk Management*, *6*, 302–318.

Westoby, M., Leishman, M., Lord, J., Poorter, H., & Schoen, D. J. (1996). Comparative ecology of seed size and dispersal [and discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *351*, 1309–1318.

Wiens, J. A. (2000). Ecological heterogeneity: An ontogeny of concepts and approaches. In M. J. Hutchings, E. A. John, & A. J. A. Stewart (Eds.), *The ecological consequences of environmental heterogeneity* (pp. 9–31). Oxford: Blackwell Science.

Zobel, M., Otsus, M., Liira, J., Moora, M., & Möls, T. (2000). Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, *81*, 3274–3282.