River corridor plants in North-western Germany are threatened by small population size and short-term environmental events

Stromtalpflanzen im nordwestlichen Deutschland sind durch kleine Populationsgrößen gefährdet

Christina Wärner[1,*], Werner Wosniok[2] & Martin Diekmann[1]

[1]*Vegetation Ecology and Conservation Biology, Institute of Ecology, FB 2, University of Bremen, Leobener Str., 28359 Bremen, Germany, cwinter@uni-bremen.de; mdiekman@uni-bremen.de;*
[2]*Institut für Statistik, FB 3, University of Bremen, Achterstr. 30, 28359 Bremen, Germany, wwosniok@math.uni-bremen.de*
*Corresponding author

Abstract

River corridor plants in Central Europe account for an above-average proportion of endangered species. The main objective of this study was to examine the effects of habitat fragmentation and abiotic conditions on the survival and changes in population size of four endangered, long-lived river corridor plant species (*Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis,* and *Senecio paludosus*) over the course of at least ten years. We sampled altogether 138 populations in the Weser and Elbe river systems in North-western Germany.

Overall, 33% of the populations went extinct during the study period. Extinction rates and changes in population size were related to initial population sizes, but not to population isolation and only marginally so to habitat quality. Large populations (> 100 individuals) had a much higher probability to survive or increase in size (to > 1000 individuals) than smaller populations. There was no general decline in population size in surviving populations, and extinction rates and changes in population size were independent of time. We therefore conclude that the high extinction rates in small populations are best explained by sudden short-term environmental events, such as changes in land use, rather than by long-term negative effects of, for example, genetic deterioration. A projection matrix for the next 117 years, however, predicted that 85% of the surveyed populations will have gone extinct. Since any establishment of new populations in the study area is unlikely owing to the lack of potential habitats and dispersal limitation, river corridor plants will probably continue to decline. Apart from preventing further habitat deterioration it will be crucial to maintain or establish an appropriate management, and to avoid sudden and adverse changes in land use.

Keywords: extinction rate, fragmentation, habitat quality, land use change, revisitation study, transition probability

Erweiterte deutsche Zusammenfassung am Ende des Manuskripts

1. Introduction

In Central Europe, more than 100 vascular plant species are exclusively or predominantly confined to the basins of large rivers. These so-called river corridor plants share a similar distribution pattern (e.g., ZACHARIAS & GARVE 1996), but otherwise show very different habitat preferences (KORSCH 1999, BURKART 2001). About 23% of the species are of high conservation priority, a proportion nearly twice as high as compared with the entire vascular plant flora in Central Europe (SCHNITTLER & GÜNTHER 1999). The main reason for the threat to these species is the destruction and deterioration of near-natural habitats along the rivers, caused by the regulation of water courses, land reclamation and agricultural intensification. At present, most populations are completely cut off from the natural river dynamics caused by the construction of dikes, and populations are therefore often small and highly isolated from each other. Especially for the North German lowlands, a large body of literature about the ecology, dynamics and restoration of riverine flood meadows has accumulated (e.g., ROSENTHAL 1992, JENSEN & SCHRAUTZER 1999). Particular attention has often been directed to the processes of seed germination and seedling establishment (JENSEN & GUTEKUNST 2003, DONATH et al. 2003, 2007, LEYER & PROSS 2009).

Habitat fragmentation in terms of decreasing population size and increasing population isolation has been shown to have negative effects on plant performance and reproduction (e.g., KÉRY et al. 2000, JACQUEMYN et al. 2002, KOLB 2005), although the selection of species used to study the effects of habitat fragmentation has been biased towards groups likely to be particularly vulnerable (HEINKEN & WEBER 2013). In a general conceptual model, GILPIN & SOULÉ (1986) suggested that populations reaching a minimum threshold number of individuals may enter into a so-called extinction vortex, a circular process in which ever decreasing plant fitness leads to a decline in population size and eventually to extinction. The increased risk of extinction for small populations is caused by a number of factors, including demographic stochasticity (LANDE 1993, KÉRY et al. 2003), environmental stochasticity (LANDE 1993), loss of genetic variation (ELLSTRAND & ELAM 1993, YOUNG et al. 1996), and the disruption of biotic interactions with pollinators and seed dispersers (JENNERSTEN 1988, ÅGREN 1996, KOLB 2005).

There is, however, little empirical evidence that small population size causes a further decline in population size and eventually leads to extinction, because long-term data on the dynamics of plant populations are scarce. Only a few studies have compared current with historical population sizes to examine extinction rates of plants and the factors causing their local disappearance (OUBORG 1993, FISCHER & STÖCKLIN 1997, ENDELS et al. 2002, LIENERT et al. 2002, MATTHIES et al. 2004, HONNAY et al. 2009, SUTTON & MORGAN 2009). The monitoring of perennial species is of particular interest, because habitat fragmentation may affect the population turnover of long-lived species only with a certain delay (FISCHER & STÖCKLIN 1997, VELLEND et al. 2006, VAN CALSTER et al. 2008, SCHLEUNING & MATTHIES 2009).

In an assessment program for endangered plant species in Niedersachsen, a federal state in North-western Germany with a high proportion (54%) of endangered river corridor plants (ZACHARIAS & GARVE 1996), the location and size of populations of these plant species has been recorded since the mid 1980s. We used these monitoring data to revisit 207 populations of four threatened species to examine the effects of habitat fragmentation and abiotic conditions on changes in population size over the course of at least 10 years. For the selected

species, a previous study had shown that plant fitness was generally negatively affected by decreasing population size and / or increasing isolation, but also influenced by habitat quality (WINTER et al. 2008).

Our intention was to test (1) whether small populations were more prone to extinction than large ones, and (2) whether the changes in population size of surviving populations were related to initial population size, isolation and environmental conditions. We aimed to provide evidence for the negative effects of reduced plant fitness (as shown in a previous study by WINTER et al. 2008) on population survival of long-lived species and to give advice for the conservation of endangered river-corridor plants.

2. Methods

2.1 Study area and species

Fieldwork was carried out in 2005 and 2006 in floodplains of the Weser and Elbe river systems in North-western Germany (Fig. 1). In this area, 85 plant species are classified as river corridor plants (ZACHARIAS & GARVE 1996), of which four endangered taxa (GARVE 2004) were selected: *Euphorbia palustris* L. (*Euphorbiaceae*), *Pseudolysimachion longifolium* (L.) Opiz (*Plantaginaceae*), *Sanguisorba officinalis* L. (*Rosaceae*), and *Senecio paludosus* L. (*Asteraceae*).
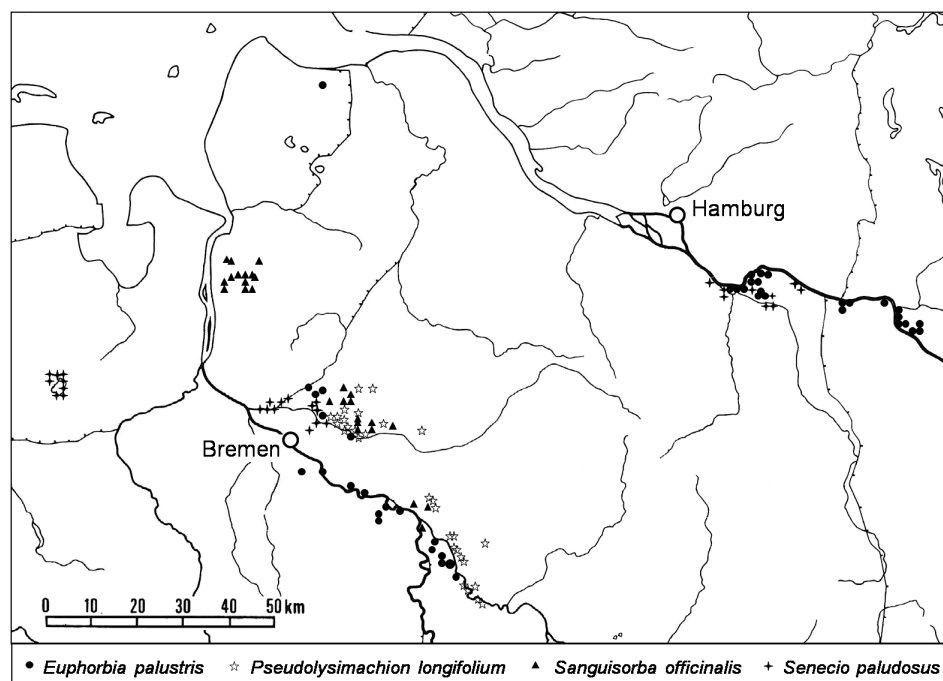

Fig. 1. Location of surveyed populations of *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis*, and *Senecio paludosus* in the floodplains of the river systems Weser and Elbe in North-western Germany.

Abb. 1. Lage der untersuchten Populationen von *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus* in den Stromtälern von Weser und Elbe im nordwestlichen Deutschland.

All species represent perennial herbs that reproduce sexually via seeds and vegetatively by means of short underground rhizomes. Natural habitats in the study area include wet meadows and the edges of nutrient-rich lakes and rivers. As a result of habitat loss, the species are at present mostly found in abandoned grasslands and ditch banks. All species have over the past decades shown a decline both in the Weser-Elbe region (CORDES et al. 2006) and in the area of Hamburg (POPPENDIECK et al. 2010, here *P. longifolium* is lacking).

2.2 Selection and revisitation of study sites

Within the framework of the assessment program for endangered plants in North-western Germany, data about the location (marks on a map 1 : 50000) and rough estimates of population sizes (in eight classes: 1, 2–5, 6–25, 26–50, 51–100, 101–1000, 1001–10000, >10000 flowering individuals) were collected by different voluntary botanists normally once-only between 1982 and to date. We were allowed to use these official data and found a total of 383 records of the four species in the study area, but used only those records that referred to estimates of population size until 1996 as the year of the first record. Furthermore, some records were omitted from the analysis because several marks on the maps were too imprecise to locate the populations in the field. In total 207 populations were selected and revisited during peak flowering of the species. Two observers searched each site for the occurrence of the studied species for up to 2 hours. All species were relatively easy to detect in the field owing to their tall stature and conspicuous inflorescence. If this search remained unsuccessful, we considered the population to have gone extinct. Populations at sites that were difficult to access were omitted from the analysis due to the unreasonably effort of time to arrive at them. By this, we avoided an overestimation of extinction events, which has been shown to be a crucial factor for the calculation of incorrect extinction probabilities of species (KÉRY et al. 2006). Altogether 138 populations were included in the final data analysis (Table 1).

Population size was determined as the number of flowering plants and assigned to the eight size classes previously mentioned. In *E. palustris* and *S. paludosus*, individuals were clearly separated from each other, whereas, in the two other species, individuals in terms of genets were difficult to identify as the shoots form dense clusters that are impossible to disentangle. Here, each ramet was treated as one individual. Population isolation as defined as the distance to the nearest population and determined with the help of detailed topographic maps ranged from 50 m to 62.5 km (median 788 m).

Table 1. Number of surveyed populations included in the multinomial logistic regression models 1, 2, and 3 for each of the studied species: *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis*, and *Senecio paludosus*.

Tabelle 1. Anzahl der untersuchten Populationen in den mit multinomialer logistischer Regression erstellten Modellen 1, 2 und 3 für die vier Arten *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus*.

	Number of populations included		
Species	model 1	model 2	model 3
Euphorbia palustris	46	34	15
Pseudolysimachion longifolium	31	22	15
Sanguisorba officinalis	27	18	15
Senecio paludosus	34	12	-
Total number of populations	138	86	45

2.3 Habitat quality

As it was not possible to locate the sites of extinct populations with sufficient accuracy, habitat quality was only assessed for sites with surviving populations. For 86 populations, patch size (area occupied by a species given in m²) and habitat type (classified in six categories: [1] ditch bank, [2] shore of a river or lake, [3] swamp forest, [4] grassland, [5] verge and [6] fallow) were determined. We furthermore selected 15 surviving populations of varying size of each of the species to collect data on additional habitat factors (Table 2). However, *S. paludosus* was omitted from this part of the study because only few populations of this species had survived. In each of these 45 populations, soil samples were collected during a rainless period in July 2006 (see WINTER et al. 2008). The samples consisted of five pooled cores (100 cm³ down to a depth of 4 cm) of mineral soil. Soil moisture was measured gravimetrically. Prior to chemical analysis, all air-dried samples were passed through a 2 mm-sieve. We determined pH in a solution of 10 g of soil and 25 ml of 0.01M $CaCl_2$ with a standard glass electrode. Plant available phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were extracted with ammonium lactate. P was measured photometrically by flow injection analysis (FIA; reagent: ammonium molybdate) and cations by Atomic Absorption Spectroscopy (all expressed in mg per 100 g soil). The contents of carbon (C) and nitrogen (N) were determined using an elemental analyzer (EuroEA 3000, HEKA-tech, Germany).

Mean vegetation height of a population was calculated from at least 5 measurements (dependent on patch size) in the patch. Light intensity was measured as photosynthetic photon flux density (PPFD) ($\mu mol\ s^{-1}\ m^{-2}$; LI-COR Quantum sensor, USA) at 20 regularly spaced locations directly above the ground on days with overcast sky. Simultaneous measurements were carried out close to each site in the open in order to calculate the relative light intensity, expressed as $PPFD_{inside}$ / $PPFD_{outside}$ in percent.

2.4 Data analysis

To increase the power of statistical analysis, analyses were performed on data sets including information for all of the studied species. Data were analyzed with a multinomial logistic regression model and a forward selection procedure of variables using the statistical software SAS 9.1.3 (SAS Institute Inc. Cary, NC, USA, 2002–2003). First, for the complete data set of 138 populations, we calculated the transition probability of each initial population size class ranging from 1 (1 individual) to 6 (101–1000 individuals) to reach another size class from 0 (extinct) to 7 (1001–10000) against the time between

Table 2. Explanatory variables included in the multinomial logistic regression models testing for the transition probability of each initial population size class to reach another size class, given separately for models 1, 2, and 3.

Tabelle 2. Erklärende Variablen in den multinomialen logistischen Regressionen, mit denen die Wahrscheinlichkeiten, von einer anfänglichen Populationsgrößen-Klasse in eine andere Klasse überzugehen, für die Modelle 1, 2 und 3 berechnet wurden.

	Included in model		
Predictor variable	1	2	3
Time between surveys	×	×	×
Isolation	×	×	×
Patch size		×	×
Habitat type		×	×
Vegetation height [m]			×
Light availability [%]			×
Soil variables (moisture, pH, C, N, C/N ratio, P, Ca, Mg and K)			×

surveys. Subsequently, we analyzed whether these probabilities were affected by population isolation (model 1; Table 2). To test for differences between transition probabilities and for significant effects of the predicting variables, an Exact Likelihood Ratio Chi-Square Test was applied. Model 2, consisting of all 86 surviving populations, served to analyze - additional to the impact of time between surveys and isolation - the effects of patch size and habitat type on the transition probabilities (Table 2). In a last step, the model was extended by the soil variables and vegetation height for the sub-set of 45 populations (model 3; Table 2).

Based on a Leslie matrix (PIELOU 1977) we finally constructed a projection matrix to predict the development of sizes of all surveyed populations using the statistical program R (version 2.12.1). For this purpose, the proportion of each initial population size class was entered into the model and related to the calculated transition probabilities.

3. Results

In *Pseudolysimachion longifolium*, *Sanguisorba officinalis* and *Euphorbia palustris*, the majority of populations were encountered on ditch banks (Table 3). In the latter species, also swamp forests and fallows served as important habitats. *Sanguisorba officinalis* was the only species where populations were found in managed grasslands. *Senecio paludosus* showed a deviating behaviour in that the species was mainly confined to the shore of rivers.

Initial population size classes ranged from 1 to 6, while populations at the time of the second survey varied in size between class 0 and 7. Overall, 55% of the populations included in the data analysis were smaller than 100 flowering individuals, and 33% of the populations had become extinct. The proportion of surviving populations varied among the four species from 88% in *E. palustris* to only 47% in *S. paludosus* (Fig. 2). In *S. officinalis* 7% of the populations had decreased and 44% increased in size, whereas in *S. paludosus* 17% had declined and only 3% increased. The proportion of populations keeping their initial size class ranged from 48% in *E. palustris* to 15% in *S. officinalis*.

Pooled over all species (model 1), the transition probabilities of reaching another size class varied considerably among the six initial size classes (Fig. 3, Table 4). Large populations (> 100 individuals) had a much higher probability of survival, of staying in their initial size class or of reaching size class 7 compared to smaller populations (≤ 25 individuals). Size classes 4 and 5 mostly showed non-significant differences to other size classes, most

Table 3. Habitat types in which the 86 populations used in model 2 were found. In the classification, six categories were distinguished: ditch bank, shore of a river or lake, swamp forest, grassland, verge and fallow.

Tabelle 3. Habitattypen der in Modell 2 benutzten 86 Populationen. Sechs verschiedene Klassen wurden unterschieden: Grabenrand, Fluss- oder Seeufer, Bruchwald, Grünland, Grünland-Saum und Brache.

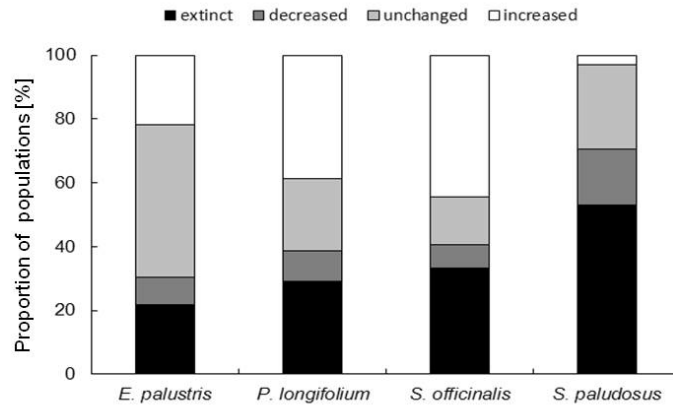| | Number of populations | | | | | |
Species	Ditch bank	Shore	Swamp forest	Grass-land	Verge	Fallow
Euphorbia palustris	15	2	6	0	2	9
Pseudolysimachion longifolium	12	6	0	0	4	0
Sanguisorba officinalis	10	0	0	4	4	0
Senecio paludosus	0	11	0	0	0	1

Fig. 2. Changes in population size (over the course of an average of 14.7 years) of all surveyed populations of the four study species *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis*, and *Senecio paludosus*. The bars show the proportions of populations that went extinct, decreased in size, remained unchanged or increased in size.

Abb. 2. Veränderungen der Populationsgröße (über einen durchschnittlichen Zeitraum von 14,7 Jahren) aller untersuchten Populationen von *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus*. Die Balken geben die jeweiligen Anteile der Populationen wieder, die ausgestorben oder in der Größe unverändert geblieben sind bzw. zu- oder abgenommen haben.
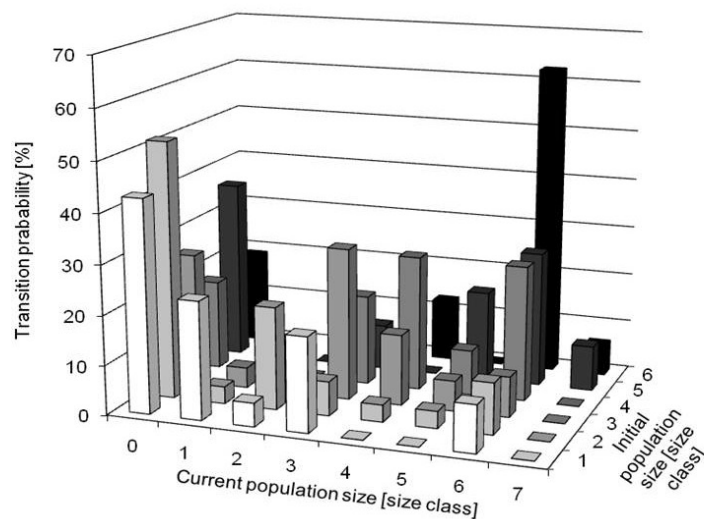

Fig. 3. Transition probabilities of initial population size classes (1 to 6) to reach another size class from 0 to 7, calculated for populations of *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis*, and *Senecio paludosus*. Transition probabilities were independent of the time between surveys (mean value: 14.7 years).

Abb. 3. Wahrscheinlichkeiten, von einer anfänglichen Populationsgrößen-Klasse (1–6) in eine andere Klasse (0–7) überzugehen, für die Populationen von *Euphorbia palustris*, *Pseudolysimachion longifolium*, *Sanguisorba officinalis* und *Senecio paludosus*. Die Übergangswahrscheinlichkeiten sind unabhängig vom Zeitraum zwischen den Untersuchungen (Mittelwert 14,7 Jahre).

Table 4. Results of Exact Likelihood Ratio Chi-Square Tests for differences in transition probabilities between the six studied initial population size classes; *p* values are given, with significant values in bold.

Tabelle 4. Ergebnisse der *Exact Likelihood Ratio Chi-Square*-Tests auf Unterschiede in den Übergangswahrscheinlichkeiten zwischen den verschiedenen Populationsgrößen-Klassen. Dargestellt sind die *p*-Werte (signifikante Werte fett).

Size class	1	2	3	4	5	6
1	—	0.154	**0.039**	**0.016**	0.059	**<0.001**
2	—	—	0.075	0.052	0.176	**<0.001**
3	—	—	—	0.454	**0.047**	**<0.001**
4	—	—	—	—	0.500	0.183
5	—	—	—	—	—	0.133
6	—	—	—	—	—	—

likely owing to low sample sizes (for both $n = 11$). The time between surveys did not affect model performance, and therefore the transition probabilities were applied for an average time between surveys of 14.7 years (range from 10 to 23 years). Including further predictor variables did not or only marginally improve the model. In model 2, patch size was found to have a significantly positive effect on the transition probabilities of the initial population size class 2 ($chi^2 = 4.26$, $df = 1$, $p = 0.039$). For model 3, transition probabilities of initial population size classes 1 and 4 were weakly positively affected by soil moisture ($chi^2 = 4.25$, $df = 1$, $p = 0.039$, and $chi^2 = 3.99$, $df = 1$, $p = 0.046$, respectively).

The construction of a projection matrix for the average time between surveys of 14.7 years resulted in the extinction of 85% of the populations in all six initial size classes after eight time intervals (about 117 years). 15% of the populations, however, developed into size class 7, but the matrix could not give any information on the fate of these populations because of the lack of populations with initial size class 7 in the data set.

4. Discussion

Small populations of the four studied, long-lived river corridor plants were more prone to become extinct than larger ones. Similar findings were also reported for seven short-lived, threatened plant species in a revisitation study in northern Germany (MATTHIES et al. 2004).

This result can be explained by various mechanisms. If population sizes are generally declining because of, for example, habitat deterioration, small populations are more likely to go extinct (faster) than larger ones (THOMAS 1994). Moreover, initial population sizes may have been small because the populations in question occurred in already deteriorated habitats. These explanations, however, were not corroborated by our study because: (i) Mean initial population size was even lower than mean current size of surviving populations, which contradicts a general decline in population size, (ii) deteriorated or deteriorating habitat quality cannot in all cases be the reason for small populations to decrease in size or go extinct, as many of these populations stayed in their initial size class or even developed into larger ones, and (iii) the measured environmental factors had hardly any effect on changes in population size, indicating that habitat quality is no main underlying cause for the extinction process or decline of populations. Despite the similar life histories of the studied river corridor plants, their responses to environmental conditions differ (WINTER et al. 2008), which is

240

why the effects of the measured habitat factors on changes in population size in a composite model of all studied species needs to be interpreted with caution. Still, the relative importance of soil quality on the reproductive success of the four studied species was shown to be much lower than the relative importance of population size (WINTER et al. 2008).

A further explanation for the high extinction rates of small populations may be that populations that fall below a certain threshold number of individuals have entered a so-called extinction vortex due to ever-decreasing plant fitness (GILPIN & SOULÉ 1986). As a consequence, one would expect a high proportion of small populations to decline, which, however, was not the case in our study where only 7% of all populations decreased in size, while 20% showed an increase. Moreover, the transition probabilities of reaching another population size class were not affected by the time between surveys. Our results therefore suggest that the increased extinction of small populations is caused by short-term rather than long-term effects. More precisely, sudden environmental events induced by human activity, such as land reclamation, changes in land use (temporary abandonment or intensification of management), or the application of herbicides, may be more important for the extinction and decline of small populations than decreasing plant fitness. In the long term (i.e., over a time span longer than the mean time between surveys of 14.7 years), however, decreasing plant fitness may have considerable negative effects on the survival of populations. We did not yet find population isolation to have any impact on extinction rates and changes in population size, suggesting that the negative effects of isolation, for example limited pollinator services and reduced gene flow (see, for example, ECKSTEIN & OTTE 2005), will influence the viability of long-lived species only over long time periods.

Even though our results show that populations above a threshold size of 100 individuals have a much higher chance of survival, to stay in their initial size class or to reach size class 7 (> 1000 individuals), a projection matrix predicted that after 117 years most of the surveyed populations will have gone extinct. The establishment of new populations is predicted to be a rare event, since all four species are on decline in the study area (GARVE 2004). Furthermore, only few suitable but empty sites are likely to be colonized, as the destruction and deterioration of the floodplain landscapes in the study area progresses and dispersal processes over long distances by water are limited as most populations are cut off from the river dynamics (see DONATH et al. 2003, 2007). In *Senecio paludosus*, seed germination and establishment of young individuals is a rare event even in existing populations (DIEKMANN & BARTELS 2012). Our findings at least suggest that the studied river corridor plants will further decline in the future.

The variation among the four study species in terms of their proportions of extinct, decreasing, unchanged, and increasing populations indicates that these differ in their responses to habitat fragmentation, possibly caused by differences in specific life history traits (cf. SUTTON & MORGAN 2009). This interpretation is supported by a previous study showing that the relative importance of population size, isolation and soil quality for the reproduction of the species varied considerably (WINTER et al. 2008). The populations of *Euphorbia palustris* had the lowest extinction rate, a high proportion of them staying in their initial size class. In a previous study of the demography of this species, however, we found that most populations were static and aged and therefore prone to extinction in the long-term (WÄRNER et al. 2011). Owing to its very long generation cycle, probably spanning several decades, the species may survive under sub-optimal environmental conditions for a relatively long time. Compared to the other study species, *Pseudolysimachion longifolium* and *Sanguisorba officinalis* had relatively high proportions of populations with increasing abundance (38–44%).

A likely explanation is their ability (also reflected in Table 3) to grow in and at the edge of pastures and meadows (KLOTZ et al. 2002), which have been developed by nature conservation in the study area over the last years. *Senecio paludosus*, in contrast, is strictly confined to reed swamps on wet, often inundated soils along the large rivers (Table 3, see also DIEKMANN & BARTELS 2012), and as these sites at present are less frequent than wet grasslands, fallows and ditch banks, *S. paludosus* shows the highest proportion of extinct (53%) and decreasing (18%) populations among the studied species.

In summary, small population size was identified as the most likely cause for the high extinction rates of populations of the four long-lived species. Small populations are mainly a result of habitat fragmentation caused by extensive river regulation and land reclamation, and this in turn can explain the high proportion of endangered river corridor plants. However, there was no indirect evidence for medium-term effects of reduced reproductive success in small and / or isolated populations on the survival of the studied species, even though this was found in a previous study (WINTER et al. 2008), indicating an extinction debt (cf. ROGERS et al. 2009). Contrary to the hypothesis that the drawbacks of small population size act slower in long-lived species (VELLEND et al. 2006, SCHLEUNING & MATTHIES 2009), the small populations of the species in this study were already affected after 15 years assumedly by sudden human activities.

Our results predict that river corridor plants will continue to decrease in the study area. To counteract this decline it will be crucial to prevent further habitat deterioration and to maintain or establish an appropriate management, avoiding sudden, adverse changes in land use, such as temporary abandonment or land intensification. The restoration of river valleys and the creation of retention areas as a result of increasing flooding events might, however, provide new suitable habitat areas for these species. On the other hand, a re-colonization of restored floodplains is unlikely because most species have already disappeared from the regional or local species pool. Re-colonization has been shown to be successful only in the vicinity of remnant stands (DONATH et al. 2003, 2007). The breeding of progeny from seeds for the reintroduction of species into restored floodplain areas offers a suitable management measure, as recently shown for *E. palustris* (C. Wärner, data not published) and *S. paludosus* (M. Diekmann et al., data not published).

Erweiterte deutsche Zusammenfassung

Einleitung – Stromtalpflanzen stellen im Vergleich zur gesamten Gefäßpflanzenflora Mitteleuropas einen überproportional großen Anteil gefährdeter Arten. Die Hauptgründe für die Bedrohung und den Rückgang dieser Arten liegen in der Zerstörung und Beeinträchtigung der natürlichen Habitate entlang der großen Flüsse, verursacht vor allem durch Eindeichung und landwirtschaftliche Intensivierung. Heute sind die meisten Populationen von der natürlichen Dynamik der Fließgewässer weitgehend abgeschnitten, weisen nur geringe Individuenzahlen auf und liegen oft stark isoliert voneinander. Viele Untersuchungen haben gezeigt, dass eine solche Habitatfragmentierung oftmals negative Auswirkungen auf das Wachstum und die Reproduktion der Pflanzen haben. Es gibt bisher jedoch nur wenige Belege dafür, dass kleine Populationen auch weiterhin abnehmen und mit großer Wahrscheinlichkeit frühzeitig aussterben. Eine Ursache dafür liegt in dem Fehlen zuverlässiger Langzeitdaten zur Dynamik von Pflanzenpopulationen. Ziel dieser Untersuchung war es, den Einfluss von Habitatfragmentierung und abiotischen Umweltfaktoren auf das Überleben und die Veränderung der Populationsgröße einiger langlebiger Stromtalpflanzen zu quantifizieren und Vorhersagen zum zukünftigen Überleben der Populationen zu machen.

Material und Methoden – Die Geländeuntersuchungen wurden in den Jahren 2005 und 2006 in den Flusssystemen von Weser und Elbe in Nordwest-Deutschland durchgeführt. Vier Arten mit typischem Stromtal-Verbreitungsmuster wurden ausgewählt: *Euphorbia palustris* L. (*Euphorbiaceae*), *Pseudolysimachion longifolium* (L.) Opiz (*Plantaginaceae*), *Sanguisorba officinalis* L. (*Rosaceae*) und *Senecio paludosus* L. (*Asteraceae*). Alle Arten sind ausdauernd und vermehren sich sexuell über Samen sowie vegetativ mit Hilfe kurzer Rhizome. In naturnahen Landschaften kommen sie meist in Feuchtwiesen und entlang nährstoffreicher Flüsse und Seen vor, sind aber heute vor allem in Sekundärbiotopen wie Brachen, Randbereichen von Grünlandflächen und Grabenrändern zu finden. Regional haben die vier Arten über die letzten Jahrzehnte hinweg in ihrer Häufigkeit abgenommen. Im Rahmen eines Pflanzenarten-Erfassungsprogramms des Landes Niedersachsen wurden die Populationen dieser Arten mit ihren ungefähren Größen (in acht Klassen: 1, 2–5, 6–25, 26–50, 51–100, 101–1000, 1001–10000, >10000 blühende Individuen) seit 1982 kartiert. Für insgesamt 138, bis spätestens 1996 erfasste Populationen wurden in den beiden Untersuchungsjahren wiederholte Zählungen der Populationsgrößen vorgenommen sowie in einer Auswahl von Populationen Habitattypen bestimmt und Umweltbedingungen (Boden, Licht) gemessen. Mithilfe von multinomialen logistischen Regressionen wurden für jede Art Wahrscheinlichkeiten des Übergangs von einer anfänglichen Populationsgrößen-Klasse zu einer anderen Klasse bei der Wiederholungs-Kartierung berechnet. In einem weiteren Schritt wurde analysiert, ob diese Übergangswahrscheinlichkeiten von der Isolation, dem Typ und der Größe des Habitats oder den Umweltbedingungen abhängen. Schließlich erstellten wir auf der Grundlage der Übergangswahrscheinlichkeiten Vorhersagen zum zukünftigen Überleben der Populationen.

Ergebnisse – Insgesamt starben 33 % der Populationen im Untersuchungszeitraum aus. Die Wahrscheinlichkeit, auszusterben bzw. deutlich ab- oder zuzunehmen, hing von der ursprünglichen Populationsgröße, nicht jedoch von der Isolation und nur wenig von der Habitatqualität ab. Große Populationen von > 100 Individuen überlebten signifikant öfter und nahmen häufiger zu als kleine Populationen von < 25 Individuen. Unter den vier Arten zeigte *Senecio paludosus* die negativste Bestandsentwicklung, *Euphorbia palustris* die relativ gesehen beste. Die Populationen, die bis 2005/06 überlebt hatten, wiesen generell keine abnehmende Populationsgröße auf, und die Veränderungen in der Bestandsgröße waren unabhängig vom Zeitraum zwischen erster und wiederholter Erfassung. Die Projektion der errechneten Übergangswahrscheinlichkeiten erlaubt die Vorhersage, dass fast alle Populationen innerhalb der nächsten 117 Jahre aussterben werden.

Diskussion – Der geringe Einfluss der Habitatqualität in den Modellen und die Unabhängigkeit der Veränderung der Populationsgröße von der Zeit in den überlebenden Populationen legen nahe, dass das Aussterben der Populationen nicht in erster Linie auf eine allmähliche Verschlechterung der Umweltbedingungen oder der genetischen Voraussetzungen zurückzuführen ist. Vielmehr spielen vermutlich plötzliche starke Veränderungen eine größere Rolle, vor allem kurzfristige Veränderungen in der Grünlandbewirtschaftung oder sonstigen Nutzung (z. B. häufigere Mahd, Verbrachung, Entwässerung). Aufgrund des Mangels an geeigneten Habitaten, der oft starken Isolation der noch bestehenden Populationen und des schlechten Ausbreitungsvermögens der Arten sind Neu-Etablierungen, die Aussterbeereignisse kompensieren könnten, unwahrscheinlich. Um ein weiteres Aussterben vieler Populationen zu verhindern wird es wichtig sein, ein für die Arten jeweils geeignetes Management zu etablieren bzw. aufrecht zu erhalten und kurzfristige, nachteilige Veränderungen im Management zu verhindern.

Acknowledgements

References

ÅGREN, J. (1996): Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. – Ecology 77: 1779–1790.

BURKART, M. (2001): River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. – Glob. Ecol. Biogeog. 10: 449–468.

CORDES, H., FEDER, J., HELLBERG, F., METZING, D. & WITTIG, B. (Eds.) (2006): Atlas der Farn- und Blütenpflanzen des Weser-Elbe-Gebietes. – Verlag H.M. Hausschild GmbH, Bremen: 512 pp.

DIEKMANN, M. & BARTELS, M. (2012): Das Sumpf-Greiskraut (*Senecio paludosus*) in Deutschland – Ökologie und Vergesellschaftung. – Tuexenia 32: 105–118.

DONATH, T.W., BISSELS, S., HÖLZEL, N. & OTTE, A. (2007): Large scale application of diaspore transfer with plant material in restoration practice - Impact of seed and microsite limitation. – Biol. Conserv. 138: 224–234.

DONATH, T.W., HÖLZEL, N. & OTTE, A. (2003): The impact of site conditions and seed dispersal on restoration success in alluvial meadows. – Appl. Veg. Sci. 6: 13–22.

ECKSTEIN, L. & OTTE, A. (2005): Effects of cleistogamy and pollen source on seed production and offspring performance in three endangered violets. – Basic Appl. Ecol. 6: 339–350.

ELLSTRAND, N.C. & ELAM, D.R. (1993): Population genetic consequences of small population size: implications for plant conservation. – Ann. Rev. Ecol. Syst. 24: 217–242.

ENDELS, P., JACQUEMYN, H., BRYS, R., HERMY, M. & DE BLUST, G. (2002): Temporal changes (1986–1999) in populations of primrose (*Primula vulgaris* Huds.) in an agricultural landscape and implications for conservation. – Biol. Conserv. 105: 11–25.

FISCHER, M. & STÖCKLIN, J. (1997): Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. – Conserv. Biol. 11: 727–737.

GARVE, E. (2004): Rote Liste und Florenliste der Farn- und Blütenpflanzen in Niedersachsen und Bremen (5. Fassung, Stand 1. 3. 2004). – Informationsd. Naturschutz Niedersachs. 24: 1–76.

GILPIN, M.E. & SOULÉ, M.E. (1986): Minimum viable populations: processes of species extinction. – In: SOULÉ, M.E. (Ed.): Conservation biology: the science of scarcity and diversity: 19–34. Sinauer Associates, Inc., Sunderland (Mass.).

HEINKEN, T. & WEBER, E. (2013): Consequences of habitat fragmentation for plant species: Do we know enough? – Perspect. Plant Ecol. Evol. Syst. 15: 205–216.

HONNAY, O., JACQUEMYN, H., VAN LOOY, C., VANDEPITTE, K. & BREYNE, P. (2009): Temporal and spatial genetic variation in a metapopulation of the annual *Erysimum cheiranthoides* on stony river banks. – J. Ecol. 97: 131–141.

JACQUEMYN, H., BRYS, R. & HERMY, M. (2002): Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. – Oecologia 130: 617–625.

JENNERSTEN, O. (1988): Pollination in *Dianthus deltoides* (*Caryophyllaceae*): effects of habitat fragmentation on visitation and seed set. – Conserv. Biol. 2: 359–366.

JENSEN, K. & GUTEKUNST, K. (2003): Effects of litter on establishment of grassland plant species: the role of seed size and successional status. – Basic Appl. Ecol. 4: 579–587.

JENSEN, K. & SCHRAUTZER, J. (1999): Consequences of abandonment for a regional fen flora and mechanism of succession change. – Appl. Veg. Sci. 2: 79–88.

KÉRY, M., MATTHIES, D. & SCHMID, B. (2003): Demographic stochasticity in population fragments of the declining distylous perennial *Primula veris* (*Primulaceae*). – Basic Appl. Ecol. 4: 197–206.

KÉRY, M., MATTHIES, D. & SPILLMANN, H.-H. (2000): Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. – J. Ecol. 88: 17–30.

KÉRY, M., SPILLMANN, J.H., TRUONG, C. & HOLDEREGGER, R. (2006): How biased are estimates of extinction probability in revisitation studies? – J. Ecol. 94: 980–986.

KLOTZ, K., KÜHN, I. & DURKA, W. (2002): BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. – Schriftenr. Vegetationskd. 38: 1–334.

KOLB, A. (2005): Reduced reproductive success and offspring survival in fragmented populations of the forest herb *Phyteuma spicatum*. – J. Ecol. 93: 1226–1237.

KORSCH, H. (1999): Chorologisch-ökologische Auswertung der Daten der Floristischen Kartierung Deutschlands. – Schriftenr. Vegetationskd. 30: 1–200.

LANDE, R. (1993): Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – Amer. Nat. 142: 911–927.

LEYER, I. & PROSS, S. (2009): Do seed and germination traits determine plant distribution patterns in riparian landscapes? – Basic Appl. Ecol. 10: 113–121.

LIENERT, J., FISCHER, M., SCHNELLER, J. & DIEMER, M. (2002): Isozyme variability of the wetland specialist *Swertia perennis* (Gentianaceae) in relation to habitat size, isolation, and plant fitness. – Am. J. Bot. 89: 801–811.

MATTHIES, D., BRAUER, I., MAIBOM, W. & TSCHARNTKE, T. (2004): Population size and the risk of local extinction: empirical evidence from rare plants. – Oikos 105: 481–488.

OUBORG, N.J. (1993): Isolation, population size and extinction: The classical and metapopulation approaches applied to vascular plants along the Dutch Rhine-system. – Oikos 66: 298–308.

PIELOU, E.C. (1977): Mathematical ecology. – John Wiley & Sons, New York: 385 pp.

POPPENDIECK, H.-H., BERTRAM, H., BRANDT, I., ENGELSCHALL, B. & V. PRONDZINSKI, J. (2010): Der Hamburger Pflanzenatlas von a bis z. – Dölling und Galitz Verlag, München: 568 pp.

ROGERS, D.A., ROONEY, T.P., HAWBAKER, T.J., RADELOFF, V.C. & WALLER, D.M. (2009): Paying the extinction debt in southern Wisconsin forest understories. – Conserv. Biol. 23: 1497–1506.

ROSENTHAL, G. (1992): Erhaltung und Regeneration von Feuchtwiesen – Vegetationsökologische Untersuchungen auf Dauerflächen. – Diss. Botan. 182: 1–259.

SCHLEUNING, M. & MATTHIES, D. (2009): Habitat change and plant demography: Assessing the extinction risk of a formerly common grassland perennial. – Conserv. Biol. 23: 174–183.

SCHNITTLER, M. & GÜNTHER, K.-F. (1999): Central European vascular plants requiring priority conservation measures - an analysis from national Red Lists and distribution maps. – Biodiv. Conserv. 8: 891–925.

SUTTON, F.M. & MORGAN, J.W. (2009): Functional traits and prior abundance explain native plant extirpation in a fragmented woodland landscape. – J. Ecol. 97: 718–727.

THOMAS, C.D. (1994): Extinction, colonization, and metapopulations - environmental tracking by rare species. – Conserv. Biol. 8: 373–378.

VAN CALSTER, H., VANDENBERGHE, R., RUYSEN, M., VERHEYEN, K., HERMY, M. & DECOCQ, G. (2008): Unexpectedly high 20th century floristic losses in a rural landscape in northern France. – J. Ecol. 96: 927–936.

VELLEND, M., VERHEYEN, K., JACQUEMYN, H., KOLB, A., VAN CALSTER, H., PETERKEN, G. & HERMY, M. (2006): Extinction debt of forest plants persists for more than a century following habitat fragmentation. – Ecology 87: 542–548.

WÄRNER, C., WELK E., DURKA, W., WITTIG, B. & DIEKMANN, M. (2011): Biological Flora of Central Europe: *Euphorbia palustris* L. – Pers. Pl. Ecol. Evol. Syst. 13: 57–71.

WINTER, C., LEHMANN, S. & DIEKMANN, M. (2008): Determinants of reproductive success: A comparative study of five endangered river corridor plants in fragmented habitats. – Biol. Conserv. 141: 1095–1104.

YOUNG, A., BOYLE, T. & BROWN, T. (1996): The population genetic consequences of habitat fragmentation for plants. – Trends Ecol. Evol. 11: 413–418.

ZACHARIAS, D. & GARVE, E. (1996): Verbreitung und Häufigkeit von Stromtalpflanzen im ehemaligen Amt Neuhaus (Mittelelbe, Lkr. Lüneburg). – Braunschw. Geobot. Arb. 4: 35–58.