

Spatiotemporal variation in
the demography of
perennial plants

Dissertation

zur

Erlangung des Doktorgrades

der Naturwissenschaften

(Dr. rer. nat.)

dem

Fachbereich Biologie

der Philipps-Universität Marburg

vorgelegt von

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aus Eschwege

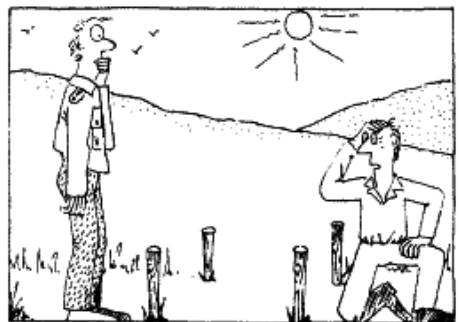
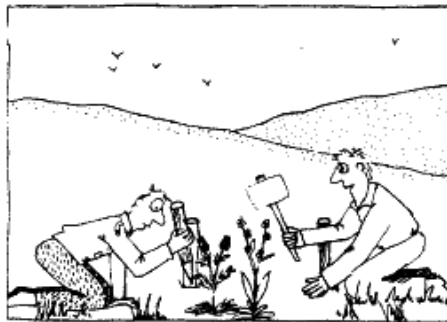
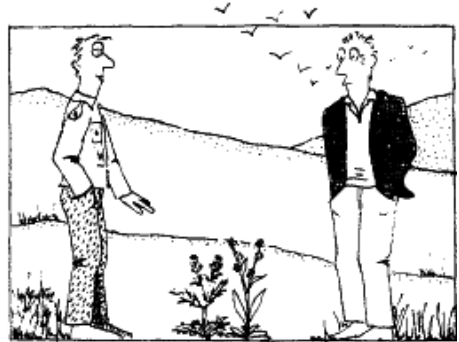
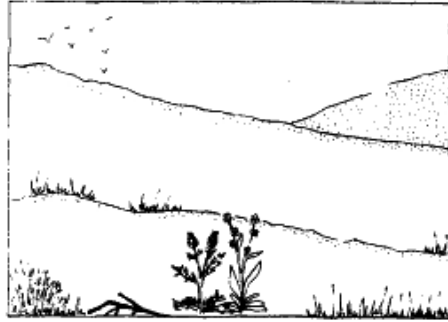
Marburg/Lahn 2007

Vom Fachbereich Biologie der Philipps-Universität Marburg
als Dissertation am 04.02.2008 angenommen.

Erstgutachter: Prof. Dr. D. Matthies

Zweitgutachter: Prof. Dr. R. Brandl

Tag der mündlichen Prüfung am 12.02.2008.



T.J. De Jong & P.G.L. Klinkhamer (1986)

*If a man will begin with certainties,
he shall end in doubts,
but if he will be content to begin with doubts,
he shall end in certainties.*

Francis Bacon

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CHAPTER 1

General introduction

POPULATION DYNAMICS OF PLANTS

To understand how plant populations respond to spatial and temporal environmental variation is an important aim of plant ecological research (Harper 1977; Crawley 1990; Jongejans & de Kroon 2005). It has been shown that plant populations strongly vary in space and time in response to the environmental variation in their habitats (van Groenendael & Slim 1988; Horvitz & Schemske 1995). Because of the deterministic and stochastic changes in environmental conditions, the eventual fate of all populations is extinction (Lande et al. 2003). Thus, the regional dynamics of plant species are usually a matter of both local extinction and colonization of new, unoccupied sites (Hanski 1999; Eriksson & Ehrlén 2001). Today in many ecosystems, fragmentation and degradation of habitats have increased the extinction risk of populations of plant species adapted to specific environmental conditions (Pitman & Jørgensen 2002; Baillie et al. 2004), while the probability of colonization of unoccupied sites by these species has strongly decreased (Hanski et al. 1996; Mildén et al. 2006). In future, climate change may further accelerate anthropogenic extinction of species with narrow ecological niches, and may also affect ecosystems, which today are still largely unaffected by human impact (Parmesan 2006; van Vuuren et al. 2006).

Plant demography

The growth rate of a population is determined by the sum of the fates of all the individuals of that population (Caswell 2001). Thus, to understand the dynamics of a population, all demographic processes which occur in a population need to be taken into account (Schemske et al. 1994). In plant populations, these processes can be divided into the life-cycle transitions survival, growth, reproduction and recruitment (Silvertown et al. 1993; Franco & Silvertown 2004). For the local persistence of a population, survival and growth of the established plants are the most important life-cycle components (Eriksson 1996; Silvertown et al. 1996). Growth of individual plants positively affects population growth, because both the probability of survival and reproduction increase with plant size (Silvertown & Charlesworth 2001). In clonal plants, growth can also be due to the vegetative propagation of ramets, which increases the probability of local persistence (Eriksson 1994; Eriksson & Ehrlén 2001). In contrast to clonal propagation, reproduction, i.e. seed formation, and subsequent seedling recruitment maintain the genetic diversity of a population (Honnay & Bossuyt 2005; Honnay et al. 2006). Various studies have shown that seedling recruitment strongly varies both in time and space (Horvitz & Schemske 1995; Jongejans & de Kroon 2005), but the longevity of dormant seeds can have a stabilizing effect on plant populations (Stöcklin & Fischer 1999).

Plant life history

The relative importance of the different life-cycle transitions for population growth strongly varies among plant species (Silvertown et al. 1993 & 1996). Plants have evolved various life-history strategies in response to the spatiotemporal variation caused by the variability in abiotic factors and by biotic interactions like competition, pathogen infestation, herbivory, pollination or seed dispersal (Silvertown & Charlesworth 2001; Ehrlén 2002). An important component of the life history of a plant species is its longevity (Stearns 1992; Ehrlén & Lehtilä 2002). Populations of short-lived species are usually more sensitive to environmental or demographic fluctuations than long-lived species, which are buffered by the survival of established plants (Fischer & Stöcklin 1997; Matthies et al. 2004). Short-lived species are therefore prone to become extinct locally and frequently have to colonize new, unoccupied sites (Eriksson 1996). Regional dynamics are important for many plant species, but it is a matter of debate whether metapopulations, which are characterized by frequent local extinction and colonization of new patches, are the rule or the exception for plants (Freckleton & Watkinson 2002; Ehrlén & Eriksson 2003). With increasing longevity of a species, the local persistence of populations becomes more important for its regional viability (Eriksson 1996). Due to the longevity of the genets, many clonal plant species can survive long periods of time despite strong fluctuations in habitat quality (Eriksson 2000; Souza & Martins 2006). Because of the difference in the life cycle between short- and long-lived plants, the distribution of short-lived plants usually reflects the actual environmental conditions, whereas long-lived plants may persist at a site despite unfavourable habitat conditions, resulting in an extinction debt (Hanski & Ovaskainen 2002). The number of extant populations of long-lived plants is therefore not a good indicator for their conservation status (Helm et al. 2006).

Environmental variability

The dynamics of plant populations strongly respond to the variability in habitat conditions due to both stochastic and deterministic factors (Lehtilä et al. 2006). Stochastic variability in habitat conditions increases the extinction risk of populations, in particular that of small populations (Menges 1998; Matthies et al. 2004). Environmental trends due to natural succession, land-use change, habitat eutrophication or climate change may cause a long period of deterministic decline in a population and may finally result in the extinction of the population (Lande et al. 2003). Deterministic factors have received less attention in studies of plant demography than stochastic factors (but see Oostermeijer et al. 1996; Lehtilä et al. 2006). However, it has been argued that deterministic changes in habitat conditions are the

main drivers of population extinction, because these changes make populations small enough to be susceptible to the effects of genetic bottlenecks and stochastic fluctuations (Oostermeijer 2000; Lande et al. 2003). To halt such deterministic trends, natural or semi-natural disturbance is important, because it abruptly changes habitat conditions and reverses successional trends (Jakalaniemi et al. 2006; Kleyer et al. 2007). Spatial and temporal patterns of disturbance are therefore seen as crucial factors for extinction and colonization processes, and thus species coexistence (Wright 2002; Wichmann et al. 2003).

In central Europe, periodic disturbance by traditional land use practices like extensive grazing or mowing has created extraordinarily species-rich grasslands at nutrient-poor sites (WallisDeVries et al. 2002; Poschlod et al. 2005). However, changes in land use have caused the loss of many of these semi-natural grasslands (WallisDeVries et al. 2002), and in the remnant grasslands the cessation of traditional management has resulted in changes in the environmental conditions and the composition of the vegetation (Poschlod et al. 2005). When habitat quality decreases after abandonment, populations of short-lived plant species become quickly extinct (Fischer & Stöcklin 1997; Matthies et al. 2004). In contrast, the demographic responses of long-lived species are more complex (Oostermeijer et al. 1994; Colling et al. 2002), but few studies have analyzed the effects of habitat change on different life-cycle phases in several remnant populations of perennial plant species (but see Vergeer et al. 2003).

In contrast to the semi-natural landscape in central Europe, large areas of species-rich tropical rainforests are still shaped by natural processes rather than by human management (Primack & Corlett 2004). Natural disturbance by flooding and treefalls are crucial processes shaping the environmental conditions in the understory of neotropical forests (King 2003; Wright et al. 2003). The environmental variability resulting from these processes strongly influences the dynamics of the plant populations in the understory (Nicotra et al. 1999; Bunker & Carson 2005). Previous demographic studies in the rainforest understory have mostly focused on tree recruitment (Wright et al. 2003; Queenborough et al. 2007), although plants that complete their life cycle in the understory constitute up to 50% of the diversity of neotropical forests (Gentry 1990). Moreover, the regional abundance of large clonal herbs that locally dominate the understory may strongly influence forest dynamics (Griffiths et al. 2007). However, very little is known about the effects of spatial environmental variation on the population dynamics of the widespread clonal herbs of Amazon forests. In addition, an understanding of the effects of seasonal environmental variation, e.g. due to seasonal flooding, is crucial to predict how plant populations of Amazon forests will respond to the strong climatic changes predicted for Amazonia (Betts et al. 2004).

Matrix population models

Matrix models provide powerful analytical tools to analyze plant demography (Schemske et al. 1994; Caswell 2001). For a profound understanding of the population dynamics of a plant species, demographic studies incorporating populations in the complete range of habitats in which a species occurs are necessary (Jongejans & de Kroon 2005; Lehtilä et al. 2006). Matrix models then can be used to compare the dynamics of the populations in the different types of habitats (van Groenendael & Slim 1988; Caswell 2001). To assess the performance of a population, the finite rate of population growth, λ , is a reliable measure (Schemske et al. 1994), but differences in population growth can be due to the variation in different life-history phases.

To identify the sensitive phases in the life cycle of a plant, the relative influence of the vital rates on λ can be analyzed by prospective and retrospective perturbation analyses (Caswell 2001). The prospective approach (elasticity analysis) explores how small changes in the vital rates would affect λ (de Kroon et al. 1986 & 2000), whereas the retrospective approach (life-table-response experiments, LTRE) quantifies the contribution of the actual variability in the vital rates to the observed variability in λ (Ehrlén & van Groenendael 1998; Caswell 2001). Recently, LTRE analyses have been successfully applied to study effects of spatial environmental variation and of experimental management on the dynamics of plant populations (Brys et al. 2004; Ehrlén et al. 2005; Colling & Matthies 2006). Temporal variation in population dynamics can also be examined in LTRE analyses, but most previous studies have focussed solely on the environmental variability among years (Brys et al. 2005; Angert 2006). However, seasonal fluctuations in environmental conditions, e.g. caused by flooding, drought or frost, are characteristic for many ecosystems (Pico et al. 2002; Myneni et al. 2007). Periodic matrix models provide a powerful, but still underutilized tool to disentangle the responses of plant populations to such seasonal fluctuations (Caswell 2001; Smith et al. 2005).

To quantify the extinction risk of a population, simulations models which incorporate the effects of environmental and demographic stochasticity can project population development into the future (Menges 1998; Morris & Doak 2002). These models can be used to compare the extinction risks among different types of populations and to assess the population viability of threatened plant species under different scenarios (Menges 2000; Brigham & Schwartz 2003).

OUTLINE OF THIS DISSERTATION

In this dissertation, I present four studies of two different model systems to analyze the relationship between the demographic processes in populations of perennial plants and the spatiotemporal variation of their habitats. In chapter two and three, I identify processes responsible for the decline of the formerly common perennial grassland plant *Trifolium montanum* L. in species-rich grasslands in central Europe, while chapter four and five examine the influence of spatial and seasonal environmental variation on the population dynamics of the widespread Amazon understory herb *Heliconia metallica* Planchon & Linden ex Hooker.

Demography of Trifolium montanum

Calcareous grasslands are one of the most species-rich habitats in central Europe (WallisDeVries et al. 2002; Dauber et al. 2006). Due to changes in land use, many of them have been destroyed, and most of the remnant sites are small and isolated (WallisDeVries et al. 2002; Hodgson et al. 2005). Small remnants of populations are susceptible to extinction because of the effects of demographic and environmental stochasticity (Matthies et al. 2004). Moreover, plants in small populations may suffer from genetic erosion (Young et al. 1996; Leimu et al. 2006), which also has been shown to increase the extinction risk of a population (Frankham 2005). In addition, cessation of traditional management in the remnant sites has strongly changed the environmental conditions (Poschlod et al. 2005). It is therefore an important aim of conservation biology to understand how these changes affect the dynamics and extinction risks of the extant populations of the long-lived plant species restricted to these grasslands.

The study species *T. montanum* was formerly a common herbaceous perennial of calcareous grasslands, but has strongly declined during the last decades and is threatened in central Europe (Hodvina et al. 1999; Garve 2004; Colling 2005). Dispersal is very limited in *T. montanum*, and thus seed transfer among the remnant populations may be very low. Vegetative propagation is rare in *T. montanum* (Klimeš & Klimešová 1999). Seed production of *T. montanum* depends on pollen transfer by bumblebees and bees, because the seed set of selfed flowerheads is strongly reduced.

In chapter 2, I analyze the effects of habitat degradation and fragmentation on different phases of the life cycle in 23 remnant populations of *T. montanum* in central Germany. To examine whether the effects of habitat degradation or those of fragmentation are more important for populations of *T. montanum*, I assess these effects on stage structure, seedling

establishment, survival and reproduction in the field populations. In addition, I grew offspring from seeds originating from the same field populations in a common garden to analyze the effects of habitat degradation and fragmentation on offspring performance.

Chapter 3 is concerned with a four-year study of the demography of *T. montanum*. I collected demographic data in nine populations and experimentally tested the effect of grassland management. With the field data, matrix models are constructed to analyze the effects of habitat degradation and experimental management on the population dynamics of *T. montanum*. I compare population growth rates between different types of habitat and management and identify the phases in the life cycle responsible for the differences in growth rates. In stochastic models, the median time to extinction and the minimum viable size of different types of populations are determined. The simulation results are then compared to the size distribution of the extant populations of *T. montanum* in central Germany to assess the extinction risk of the remnant populations of this declining grassland plant.

Demography of Heliconia metallica

Floodplain forests constitute c. 20% of Amazon rainforests (Junk 1997). Lack of light and disturbance by flooding are the dominant environmental factors in these forests (Myster 2007). Small-scale environmental differences due to the formation of small canopy gaps and to the variation in micro-topography strongly influence the plants living in the understory of these forests (Montgomery & Chazdon 2002; King 2003). Seasonal fluctuations in environmental conditions may be another crucial factor influencing the plant populations (Bunker & Carson 2005; Engelbrecht et al. 2007), because precipitation is seasonal in Amazon rainforests (Myneni et al. 2007). The effects of seasonal environmental variation on plant populations are of particular interest for tropical ecology, because during the last decades an increase in the length of the dry season has been observed in Amazonia, which is predicted to intensify in the near future (Betts et al. 2004; Aragão et al. 2007).

Large clonal herbs, e.g. of the genus *Heliconia*, are a typical component of Amazon floodplain forests and can influence tree recruitment because of their local dominance in the understory (Berry & Kress 2001; Stevansson 2007), but little is known about the population dynamics of these clonal herbs. The study species *H. metallica* is a widespread clonal herb distributed from Honduras to Bolivia (Berry & Kress 1991). The plant spreads laterally by rhizomes, which produce shoots (ramets) of up to 3.5 m height. The flowers of *H. metallica* are a key nectar resource visited by various species of hummingbirds (see Bruna & Kress 2002), and its fruits are eaten and dispersed by frugivorous birds (see Stiles 1979).

Chapter 4 deals with the effects of spatiotemporal environmental variation on the population dynamics of *H. metallica*. Demographic data were collected in 16 populations of *H. metallica* during two rainy and two dry seasons in a Peruvian floodplain forest. Using periodic matrix models, I analyze the influence of seasonal climatic fluctuations and of the interacting effects between flooding and canopy gaps on the dynamics of populations of *H. metallica*. I assess the importance of clonality for population persistence, identify limiting life-cycle phases during the wet and dry season and compare the viability of populations situated in the lower and moister parts of the floodplain to those in the higher and dryer parts.

Chapter 5 is concerned with the role of seed ecology for the local and regional population dynamics of *H. metallica*. In this study, I combine the results from an experiment of seed addition and predator exclusion with observations of natural seedling recruitment. Over a two-year study period, seed predation, seedling establishment and survival were recorded in the same Peruvian floodplain forest to investigate whether the presence of clonally propagated ramets inhibits seedling recruitment, whether disturbance by flooding is necessary for the colonization of new sites and whether the regional abundance of *H. metallica* is limited by dispersal.

CHAPTER 2

Negative effects of habitat degradation
and fragmentation on the declining
grassland plant *Trifolium montanum*

Basic and Applied Ecology, in press
with Marc Niggemann, Ute Becker and Diethart Matthies

ABSTRACT

Changes in land use have resulted in a strong decline in the plant diversity of nutrient-poor grasslands, but little is known about the combined effects of habitat degradation and fragmentation on populations of individual species. We studied these effects on stage structure, recruitment, reproduction and offspring performance in populations of the declining grassland plant *Trifolium montanum* in central Germany. Density and survival probability of juvenile plants decreased with light competition, measured as leaf area index (LAI) above *T. montanum* plants, resulting in aged populations with few juvenile plants at unmanaged sites with higher LAI. Reproduction of *T. montanum* was not related to LAI, but increased strongly with local density, suggesting pollinator limitation in fragmented populations with a low density of flowering plants. In the common garden, the survival of sown offspring increased with mean seed size, whereas seed production of offspring decreased with isolation, and in strong contrast to previous studies of fragmentation, also decreased with size and density of the population of origin. This could be due to increased inbreeding because of pollination between closely related neighboring plants in dense and large populations. Our results indicate that both habitat degradation and fragmentation have negative effects on populations of *T. montanum*, but affect different phases of the life cycle. In the short term, the effects of habitat degradation are more important than those of fragmentation, and populations of *T. montanum* are primarily threatened by an increase in light competition on unmanaged sites that rapidly affects the dynamics of the populations. The observed opposite effects of habitat fragmentation on reproduction and offspring performance indicate that the effects of population size, density and isolation on plant fitness and population viability may be complex.

INTRODUCTION

Many formerly common plants of nutrient-poor grasslands have strongly declined in central Europe in recent decades (Korneck et al. 1996). The main driving force for their decline is a change in land use and subsequent habitat loss and degradation (Hodgson et al. 2005; Poschlod et al. 2005). In the remnant grasslands, cessation of traditional management like grazing or mowing has resulted in changes in the composition of the vegetation (Poschlod et al. 2005). While populations of short-lived species become quickly extinct when habitat quality decreases (Fischer & Stöcklin 1997; Matthies et al. 2004), established perennial plants can survive for a long time (Ehrlén & Lehtilä 2002). However, reduced recruitment of long-lived plants in degraded habitats, often caused by increased light competition (Lepš 1999), may result in the formation of aged populations with few juvenile plants, which are doomed to become extinct in the long-term (Oostermeijer et al. 1994; Colling et al. 2002).

The negative effects of habitat degradation may be exacerbated by the effects of habitat fragmentation that result in increased isolation and reduced size and density of plant populations (Lienert & Fischer 2003). Because of their greater sensitivity to environmental and demographic stochasticity, small populations face an increased risk of extinction (Matthies et al. 2004). Moreover, small and isolated populations may suffer from genetic erosion (Young et al. 1996), and reduced genetic diversity has been found to reduce offspring fitness (Leimu et al. 2006) and population viability (Frankham 2005). However, plant fitness and population viability are not always affected by a reduction of genetic diversity, in particular during early phases of the genetic erosion process (Ouborg & van Treuren 1995). In addition, small and low density populations may be less attractive to pollinators and experience pollinator limitation (Kunin 1997).

Fragmentation of nutrient-poor grasslands has strongly reduced the probability of colonization of unoccupied sites and today the regional survival of long-lived grassland plants mainly depends on the survival of the remaining populations (Soons et al. 2005; Herben et al. 2006). However, few studies have investigated different demographic processes in a large number of remnant populations to unravel the effects of habitat degradation and fragmentation on the declining long-lived grassland species (but see Vergeer et al. 2003). We studied habitat conditions and stage structure of 23 populations of the long-lived declining grassland plant *Trifolium montanum* L. in central Germany and analyzed establishment, seedling survival and reproduction in the field in a subset of these populations, and offspring performance in a common garden experiment.

We addressed the following questions: (1) Do habitat quality and fragmentation affect population structure, establishment and seedling survival of *T. montanum*? (2) Are reproduction in field populations and the performance of offspring in the common garden affected by habitat quality and fragmentation of *T. montanum* populations?

MATERIALS AND METHODS

Study species

Trifolium montanum is a long-lived herbaceous perennial of calcareous grasslands, which has strongly declined in central Germany during the last decades and is threatened in several German states (Hodvina et al. 1999; Garve 2004). *T. montanum* has very limited clonal growth (Klimeš & Klimešová 1999). From June to July plants produce 1-5 flowering shoots, each bearing 1-6 flowerheads with c. 150 white flowers each, which are pollinated by bumblebees and bees. The flowers are not self-pollinating and seed set of selfed flowerheads is c. 70% lower than that of outcrossed flowerheads. Seeds have a mass of c. 0.7 mg and are dispersed from July on, but dispersal distance is very limited. Most seeds germinate in spring of the following year, when the height of the surrounding vegetation is c. 20 cm. Very few seeds survive to the next year (Thompson et al. 1997).

Study sites

In summer 2000, we searched for remnant populations of *T. montanum* in a continuous landscape in northern Hesse and southern Lower Saxony (Germany). In all 23 populations found, stage structure and habitat conditions were studied in 2003. Seedling establishment and survival were studied in eight large populations from 2002-2004. For studies of reproduction in the field in 2003 and offspring performance in a common garden starting in 2000, the same set of populations was used, but some of the populations were too small or had already been grazed or mown before seed collection. From 2000-2005, we recorded whether a site was managed (annually grazed or mown) or not managed (Appendix A).

Habitat conditions and population characteristics

In summer 2003, several study plots (50 x 50 cm) were randomly selected in areas with *T. montanum* present. Depending on population size, the number of plots per population ranged from 2-13 (179 plots in total). In each plot, the area covered by bare soil and the thickness of the litter layer were determined. To estimate light competition for *T. montanum*

plants, in each population several plots of 25 x 25 cm were selected close to the 50 x 50 cm plots (148 plots in total). In each plot, the leaf area index (LAI) was measured at two random points 10 cm above the ground (i.e. above the canopy of the *T. montanum* plants) using a plant canopy analyser (LAI 2000, Li-Cor, Lincoln, Nebraska, USA).

In 2003, the number of flowering plants was counted (range of population size: 10-4360 flowering plants, median = 160) and the distance to the next population was measured (range of isolation: 0.11 km-15.7 km, median = 0.21 km). To measure the local density of flowering plants, we randomly chose 3-41 target plants (depending on population size) and counted the number of conspecific flowering plants within radii of 25 cm, 50 cm and 100 cm (measured in 16 of the populations). We then calculated population means of the number of conspecific flowering plants in circles (radii of 25 cm, 50 cm and 100 cm) and annuli (0-25 cm, 26-50 cm and 51-100 cm) around the target plants to analyze the effect of local density on reproduction and offspring fitness at different spatial scales (Appendix A).

Stage structure of populations

In summer 2003, the stage structure of *T. montanum* was analyzed in the same plots in all 23 populations. Reproductive shoots of each plant were counted and the length of the longest leaf and the basal diameter of the thickest shoot were measured. The basal shoot diameter was strongly correlated with leaf length ($r = 0.92$, $p < 0.001$) and could also be measured when shoots had been grazed. We therefore used the basal shoot diameter to distinguish two vegetative stages in addition to the reproductive stage: Juveniles with a basal shoot diameter ≤ 0.5 mm and non-reproductives with a basal shoot diameter > 0.5 mm.

Recruitment

In August 2002, ripe fruitheads were collected in eight large populations of *T. montanum*, and in October 2002 65 transects of 1 m length were marked with metal rods (5-12 transects per population, depending on the number of seeds available). Along each transect two plots of 10 x 10 cm were set up and in one of them 100 seeds of *T. montanum* were sown. To analyze the effect of disturbance on recruitment, in the largest population the 12 transects were extended by 1 m each and in the additional sowing and control plots vegetation was clipped and litter removed. In May and July of the following year, the number of emerged seedlings was counted in each plot. The small number of seedlings in the control plots was subtracted from that in the sowing plots and the proportion of seeds that had developed into seedlings was calculated. In the same eight populations that had been used for the sowing experiment, we

followed the fate of individually marked juvenile plants in 89 permanent plots (50 x 50 cm) from July 2003 to July 2004 to study the mortality of established seedlings.

Reproduction in the field and offspring fitness in the common garden

To analyze reproduction, we randomly selected 4-59 fruiting plants (depending on population size) in 14 field populations in August 2003. We counted the number of fruitheads as an estimate of plant size, collected 1-3 fruitheads per plant and determined the number of seeds per fruithead in the laboratory.

To study offspring performance in the common garden, we selected 381 plants from 20 populations in 2000 (4-30 plants per population), counted the number of fruitheads of each plant, and collected a single fruithead from each plant. In the laboratory, we counted and weighed the seeds and calculated the mean size of the seeds [mg] produced by each plant. Seeds were stored at 7 °C, and in April 2002 c. 100 seeds from each plant were sown into two petri dishes that were placed into a climate chamber at 18 °C. Germination was recorded 28 days after sowing. Of the germinated seedlings, three were selected randomly per mother plant, planted individually into pots, and grown for 16 months in the Botanical Garden of the University of Marburg. We recorded survival during the 16 months, and in summer 2003 we determined for each plant (358 plants in total) the number of fruitheads and the number of seeds in three randomly selected fruitheads. We calculated seed production per plant as the number of fruitheads times the mean number of seeds per fruithead. As an estimate of mean fitness of offspring from a population, we calculated multiplicative fitness as the product of germination, plant survival until flowering and seed production.

Data analysis

Habitat conditions, population characteristics, stage structure and reproduction of populations were compared between managed and unmanaged sites by analyses of variance (ANOVA). We also compared offspring performance and seed production of plants from these two types of populations in the common garden. The effects of habitat quality (LAI, litter thickness and proportion of bare soil) and of fragmentation (population isolation, population size and local density of flowering plants) on the mean density of juvenile plants, percent seedling establishment and mortality of juvenile plants were investigated by simple and multiple regression analyses (backward elimination, $p > 0.05$). To analyze the effect of disturbance on seedling establishment, we carried out an analysis of deviance using a logit-link and a

binomial error distribution (Crawley 2002). Effects of independent variables on reproduction in the field and offspring performance in the common garden were investigated by simple and multiple regression analyses (backward elimination, $p > 0.05$). Statistical analyses were carried out with SPSS 12.0.1 (SPSS Inc. 2003). LAI, population size and isolation and the densities of plant stages were log-transformed, and proportion of bare soil and percent seedling establishment were arcsine square-root transformed prior to analysis.

RESULTS

Habitat conditions and population characteristics

From 2000-2005, management differed among sites. Calcareous grasslands at hilltops and slopes were frequently managed ($n = 13$), whereas relicts of calcareous grasslands along field paths and fertilized meadows were rarely managed ($n = 10$). LAI was significantly lower on managed than on unmanaged sites (0.33 vs. 0.89, $F_{1,21} = 16.0$, $p < 0.001$), whereas litter thickness and the proportion of bare soil did not differ between managed and unmanaged sites ($p > 0.5$ in both cases). Population size and mean density of flowering plants (100 cm radius) were positively correlated ($r = 0.78$, $p < 0.001$), and were larger for managed than unmanaged sites (size: 469 vs. 43 flowering plants, $F_{1,21} = 18.7$, $p < 0.001$; density: 17.2 vs. 6.9 flowering plants per 3.1 m², $F_{1,14} = 10.2$, $p = 0.006$), whereas isolation did not differ between management types ($F_{1,21} = 1.3$, $p = 0.267$).

Stage structure of populations

Population in managed and unmanaged sites differed strongly in stage structure. At managed sites, populations were characterized by a high proportion of juvenile plants (dynamic populations), whereas at unmanaged sites a high proportion of the plants was large and presumably old (aged populations, Fig. 1A). Managed and unmanaged populations differed strongly in the density of juvenile plants, but only slightly in that of non-reproductive and reproductive plants (Fig. 1B).

The density of juvenile plants strongly decreased with LAI ($r = -0.58$, $p = 0.004$; Fig. 2A), but not that of non-reproductive and reproductive plants ($p > 0.1$ in both cases). The density of juvenile plants increased with population size ($r = 0.58$, $p = 0.004$) and with the local density of flowering plants (100 cm scale, $n = 16$: $r = 0.53$, $p = 0.035$), but was not related to population isolation, litter thickness and proportion of bare soil ($p > 0.1$ in all cases). In a multiple regression, juvenile plant density was only influenced by LAI.

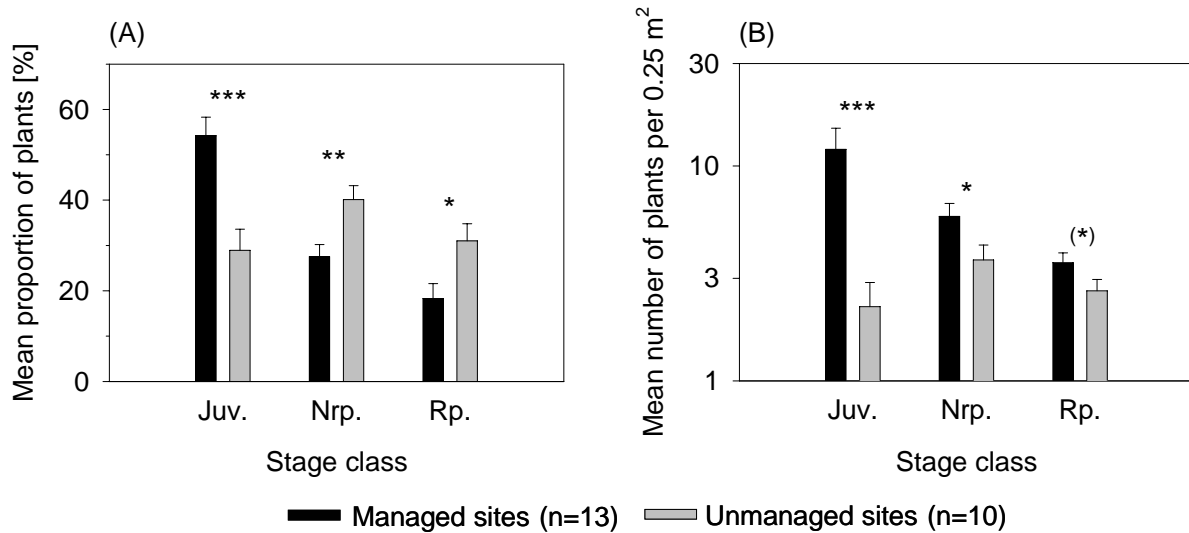


Figure 1. Stage structure of populations of *T. montanum*. (A) Mean proportion of juveniles (Juv.), non-reproductives (Nrp.) and reproductives (Rp.), and (B) the mean density of each stage class for populations at 13 managed and 10 unmanaged sites. Asterisks indicate significant differences between managed and unmanaged populations (ANOVA; (*), $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Error bars denote +1SE.

Recruitment

Seedling establishment of the sown seeds was low (overall mean of 1.1% in July 2003) and in 30% of the plots no seedlings established at all. In a multiple regression, proportion of bare soil positively ($\beta = 0.68$, $t = 4.9$, $p = 0.005$), and thickness of the litter layer negatively ($\beta = -0.49$, $t = -3.5$, $p = 0.017$) affected establishment ($R^2 = 0.91$, $p = 0.002$), but LAI had no effect ($p = 0.715$). In the one population studied, disturbance had a positive effect on recruitment. The proportion of seeds producing a seedling was higher in disturbed than in undisturbed plots, both in May (5.0% vs. 2.0%) and in July (4.3% vs. 2.4%). However, the effect of disturbance was only marginally significant in May and not significant in July (Quasi- $F_{1,11} = 4.14$, $p = 0.067$ and Quasi- $F_{1,11} = 1.62$, $p = 0.229$, respectively).

In the eight populations studied, the overall mortality of juvenile plants was 32.5% (July 2003 - July 2004). The mortality of juvenile plants increased with LAI (Fig. 2B), but was not related to litter thickness and the proportion of bare soil ($p > 0.4$ in both cases). The mortality of juvenile plants decreased with population size ($r = -0.79$, $p = 0.019$), but was not related to the isolation, local density, mean plant size and seed size in a population ($p > 0.2$ in all cases).

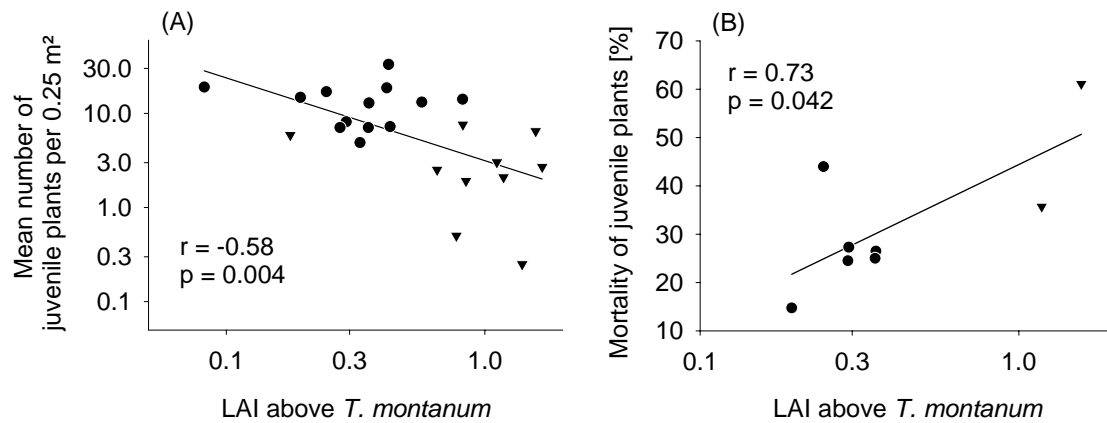


Figure 2. The effects of light competition, measured as the LAI above *T. montanum* plants, on (A) the density of juvenile plants of *T. montanum* in 23 populations, and on (B) the mortality of juvenile plants of *T. montanum* in eight populations. Circles denote populations at managed and triangles populations at unmanaged sites.

Reproduction in the field populations

Managed populations tended to produce more seeds than unmanaged populations (82.2 vs. 63.9 seeds per fruithead, $F_{1,12} = 3.8$, $p = 0.074$). The number of seeds per fruithead was not influenced by LAI ($r = -0.24$, $p = 0.410$) and isolation ($r = 0.39$, $p = 0.164$), but tended to increase with population size ($r = 0.46$, $p = 0.097$). There were strong positive relationships between the number of seeds per fruithead and the local density of flowering plants of *T. montanum* within circles of 25 cm ($r = 0.62$, $p = 0.019$), 50 cm ($r = 0.74$, $p = 0.003$) and 100 cm ($r = 0.80$, $p < 0.001$; Fig. 3). While the number of seeds per fruithead increased with the number of fruitheads per plant ($r = 0.57$, $p = 0.035$), seed set was only influenced by the flowering plant density within a radius of 100 cm in a multiple regression including all explanatory variables.

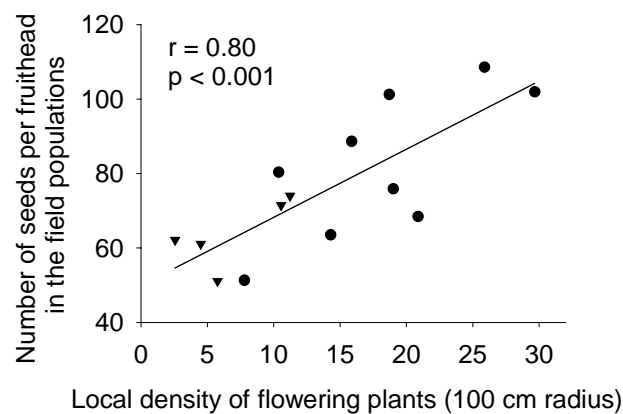


Figure 3. The relationship between the number of seeds per fruithead in the field populations and the mean number of conspecific flowering plants within a radius of 100 cm around randomly selected flowering plants in 14 populations of *T. montanum*. Circles denote populations at managed and triangles populations at unmanaged sites.

Offspring fitness in the common garden

Seed size, germination and plant survival in the common garden did not differ between managed and unmanaged populations ($p > 0.2$ in all cases). Seed size and germination were not related to LAI, population size, local density, isolation and mean plant size in the population of origin ($p > 0.1$ in all cases), and germination was not affected by the mean seed size in the population of origin ($r = 0.20$, $p = 0.410$). Plant survival in the common garden was also not related to habitat quality and fragmentation of the population of origin ($p > 0.3$ for all variables), but decreased with mean plant size ($r = -0.43$, $p = 0.062$) and strongly increased with mean seed size in the population of origin ($r = 0.67$, $p = 0.001$).

In contrast, offspring seed production in the common garden was not related to plant size and seed size ($p > 0.2$ in both cases). Offspring from unmanaged populations tended to produce more seeds than those from managed populations (734 vs. 640 seeds, $F_{1,18} = 3.4$, $p = 0.082$). Seed production was not related to LAI ($r = 0.35$, $p = 0.129$), but decreased with the size of the population of origin ($r = -0.51$, $p = 0.020$; Fig. 4A) and with isolation ($r = -0.75$, $p < 0.001$; Fig. 4B). The local density within circles of 25 cm radius in the population of origin negatively affected seed production ($n = 15$: $r = -0.74$, $p = 0.002$; Fig. 4C), but the density in annuli from 26 to 50 cm ($n = 15$: $r = -0.48$, $p = 0.070$) and 51 to 100 cm ($n = 15$: $r = -0.22$, $p = 0.440$) had less effect. In a multiple regression including all explanatory variables, isolation (beta = -0.44, $t = -3.2$, $p = 0.009$) and the local density of the population of origin (0-25 cm annulus: beta = -0.83, $t = -4.4$, $p = 0.001$) negatively, and the density of plants within the 51-100 cm annulus positively (beta = 0.48, $t = 2.9$, $p = 0.014$) affected offspring seed production ($R^2 = 0.85$, $p < 0.001$).

The multiplicative offspring fitness in a population, i.e. the product of germination, plant survival and seed production, decreased with isolation ($r = -0.51$, $p = 0.021$) and local density (25 cm scale, $n = 15$: $r = -0.56$, $p = 0.030$), but was not related to any other explanatory variable ($p > 0.1$ in all cases) and did not differ between managed and unmanaged populations ($p > 0.3$). In a multiple regression, only the isolation of the population of origin affected multiplicative offspring fitness.

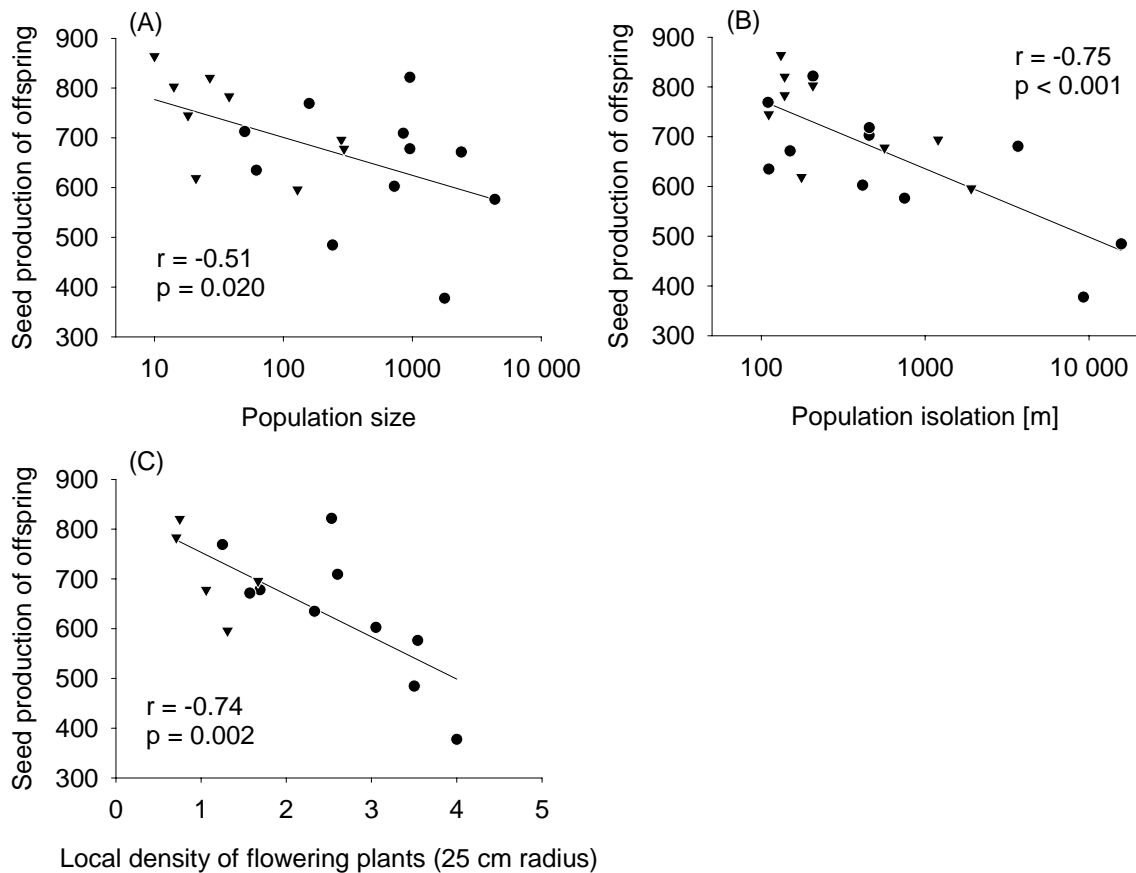


Figure 4. The relationship between seed production of offspring of *T. montanum* in the common garden and (A) the number of flowering plants in 20 populations of origin, and (B) the distance to the next population of the same populations, and (C) the mean number of conspecific flowering plants within a radius of 25 cm around randomly selected mother plants in 15 populations of origin. Circles denote managed and triangles unmanaged populations of origin.

DISCUSSION

Populations of many plants of nutrient-poor grasslands are expected to become gradually extinct in the changing landscape of central Europe. In the case of *T. montanum*, increased light competition due to cessation of traditional management like grazing or mowing may be the main cause for its decline in central Germany. At regularly managed sites with low LAI, populations of *T. montanum* contained many juvenile plants, whereas at unmanaged sites populations were of the aged type and contained only few juvenile plants. The density of juvenile plants strongly decreased with LAI, whereas the density of adult plants (flowering and non-flowering) was not influenced by LAI, indicating that adult plants may be less sensitive to habitat degradation than juvenile plants.

Our results are in line with those of previous studies of long-lived plants. Aged populations of the perennials *Gentiana pneumonanthe* and *Scorzonera humilis* mainly grew in unmanaged or nutrient-enriched grasslands (Oostermeijer et al. 1994; Colling et al. 2002), and mostly had a growth rate < 1 (Oostermeijer et al. 1996; Colling & Matthies 2006). In perennial plants like *T. montanum*, the longevity of adult plants may delay the extinction of the aged populations. However, vegetation succession and habitat degradation may proceed on unmanaged sites in the near future and only frequent grazing or mowing of currently unmanaged sites can restore habitat quality and rescue populations of grassland species like *T. montanum* in the long term.

The failure of population regeneration in aged populations of *T. montanum* was mainly due to habitat degradation. The recruitment of new plants was limited by the increased mortality of juvenile plants in small unmanaged populations with high LAI, suggesting recruitment limitation due to strong light competition (see Lepš 1999). In contrast, the first phase of recruitment in *T. montanum*, i.e. seedling establishment, was mainly influenced by litter, but not by LAI. Experimental disturbance by removing litter and vegetation slightly increased seedling establishment, and establishment was higher in populations with a thin litter layer and a high proportion of bare soil (see Bosy & Reader 1995). Thus, different factors might affect the recruitment process. In the case of *T. montanum*, the negative effects of increased light competition are restricted to later stages of the recruitment process, i.e. the survival of juvenile plants.

Reduced reproduction in populations of low local density of flowering *T. montanum* plants may also contribute to the formation of aged populations with little recruitment. The reduced density of flowering plants might be caused by smaller habitat size and thus increasing edge effects in fragmented populations of *T. montanum* (see Lienert & Fischer 2003). Lower reproduction in these populations could be due to the behaviour of pollinators, which have been reported to visit dense populations more frequently and to transfer pollen among neighboring plants more efficiently (Kunin 1997). Indeed, observations of pollinator behaviour indicate that the number of pollinators visiting *T. montanum* strongly increases with the density of flowering *T. montanum* plants in a population (M. Niggemann, unpublished data).

Offspring survival in the common garden strongly increased with the mean seed size in the population of origin. Similar maternal effects on the early development of offspring have been found in other studies (Schmid & Dolt 1994; Pico et al. 2003). Maternal effects usually decrease as development proceeds (Helenum & Schaal 1996). In line with that, seed production and multiplicative offspring fitness of *T. montanum* were not affected by mean

seed size in the population of origin. In contrast, offspring seed production and fitness in the common garden decreased with isolation and with the local density of the population of origin. The reduced offspring fitness in isolated populations might be due to genetic erosion, which is caused by lack of pollen or seed transfer from neighboring populations. This negative effect was independent of population size, suggesting that even large populations suffer from isolation. Surprisingly, high local density of mother plants in large populations negatively affected offspring fitness of *T. montanum*. In dense and large populations, the probability of cross-pollination between closely related neighboring plants may be increased, resulting in biparental inbreeding (see Becker et al. 2006). In contrast to the negative relationship between offspring seed production and population size in our study, previous studies have found an overall positive effect of population size on offspring fitness (Leimu et al. 2006). Our results strongly suggest that the density and spatial distribution of plants may be more important for the quality of transferred pollen than the total number of flowering plants in a population.

In the field populations, however, the negative effect of density on offspring seed production appears to be more than compensated by the positive effect of higher density on reproduction. Natural selection in the field might also purge inbred progeny during early phases of seedling establishment, and inbreeding depression may not affect all families of a population (Ouborg et al. 2006). Still, our results suggest that the effects of population size, density and isolation on individual plant fitness and population viability may be more intricate than previous studies have suggested. In conclusion, both habitat degradation and fragmentation have negative effects on populations of *T. montanum*, but affect different phases of the life cycle. In the short term, the effects of habitat degradation are more important than those of fragmentation, and the populations of *T. montanum* are primarily threatened by an increase in light competition on unmanaged sites, which rapidly affects the dynamics of the populations.

ACKNOWLEDGEMENTS

We thank H. Berg and T. Becker for their support and anonymous reviewers for their helpful comments. This study was supported by the research program TRANSPLANT of the European Union (EVK2-1999-00042) and by a Ph.D. scholarship of Studienstiftung des deutschen Volkes.

APPENDIX A

Habitat and population characteristics of the 23 study sites with *Trifolium montanum*. Land use of grasslands was managed (M), i.e. grazed or mown, or unmanaged (U). Mean leaf area index (LAI), size (number of flowering plants), isolation (distance to the nearest population) and mean local density (mean number of flowering plants in circles with radii of 25 cm and 100 cm) are given. For studies of stage structure (SS), seedling establishment (SE) and juvenile survival (JS), the number of study plots per population is given. For measurements of local density (LD), and for studies of reproduction in the field (RE) and offspring fitness in the common garden (OF), the number of sampled plants per population is given. Population 6 and 7 were pooled for studies of seedling establishment, juvenile survival and offspring fitness.

Site	Use	LAI	Population size	Isolation [m]	Density (25 cm)	Density (100 cm)	SS	SE	JS	LD	RE	OF
1	M	0.19	4360	750	3.5	20.9	11	12	11	41	59	20
2	M	0.36	950	3680	1.7	15.9	10	8	10	16	20	30
3	U	1.57	280	1200	1.7	10.6	8	6	8	9	17	20
4	M	0.29	950	210	2.5	29.7	10	9	10	15	12	20
5	M	0.24	860	460	2.6	18.7	10	10	10	10	20	30
6	M	0.27	1980	150	1.7	14.3	13	{7} {20}		20	30	{16}
7	M	0.33	400	150	1.3	7.8	7			10	10	
8	M	0.35	1760	9240	4.0	25.9	11	8	11	18	25	20
9	U	1.18	292	570	1.1	11.2	10	5	9	17	18	20
10	M	0.08	730	420	3.1	19.0	10	-	-	20	20	19
11	U	0.18	40	110	-	-	10	-	-	-	-	-
12	M	0.42	160	110	1.3	10.4	9	-	-	8	10	20
13	U	1.39	10	130	-	-	4	-	-	-	-	4
14	U	0.82	21	180	-	-	2	-	-	-	-	19
15	U	1.67	38	140	0.7	2.6	6	-	-	7	7	20
16	U	0.65	27	140	0.8	4.5	6	-	-	4	4	18
17	U	1.11	14	210	-	-	3	-	-	-	-	12
18	M	0.43	50	460	-	-	6	-	-	-	-	20
19	M	0.57	130	120	-	-	8	-	-	-	-	-
20	U	0.78	18	110	-	-	4	-	-	-	-	15
21	M	0.82	62	110	2.3	10.3	6	-	-	3	-	20
22	U	0.85	129	1910	1.3	5.8	10	-	-	13	13	19
23	M	0.42	240	15 740	3.5	16.8	5	-	-	10	-	19

CHAPTER 3

Habitat change and plant demography:

Assessing the extinction risk of a
formerly common grassland perennial

Submitted
with Diethart Matthies

ABSTRACT

An important aim of conservation biology is to understand how habitat change affects dynamics and extinction risks of populations of animal and plant species. We used matrix models to analyze the effect of habitat degradation on the demography of the declining perennial plant *Trifolium montanum* in nine calcareous grasslands in Germany over four years and experimentally tested the effect of grassland management. In stochastic simulations of population dynamics, we determined minimum viable population sizes and compared these to the size distribution of extant populations of *T. montanum*. Finite population growth rate decreased with light competition, measured as leaf area index above *T. montanum* plants. At unmanaged sites, population growth was <1 due to lower recruitment and lower survival and flowering probability of large plants. In stochastic simulations, median time to extinction of unmanaged populations of 100 flowering individuals was still about 50 years. Simulated management rapidly increased population growth because of higher survival and flowering probability of large vegetative plants. Management every second year would be sufficient to ensure a projected growth rate ≥ 1 . At frequently managed sites, the finite growth rate was ≈ 1 in most populations of *T. montanum*. Because of the effects of environmental and demographic stochasticity, these populations required 60 flowering plants to survive with 95% probability over the next 100 years. However, most populations of *T. montanum* in central Germany consist of less than 50 flowering plants. We conclude that habitat change after cessation of management strongly affects recruitment and the fate of established individuals of this perennial plant. Even if management is frequent, many remnant populations might be prone to extinction because of their small size. However, the results indicate that the extinction process may take a long time in perennial plants, resulting in an extinction debt.

INTRODUCTION

Many animal and plant species have strongly declined during the last decades as a result of changes in land use (Baillie et al. 2004). Understanding the consequences of habitat change for population viability and long-term persistence of both animal and plant species is a major goal of conservation research (Debinski & Holt 2000; Henle et al. 2004). One of the most species-rich habitats in Europe are calcareous grasslands, but many of them have been severely affected by the cessation of traditional management practices (WallisDeVries et al. 2002). Subsequent degradation of habitat quality is considered a main driving force for the decline of formerly common species of these grasslands (Hodgson et al. 2005; Dauber et al. 2006).

The effect of habitat change may strongly differ among plant species. Populations of short-lived species usually become quickly extinct when habitat quality decreases (Fischer & Stöcklin 1997; Matthies et al. 2004), but some species might recover due to their long-lived seed bank, if habitat conditions improved (Stöcklin & Fischer 1999). In contrast, populations of long-lived plants may be buffered by the longevity of established perennial plants (Ehrlén & Lehtilä 2002), although early phases of the life cycle might already be affected by habitat degradation (Oostermeijer et al. 1994; Colling et al. 2002). The response of populations of perennial plants to habitat degradation may therefore be delayed and patch occupancy of these species is often not in equilibrium with the environmental conditions in the habitat patches, resulting in an extinction debt (Hanski & Ovaskainen 2002). Many populations of formerly common plants that appear to be viable may actually be doomed in the long term, and the remnants of formerly larger populations may be in a process of deterministic decline that is exacerbated by a higher susceptibility of small populations to demographic and environmental stochasticity (Holsinger 2000; Matthies et al. 2004).

To determine whether remnant populations of perennial plants are viable and to guide actions of conservation management, a detailed study of the demography of a species using stage-structured matrix models is required (Schemske et al. 1994; Menges 2000). Because of the strong spatiotemporal variation in the dynamics of plant populations (Horvitz & Schemske 1995; Jongejans & de Kroon 2005), demographic information from several populations and years is necessary to determine the temporal and spatial variability of population dynamics and to investigate the relationship between population viability and habitat conditions, but such studies are time-consuming and therefore still rare (but see Menges & Dolan 1998; Colling & Matthies 2006). Even rarer are studies that have experimentally analyzed the demographic effects of management actions and that may help to identify suitable

management strategies for declining plant species (but see Brys et al. 2004; Ehrlén et al. 2005). Changes in environmental conditions or management may differently affect the phases of a plant's life cycle (Ehrlén et al. 2005; Lehtilä et al. 2006). Although the recruitment process of perennial plants is thought to be more sensitive to changes in habitat quality (Colling et al. 2002; Ehrlén et al. 2005), minor effects on vital rates involving adult plants may be more important for population growth (Colling & Matthies 2006). To decompose the overall effect on population growth into the contributions of the various vital rates, life-table response experiment (LTRE) analysis has been developed (Caswell 2001) and has been successfully applied to elucidate the effects of different habitat quality and management practices on plant population dynamics (Brys et al. 2005; Colling & Matthies 2006). Demographic information obtained over various years and in different populations can be used to construct simulation models that incorporate the effects of demographic and environmental stochasticity to assess and compare the long-term viability of different types of populations (Menges 2000).

Changes in the configuration of the cultural landscape of central Europe have strongly reduced the probability of colonization of unoccupied sites, and today the survival of grassland plants mainly depends on the survival of the extant populations (Soons et al. 2005; Herben et al. 2006). However, very few studies have investigated the demography of various extant populations of a declining grassland plant to assess the effects of changes in habitat quality on the dynamics and extinction risk of these populations. We studied the demography of the strongly declining perennial grassland plant *Trifolium montanum* L. in nine populations of different habitat quality over four years, estimated minimum viable population sizes using stochastic models and compared these to the size distribution of extant populations of *T. montanum* in central Germany.

We addressed the following questions: (1) Do differences in habitat quality affect the finite growth rate of extant populations of *T. montanum*? (2) Which parts of the life cycle contribute most to the differences in growth rate among populations and between an experimentally managed and an unmanaged population? (3) Which frequency of management and which population size are required for the long-term viability of populations of *T. montanum*?

METHODS

Study species and sites

Trifolium montanum is a formerly common herbaceous perennial of calcareous grasslands, which has strongly declined during the last decades and is threatened in central Europe (Hodvina et al. 1999; Garve 2004; Colling 2005). Vegetative propagation is rare in *T. montanum* (Klimeš & Klimešová 1999). From June to July, flowering plants produce 1-5 flowershoots, each bearing 1-6 flowerheads with c. 150 white flowers each that are pollinated by bumblebees and bees. Seeds are dispersed from July on, but dispersal distance is very limited. Most seeds germinate in spring of the following year (Thompson et al. 1997) and of the dormant seeds <1% produces a seedling (M. Schleuning, unpublished data).

In summer 2002, we selected nine calcareous grassland sites of different habitat quality with populations of *T. montanum* in a continuous landscape in central Germany (Hesse and Lower Saxony). Grazing is the usual management type of the study sites, but two sites were not managed during the study period. In each population, we counted the number of flowering plants of *T. montanum* (range of population size: 280-4360, median = 950) and measured light competition for plants of *T. montanum* using a plant canopy analyzer (LAI 2000, Li-Cor, Lincoln, Nebraska). To determine population means of light competition, we selected several plots of 25 x 25 cm with *T. montanum* in each population in July 2005 (90 plots in total) and measured the leaf area index (LAI) from two points 10 cm above the ground, i.e. above the canopy of the *T. montanum* plants. For statistical analyses, LAI was log-transformed.

Demographic field methods

In summer 2002, we randomly selected 90 permanent plots of 50 x 50 cm in the nine populations of *T. montanum* (7-13 plots per population, depending on population size). The corners of the plots were marked by metal tubes driven into the soil and could be relocated in the following years using a metal detector. During the initial census in July 2002, we assigned coordinates with a precision of 0.5 cm to each *T. montanum* plant inside the permanent plots. For each plant, we counted the number of flowershoots and measured the length of the longest leaf with a ruler and the basal diameter of the thickest shoot with calipers. We used the basal shoot diameter to estimate the size of the plants, because it was strongly correlated with leaf length ($r = 0.92$, $p < 0.001$) and could also be measured when shoots had been grazed. In July of 2003, 2004 and 2005, permanent plots were revisited before sites were grazed, plants were relocated and the same traits were measured. The survival of each plant recorded in the

previous year was checked and those that had not reappeared were considered dead. Most new plants were easily identified by their cotyledons or the first leaf that differed in shape from the following leaves. If such leaves were not found, we carefully checked if the new plant was connected to the root of one of the neighboring plants. If this was the case, the plant was considered to be a daughter ramet formed by fission, i.e. vegetative propagation, otherwise the plant was classified as having been formed by seedling establishment. Coordinates were assigned to all new plants. Overall, from 2002-2005, we observed 6861 demographic transitions.

In addition, in 2002 we set up 33 permanent plots of 50 x 50 cm in a large population that had not been managed frequently. Permanent plots were marked and plants of *T. montanum* were measured in July 2002 using the methods described above. In August 2002, plots randomly received one of three clipping treatments: (1) intensive management, i.e. clipping of the whole vegetation 5 cm above ground, (2) extensive management, i.e. clipping of c. 25% of the vegetation 5 cm above ground, and (3) no management. Cut plant material was removed from the plots. Clipping treatments simulated management practices like mowing or grazing. In July 2003, treatment plots were revisited and demographic data recorded (1286 transitions observed).

Matrix model construction

We constructed size-based transition matrices to compare recruitment, growth and survival of *T. montanum* plants among the nine study populations and among clipping treatments. We distinguished four different size classes: (1) juveniles with a basal shoot diameter <0.4 mm, (2) small vegetative plants with a basal shoot diameter of 0.4 mm or 0.5 mm, (3) large vegetative plants with a basal shoot diameter >0.5 mm, and (4) flowering plants. The projection matrix model for the analysis was a linear, time-invariant model of the form $\mathbf{n}_{(t+1)} = \mathbf{A} \cdot \mathbf{n}_{(t)}$, where \mathbf{n} is a vector of the stage-classified plants at times t and $t + 1$, and \mathbf{A} is the 4 x 4 matrix of transition probabilities a_{ij} . Demographic data from all permanent plots of a population or treatment type were pooled for the calculation of transition probabilities (see Horvitz & Schemske 1995). Transition probabilities were calculated as the number of plants developing from stage i to stage j in one year, divided by the number of plants in stage i in the previous year. Rare events of fission were handled by enabling two simultaneous transitions by the same plant. Newly recruited plants from seeds had been formed by the seeds of the flowering plants of the previous year, as germination from the seed bank was negligible (M. Schleuning, unpublished data). Transition matrices \mathbf{A} were constructed for all populations

pooled (one overall matrix and a matrix for each of the three annual transitions), for each population (an overall matrix from 2002-2005 that consisted of the pooled data from all study years) and for each type of clipping treatment. In addition, we distinguished three types of populations according to their finite growth rate (decreasing, stable or increasing in size), and constructed an overall matrix for each type of population.

Matrix model analysis

Differences in the fate of plants among years, populations and different clipping treatments were analyzed using log-linear models (Caswell 2001). From each transition matrix, we calculated the dominant eigenvalue, i.e. the finite rate of population growth, λ (Caswell 2001). The effect of light competition (LAI) on finite population growth rate was analyzed by linear regression. To estimate sampling errors in λ , we randomly sampled individual fates from the observed vector of fates with replacement, generated a bootstrap fate vector of the same sample size, and calculated bootstrap transition probabilities and λ . We ran 10 000 bootstrap replications to calculate bias-corrected 95% confidence intervals (CI) around the estimates of λ (Caswell 2001). To test for significant differences in λ between population and treatment types, we carried out two-tailed, pair-wise permutation tests with the null hypothesis that $\theta = |\lambda_{\text{type1}} - \lambda_{\text{type2}}| = 0$ (Caswell 2001; Colling & Matthies 2006). We randomly permuted individuals between population (treatment) types and then constructed bootstrap matrices for each population (treatment) type to calculate the test statistic $\theta_{(i)}$ as the absolute difference between the finite growth rates of the respective population (treatment) types (10 000 replications). Then, the probability p of obtaining a value of $\theta \geq \theta_{\text{observed}}$ was calculated as (Caswell 2001):

$$p[\theta \geq \theta_{\text{observed}} | H_0] = \frac{\#\{\theta_{(i)} \geq \theta_{\text{observed}}\} + 1}{10\,000 + 1}$$

From the overall matrix for each population type, excluding recruitment and vegetative propagation, we calculated the conditional total life span of reproductive plants of *T. montanum* using equation 6 in Cochran and Ellner (1992) and subtracted one year from the estimated ages as recommended by Ehrlén and Lehtilä (2002). We carried out a life table response experiment (LTRE) analysis to decompose the observed differences in λ among the three different types of populations and among clipping treatments into the contributions of each vital rate using standard methods of LTRE analysis (Caswell 2001). We chose the transition matrix of the population type with a finite growth rate ≈ 1 , i.e. stable in size, as the reference matrix to analyze the effect of population type, and the matrix of unclipped plots as

the reference matrix to analyze the effect of simulated management. The effect of management frequency on population growth was tested by projecting the dynamics of a population over 100 000 time intervals. We incorporated the transition matrix of unmanaged plots as the standard matrix into the model and sampled at certain time intervals the matrix of experimentally managed plots (each second, each third, each (...) year). The log growth rate was then calculated as the arithmetic mean of all pairs of $\log(\mathbf{n}_{(t+1)}/\mathbf{n}_{(t)})$. Matrix model and regression analyses were carried out with R 2.4.1 (R Development Core Team 2006).

We simulated the stochastic population dynamics over 100 years using RAMAS[®]-Metapop (Akçakaya & Root 1998) and estimated minimum viable population sizes for three types of populations differing in finite growth rates. We constructed annual matrices for each type of these populations from the field observations and then calculated an arithmetic mean matrix and a standard deviation matrix for each population type and incorporated these into the program. The program assigns during each time step to each transition rate a random value drawn from a normal or log-normal distribution whose mean and standard deviation are given by the empirical matrices. We chose a log-normal distribution for stochastic simulations, because several matrix elements had small mean values, but large standard deviations (see Akçakaya & Root 1998). Demographic stochasticity was included using the procedure implemented in RAMAS[®]-Metapop. The stage structure introduced into the model was based on the initial field census in each of the three types of populations. We ran 10 000 replications of the model and determined the proportion of runs in which no plants (including juveniles) survived, i.e. estimated real population extinction. Minimum viable population sizes were calculated as the number of flowering plants required for a 95% probability of survival over 100 years (see Menges 2000). Current data on the sizes of all 86 populations of *T. montanum* in the German state of Lower Saxony were provided by A. Schacherer (NLWKN). Methodology and results (1982-1992) of the plant species monitoring program in Lower Saxony are published in Garve (1994).

RESULTS

Spatiotemporal variation in demography

Plant survival was high in the large size classes, but about 50% of the juvenile plants died during each year (Table 1). Most plants stayed in their respective size class from one year to the next. Retrogression into previous size classes was observed, but not to juvenile plants and not from flowering to small vegetative plants. The flowering probability of small vegetative

plants was only 6%, whereas that of large vegetative plants was 31%. Of the flowering plants only 56% flowered again in the following year. We observed 1438 newly recruited plants from seeds during the three one year time intervals. Of these 12% developed into small vegetative plants during the first year. In a log-linear analysis, the fate of plants strongly differed among years ($\Delta G^2 = 190.2$, $p < 0.001$) and among populations ($\Delta G^2 = 383.4$, $p < 0.001$). The fate of all vegetative plant stages strongly differed both in time and space ($p < 0.001$ in all cases), whereas that of flowering plants was less variable ($p = 0.076$ and $p = 0.015$, respectively).

Table 1. Transition probabilities of individuals of *T. montanum* from year t (columns) to year $t + 1$ (rows). To calculate transition probabilities, demographic data were pooled over the nine populations and the three one year time intervals recorded. Fecundity transitions from flowering to newly recruited plants from seeds are given in bold. Mean plant survival in each stage is given in the last row.

	Juvenile	Small vegetative	Large vegetative	Flowering
Juvenile	0.323	0	0	1.275
Small vegetative	0.144	0.442	0.083	0.172
Large vegetative	0.018	0.351	0.541	0.391
Flowering	0	0.058	0.309	0.560
Survival	0.485	0.850	0.934	0.952

From 2002-2005, population size slightly increased over all populations of *T. montanum* (finite rate of population growth (λ) = 1.054, 95% confidence interval (CI) 1.039-1.070), but temporal variation among years was considerable (coefficient of variation (CV) = 11.7%), probably due to weather variation. Overall population size increased from 2002 to 2003 ($\lambda = 1.097$, CI 1.061-1.135) and from 2003 to 2004 ($\lambda = 1.162$, CI 1.134-1.193), but decreased from 2004 to 2005 ($\lambda = 0.923$, CI 0.909-0.950). Spatial variation in overall λ was strong and varied from 0.880-1.144 among populations (CV = 7.9%). In two of the populations, overall λ was less than 1 (pooled matrix: $\lambda = 0.921$, CI 0.879-0.963). At four sites, population size was stable ($\lambda = 1.031$, CI 1.010-1.051), whereas three populations increased in size ($\lambda = 1.123$, CI 1.098-1.149). In pair-wise permutation tests, finite growth rates differed significantly among these three types of populations ($p < 0.001$ in all cases). Finite growth rates strongly decreased with the mean leaf area index at a site (Fig. 1). The leaf area index above *T. montanum* plants was much higher in the two declining populations that had not been managed during the study period. These two populations were also the smallest (each <300 flowering plants). The conditional total life span of flowering plants was much lower in declining populations at sites with high light competition (10.4 years) than in those that were stable (18.7 years) or increased (21.4 years) in size.

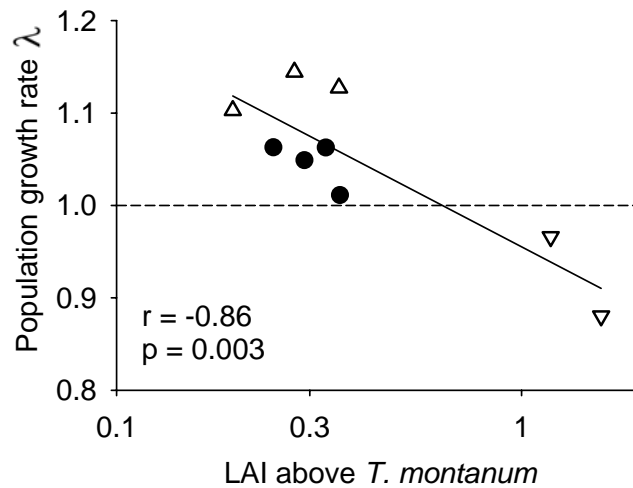


Figure 1. The relationship between the finite rate of population growth, λ , and the mean leaf area index (LAI) measured above *T. montanum* plants in nine populations of *T. montanum*. Growth rates <1 , ≈ 1 , and >1 are indicated by different symbols.

We carried out a LTRE analysis to investigate which demographic transitions were responsible for the differences in growth rates. In populations with a $\lambda < 1$, recruitment was much lower indicating a lower probability of seedling establishment and of survival and growth of newly recruited plants in the first growing season (Fig. 2A, Appendix A), but recruitment did not cease completely in these populations (0.9 newly recruited plants per flowering plant). Survival of juvenile plants was lower in declining than in stable populations and a slightly lower proportion of large vegetative and flowering plants survived and flowered in the next year. These small differences in the fate of large plants made the strongest contribution to the lower population growth rate in declining populations, but lower recruitment also contributed considerably to population decline (Fig. 2B). In populations with a $\lambda > 1$, a higher proportion of vegetative and flowering plants flowered in the next year, whereas plant survival was very similar in large vegetative and flowering plants in growing and stable populations (Fig. 3A, Appendix A). The very similar survival is indicated by the fact that the sum of the differences in the transitions to vegetative and flowering plants nearly equals zero in these stages. Higher probabilities of flowering and thus seed production made the strongest contribution to higher population growth in growing populations (Fig. 3B).

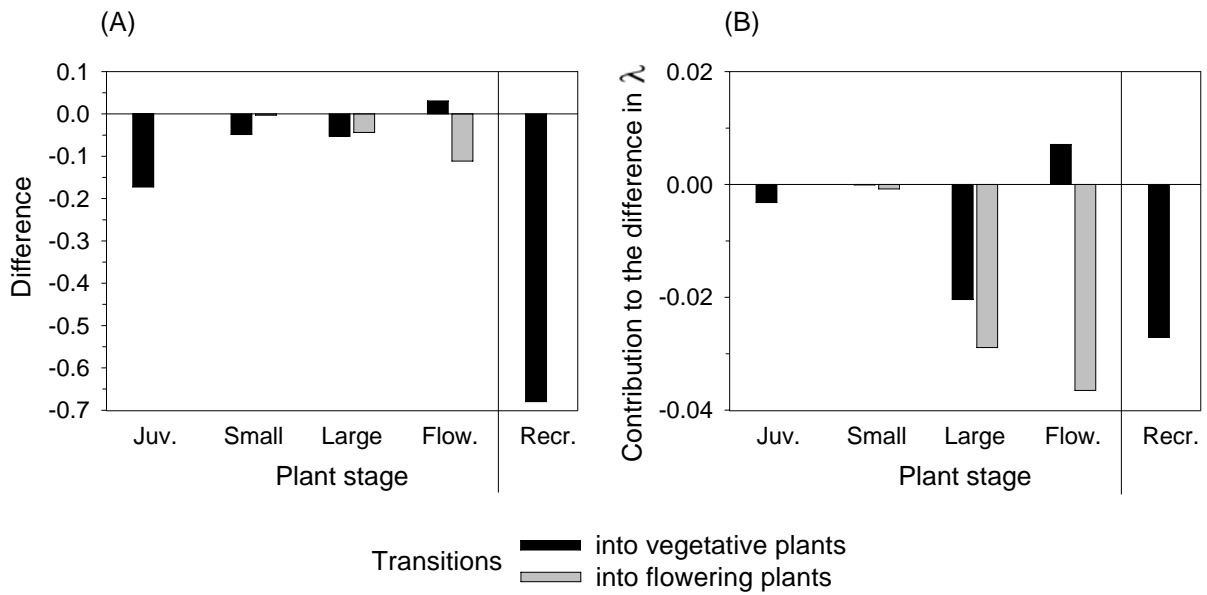


Figure 2. Life-cycle differences between declining ($\lambda < 1$) and stable ($\lambda \approx 1$) populations of *T. montanum*. (A) Differences between transition probabilities, (B) and the contributions of these differences to the difference in λ . Transitions involving different plants stages are abbreviated as: Juv. = juvenile, Small = small vegetative, Large = large vegetative, Flow. = flowering. Recr. = fecundity transitions from flowering to newly recruited plants from seeds.

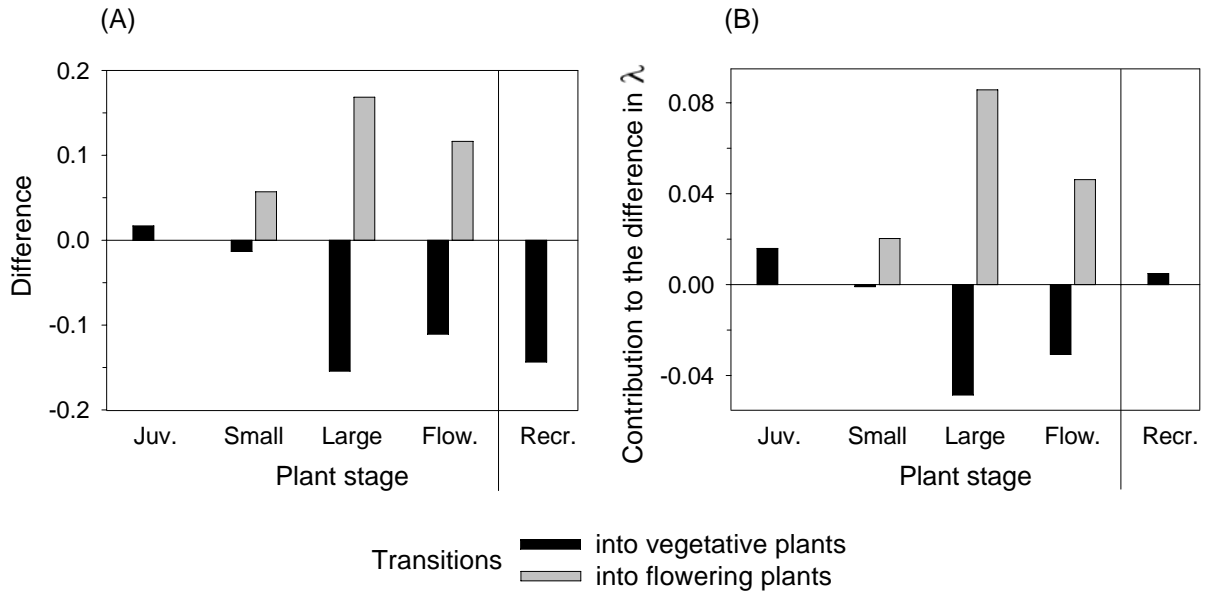


Figure 3. Life-cycle differences between growing ($\lambda > 1$) and stable ($\lambda \approx 1$) populations of *T. montanum*. (A) Differences between transition probabilities, (B) and the contributions of these differences to the difference in λ . Transitions involving different plants stages are abbreviated as: Juv. = juvenile, Small = small vegetative, Large = large vegetative, Flow. = flowering. Recr. = fecundity transitions from flowering to newly recruited plants from seeds.

Effects of simulated management

Experimental management strongly affected the demography of *T. montanum*, but plant fate did not differ between the two types of experimental management ($\Delta G^2 = 13.7$, $p = 0.623$), whose data therefore were pooled for further analyses. The fate of plants strongly differed between managed and unmanaged plots ($\Delta G^2 = 37.8$, $p = 0.002$), in particular that of large vegetative plants ($\Delta G^2 = 18.7$, $p = 0.001$). Survival (89.2% vs. 76.1%) and flowering probability (21.5% vs. 6.0%) of large vegetative plants were higher in managed than in unmanaged plots. The finite rate of increase, λ , was significantly higher in managed ($\lambda = 1.128$, CI 1.044-1.222) than in unmanaged plots ($\lambda = 0.912$, CI 0.807-1.014, permutation test: $p = 0.009$). We compared managed and unmanaged plots in a LTRE analysis. Recruitment was much higher in managed than in unmanaged plots, and the flowering probability of all stages was increased (Fig. 4A). Higher probabilities of flowering and thus seed production contributed most to the differences in λ , whereas the increased probability of recruitment only made a small positive contribution (Fig. 4B). We projected population growth under different management frequencies by alternate sampling of the observed transition matrix in managed and unmanaged plots, respectively. If management was assumed to take place each second year, populations would increase (1.028), whereas management each third (0.993) or each fourth year (0.974) would not be sufficient to halt population decline.

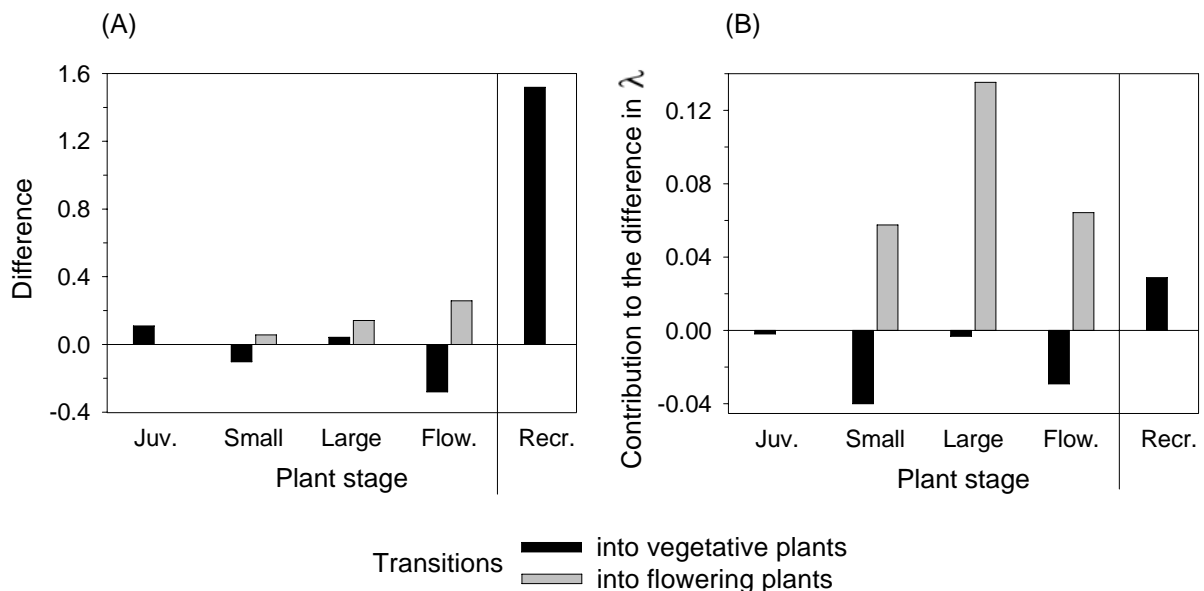


Figure 4. Life-cycle differences between an experimentally managed and an unmanaged population of *T. montanum*. (A) Differences between transition probabilities, (B) and the contributions of these differences to the difference in λ . Transitions involving different plants stages are abbreviated as: Juv. = juvenile, Small = small vegetative, Large = large vegetative, Flow. = flowering. Recr. = fecundity transitions from flowering to newly recruited plants from seeds.

Minimum viable population size

For each of the three types of populations with different finite growth rate, we determined the number of plants a population would require for a 95% probability of survival over the next 100 years, i.e. the minimum viable population size (MVP). Populations with a $\lambda < 1$ would of course go deterministically extinct, but median time to extinction was long for populations with an initial size of 1000 flowering plants (68 years) and even for those starting with 100 flowering plants (46 years). Populations with a $\lambda \approx 1$ would require 60 flowering plants to fulfil the MVP criterion, whereas populations with a $\lambda > 1$ required only 10 flowering plants (Fig. 5A). For the German state of Lower Saxony, data on the size of all populations of *T. montanum* indicate that 55% of the populations consist of less than 50 flowering plants (Fig. 5B). Since most of the extant populations will have at best a $\lambda \approx 1$, >50% of the populations of *T. montanum* in this state are smaller than MVP.

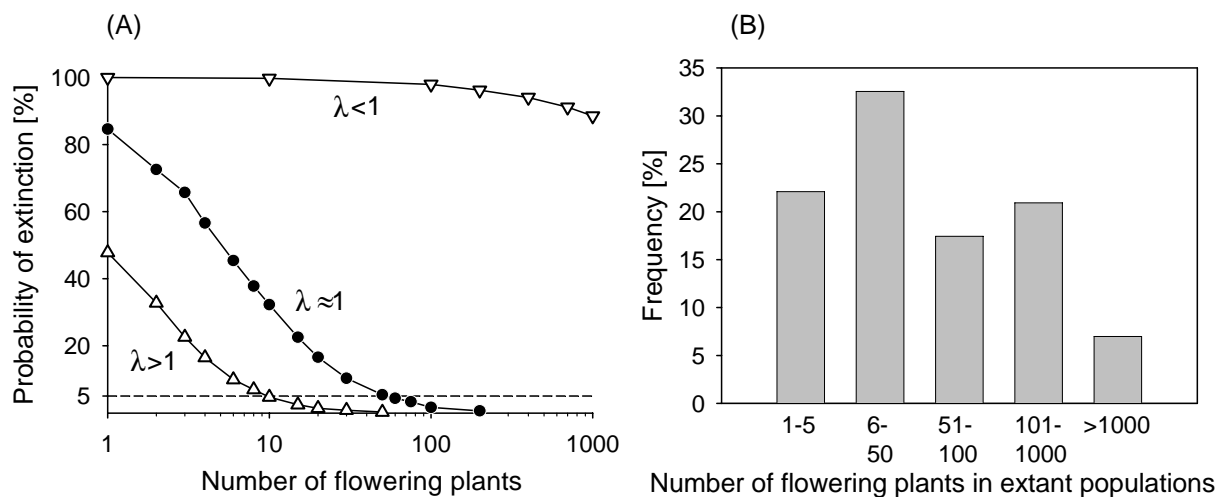


Figure 5. (A) The relationship between the probability of extinction of a population and its size for populations of *T. montanum* of different finite rate of increase, λ . Results are shown of simulations including demographic and environmental stochasticity of the population dynamics over 100 years based on data from four years. The dashed line denotes a probability of population extinction of 5% over 100 years. (B) The size distribution of the 86 extant populations of *T. montanum* in Lower Saxony, Germany (see Garve 1994).

DISCUSSION

Our study demonstrates that habitat change plays a crucial role in the process of population decline of formerly common grassland plants. An increase in light competition, measured as leaf area index above *T. montanum* plants, strongly reduced growth rate and viability of populations of *T. montanum*. This was due to lower recruitment and a lower survival and flowering probability of large plants at unmanaged sites. Our results support conclusions of other studies that cessation of management negatively affects populations of nutrient-poor grassland plants (Brys et al. 2004; Ehrlén et al. 2005). In most of these studies, early phases of the life cycle were more strongly affected by cessation of management than those involving adult plants (Bullock et al. 1994; Ehrlén et al. 2005). In contrast, transitions involving large plants contributed most to population decline in *T. montanum* and the conditional total life span of flowering plants dropped from 20 to 10 years at unmanaged sites. This indicates that established plants may not in all cases be able to buffer the negative effects of habitat degradation on populations of perennial plants (see also Brys et al. 2005), suggesting shorter time delays to population extinction than previously suggested (Eriksson & Ehrlén 2001; Hanski & Ovaskainen 2002). Many populations of *T. montanum* may be doomed, but in contrast to other species some recruitment does still occur in unmanaged populations. Continued recruitment is responsible for the rather long median time to extinction of c. 50 years even for populations of only c. 100 flowering plants. Such delays in the extinction process increase the time available for conservation management to rescue declining plant populations by a renewal of grassland management (Helm et al. 2006).

Our results indeed demonstrate that declining populations of *T. montanum* can rapidly be rescued by grassland management. In *T. montanum*, grassland management every two years would be sufficient to halt deterministic population decline. Management simulating the effect of grazing or mowing after the growing season increased the probability of flowering and recruitment in the following year, although plants of *T. montanum* were also mown and the litter layer was not disturbed (see Ehrlén et al. 2005), indicating that light competition is the limiting factor for these populations of *T. montanum*. Similar results have been found in studies of the grassland perennial *Primula veris* (Brys et al. 2004).

How to interpret the results of demographic studies to further plant conservation is a matter of debate (Ehrlén & van Groenendael 1998; Caswell 2000; Lehtilä et al. 2006). We separately examined the contributions of transitions to vegetative and flowering plants to the observed differences in population growth. This approach was very insightful, because it showed that both differences in survival and flowering probability of large plants contributed

to population decline in unmanaged populations. Transitions involving flower formation, i.e. seed production, immediately affected the dynamics of the populations and contributed most to the actual differences in growth rates among populations, indicating that *T. montanum* is seed-limited. Differences in the probability of flowering also contributed strongly to differences in population growth rates in *P. veris* (Brys et al. 2004 & 2005), suggesting that the flowering probability of established plants may be a key transition for the conservation of perennial plants. Because seed production and seedling establishment are consecutive processes, their reduction can have multiplicative negative effects on the population dynamics as observed in unmanaged populations of *T. montanum*. Conservation management of perennial plants should aim to increase both the probability of flowering of established plants and the availability of safe sites for seedling establishment (see also Lehtilä et al. 2006).

Stochastic simulations indicated that the long-term viability of unmanaged populations of *T. montanum* is very low. Many of the extant populations may actually only still exist because populations consisting even of only 100 flowering plants typically persist for several decades after the cessation of management. This suggests that because of an extinction debt the current distribution of perennial grassland plants is not a good indicator of their regional viability (see also Helm et al. 2006). For the conservation of declining grassland plants, management actions are urgently required and should be frequent to restore and maintain an open vegetation structure. Grassland management should be carried out after seed shed at the end of the growing season, because the population dynamics of most grassland plants are rapidly affected by seed shortage (Lennartsson & Oostermeijer 2001; Brys et al. 2004).

At frequently managed sites, the finite growth rate of most populations of *T. montanum* was ≈ 1 . In stochastic simulations the risk of extinction for these populations was nevertheless considerable, and they required c. 60 flowering plants to be viable. However, in central Germany most populations of *T. montanum* are smaller and thus face a considerable risk of extinction, even if management is frequent. Many other declining grassland plants have also a high proportion of small populations (Garve 1994), which are prone to extinction in the long-term (Matthies et al. 2004). Due to the lack of suitable habitats and insufficient dispersal in the fragmented landscape, there is currently probably no founding of new populations (Hanski et al. 1996), and small populations are therefore important for the future evolutionary potential and regional viability of declining grassland plants (Volis et al. 2005). To halt the ongoing loss of these populations, conservation management should explicitly include small remnants of nutrient-poor grasslands in management plans and aim to restore adjacent habitats to enlarge the size of small populations.

ACKNOWLEDGEMENTS

We thank "Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN)" and in particular A. Schacherer for data on sizes of populations of *T. montanum* in the German state of Lower Saxony. Support from U. Becker, H. Berg and M. Niggemann during site selection and data collection is gratefully acknowledged. This study was supported by the research program TRANSPLANT of the European Union (EVK2-1999-00042) and by a Ph.D. scholarship of Studienstiftung des deutschen Volkes.

APPENDIX A

Transition probabilities of individuals of *T. montanum* from year t (columns) to year $t + 1$ (rows) in the three types of populations with different projected growth rate, λ . (A) $\lambda < 1$, (B) $\lambda \approx 1$, and (C) $\lambda > 1$. Individuals were classified into four size stages. For the calculation of transition probabilities, demographic data were pooled over populations belonging to the same population type and the three one year time intervals (2002-2005) recorded. Fecundity transitions from flowering to newly recruited plants from seeds are given in bold. Mean plant survival in each stage is given in the last row.

(A) $\lambda = 0.921$ (95% confidence interval 0.879-0.963)

	Juvenile	Small vegetative	Large vegetative	Flowering
Juvenile	0.163	0	0	0.813
Small vegetative	0.116	0.296	0.080	0.119
Large vegetative	0.039	0.459	0.555	0.470
Flowering	0	0.031	0.217	0.410
Survival	0.318	0.786	0.853	0.881

(B) $\lambda = 1.031$ (95% confidence interval 1.010-1.051)

	Juvenile	Small vegetative	Large vegetative	Flowering
Juvenile	0.353	0	0	1.476
Small vegetative	0.129	0.481	0.112	0.136
Large vegetative	0.009	0.322	0.576	0.439
Flowering	0	0.033	0.261	0.522
Survival	0.490	0.837	0.949	0.961

(C) $\lambda = 1.123$ (95% confidence interval 1.098-1.149)

	Juvenile	Small vegetative	Large vegetative	Flowering
Juvenile	0.325	0	0	1.257
Small vegetative	0.159	0.450	0.057	0.212
Large vegetative	0.023	0.340	0.477	0.329
Flowering	0	0.091	0.429	0.638
Survival	0.507	0.881	0.963	0.967

CHAPTER 4

Flooding and canopy dynamics shape the
demography of an Amazon understory herb

Submitted

with Vicky Huaman and Diethart Matthies

ABSTRACT

Clonal understory herbs are an important component of Amazon rainforests and can influence forest regeneration because of their local dominance. However, little is known about the demographic response of clonal herbs to the spatial and temporal environmental variation in the rainforest understory. In a factorial design, we studied the influence of flooding and canopy gaps on the demography of the widespread clonal understory herb *Heliconia metallica* in 16 populations in a Peruvian floodplain forest over two wet and two dry seasons using periodic matrix models. The life history of *H. metallica* was dominated by ramet survival and clonal growth, whereas recruitment of seedlings in established populations was very rare and contributed little to population growth. In recently formed small canopy gaps, growth and clonal expansion of the ramets were rapid and reproduction was frequent, whereas in non-gaps ramets grew and expanded little and rarely flowered. All populations increased in size during the wet and decreased during the dry season. Projected annual growth rates of non-flooded populations at both gap and non-gap sites were <1 . In contrast, growth rates of flooded populations were close to 1 at non-gap sites and significantly >1 in recently formed gaps. Life table response analyses indicated that the lower growth rate at non-flooded sites was mainly due to the lower survival of ramets during the dry season. In stochastic matrix models, the extinction risk of non-flooded populations of *H. metallica* was high even if gaps were assumed to be formed in 5% of the years, whereas that of flooded populations was low and decreased with the frequency of gap formation. The effects of flooding and canopy gaps interact and determine the dynamics of the populations of *H. metallica*. The clonal life form and the plasticity of the ramets enable populations of clonal herbs like *H. metallica* to persist under variable light conditions, but may not be able to buffer the drought stress during the longer dry seasons predicted by climate change models.

INTRODUCTION

To understand how plant populations in tropical rainforests respond to spatial and temporal environmental variation is a major goal of tropical ecology and is critical for the prediction of the potential consequences of habitat fragmentation and climate change for plant diversity (Bruna & Oli 2005; Engelbrecht et al. 2007). Structure and composition of tropical forests are strongly affected by the dynamics of plant populations in the understory (Nicotra et al. 1999; Bunker & Carson 2005), but most studies of these processes have focused on the recruitment of rainforest trees (Wright et al. 2003). However, plants that complete their life cycle in the understory constitute up to 50% of the diversity of neotropical forests and provide key resources for many species of animals (Gentry & Emmons 1987; Gentry 1990). Many understory herbs of tropical forests are clonal (e.g. of the genus *Heliconia*, Berry & Kress 1991). These herbs can strongly affect forest dynamics because of their local dominance and inhibition of tree recruitment (Griffiths et al. 2007; Stevenson 2007), but previous studies of the population dynamics of tropical herbs have focused on the non-clonal *Calathea ovandensis* (Horvitz & Schemske 1995) and *Heliconia acuminata* (Bruna & Oli 2005).

The dominant environmental factor for plants in the understory of tropical lowland forests is lack of light, as only 1-2% of the photosynthetically active radiation typically reaches the understory (Chazdon & Fetcher 1984). An increase in light availability by the formation of a gap is beneficial for growth, reproduction and recruitment of understory species (Horvitz & Schemske 1994; Valverde & Silvertown 1995; Bruna & Ribeiro 2005), and the population growth rate of understory herbs is usually positively related to canopy openness (Horvitz & Schemske 1995; Valverde & Silvertown 1998). It has been suggested that understory herbs form metapopulations that are characterized by frequent population extinction and colonization events in response to canopy closure and opening (Valverde & Silvertown 1997). However, populations may be buffered by the existence of a seed bank or by the longevity of plants, which both increase the temporal stability and decrease the probability of population extinction (Doak et al. 2002; Nicolè et al. 2005). In tropical forests, seed banks are rare (Vásquez-Yanes & Orozco-Segovia 1993), but clonal understory herbs may be buffered by a meristem bank of small vegetative ramets against fluctuations in habitat quality.

Another crucial factor influencing the population dynamics of understory plants in many neotropical forests may be flooding, since c. 20% of the Amazon rainforests are exposed to seasonal flooding in the rainy season (Junk 1997). Flooding frequency and duration vary at a small spatial scale due to the heterogeneous micro-topography that is the

result of historical river dynamics (Terborgh 1990). In the lower parts of a floodplain, herbs are frequently subjected to scouring floods, but those that withstand disturbance may flourish due to increased water availability and reduced competition at frequently flooded sites (Menges 1990; Elderd & Doak 2006). During the dry season, local differences in water availability and drought stress strongly influence the dynamics of plant populations in tropical forests (Bunker & Carson 2005). Understory herbs are sensitive to water limitation (Skillman et al. 1999), which might explain the decreasing density and diversity of tropical understory plants with increasing severity of the dry season (Gentry & Emmons 1987; Wright 1992). These plants might therefore be very sensitive to droughts that have been observed during the last decades (Aragão et al. 2007) and are predicted to intensify in Amazonia in the future (Betts et al. 2004). However, the potential effects of drought on the population dynamics of tropical understory herbs are difficult to predict, because all previous demographic studies were carried out in non-flooded forests and did not analyze the effects of spatial and seasonal differences in water availability (see Horvitz & Schemske 1995, Bruna & Oli 2005).

For a profound understanding of the demography of a plant, demographic studies incorporating populations in the complete range of habitats in which a species occurs are necessary (Lehtilä et al. 2006). In tropical forests, the spatial heterogeneity in light and water availability can create a mosaic of different habitats, in which the demography of understory plants may differ strongly. However, no study has investigated the interacting effects of canopy openness and flooding on the population dynamics of tropical understory plants, and even in temperate regions studies that analyze the effects of more than one factor on plant demography are very rare (but see Elderd & Doak 2006). In regions with a seasonal climate, periodic fluctuations in environmental factors may also strongly affect the population dynamics of plants. Periodic matrix models provide a powerful, but underutilized tool for understanding the responses of plant populations to seasonal fluctuations in environmental factors, e.g. caused by flooding, drought or frost (Smith et al. 2005).

Spatiotemporal variation in population dynamics may be due to variation in different life-history components and their relative influence on the finite rate of population growth (λ) can be analyzed by means of periodic prospective and retrospective perturbation analyses (Smith et al. 2005). The prospective approach (elasticity analysis) explores how small changes in the vital rates would affect λ (de Kroon et al. 1986 & 2000), whereas the retrospective approach (life-table-response experiments, LTRE) quantifies the contribution of the actual variability in the vital rates to the observed variability in λ (Caswell 2001).

We analyzed the effects of spatial and seasonal environmental variation on the demography of an Amazon understory herb (*Heliconia metallica* Planchon & Linden ex Hooker, Heliconiaceae). In a Peruvian floodplain forest, we studied the influence of flooding and gaps on the demography of *H. metallica* in 16 populations over two wet and two dry seasons. We used periodic matrix models to address the following questions: (1) Is the demography of *H. metallica* influenced by flooding and canopy dynamics? (2) Are demographic processes in the dry or the wet season more important for the population dynamics of *H. metallica*? (3) Which demographic transitions contribute most to the spatial and temporal variation in population growth rate?

METHODS

Study system

The more than 200 *Heliconia* spp. are important components of the understory of neotropical forests (Bruna & Kress 2002). *Heliconia metallica* is distributed from Honduras to Bolivia (Berry & Kress 1991) and is a common component of the floodplain community in south-eastern Peru, where it grows both under a closed canopy and in small canopy gaps. Like most *Heliconia* spp., it is clonal and spreads laterally by rhizomes which produce above-ground shoots (ramets) that can reach a height of up to 3.5 m. The maximum distance observed between two connected ramets was 65 cm. New ramets remain connected to the mother ramet during establishment, but become independent later. Experimental separation of connected ramets by cutting the rhizome did not affect the survival probability of the ramets ($n = 48$, $\chi^2 = 1.51$, $p = 0.220$). Ramets of *H. metallica* may generate a single terminal inflorescence and eventually die after reproduction, but new shoots are formed from their rhizome. In the study area, *H. metallica* is the only understory herb that flowers and produces nectar throughout the whole year and its flowers are visited by at least seven species of hummingbirds. Most of the ripe fruits are removed by frugivorous birds. Seeds mainly germinate during the wet season from October to April and do not form a long-lived seed bank.

Study site

The field studies were carried out in a white-water floodplain forest of the Madre de Dios River that grows on rich alluvial soils close to Manu Wildlife Centre in south-eastern Peru (270 m asl, 12°21'20"S , 70°42'44"W). We studied 16 populations of *H. metallica* separated from each other by at least 100 m and distributed over an area of 2 km² of mature floodplain

forest. We chose study populations that were situated both under a closed forest canopy and in c. one-year-old small canopy gaps, and that occurred at different elevations above the river (maximum difference in elevation c. 6 m). The relief of the floodplain varies on a small spatial scale as a result of historical river and stream dynamics (Terborgh 1990). Precipitation in the study area is c. 2500 mm per year and strongly varies between a dry season from May to September and a rainy season from October to April (>80% of the precipitation). The river level fluctuates strongly within a year with peak water levels and occasional inundation of the floodplain between November and April (Amazon Conservation Association, unpublished data).

Installation of permanent plots and measurement of habitat variables

In October 2004, we established in each population 9-17 permanent plots of 2 x 2 m (a total of 195 plots). Plots were set up along transects from the centre to the edge of each population that were marked by wooden poles. The corners of the plots were marked with large metal nails to which strips of color tape were attached. Plots could easily be relocated by their position along and distance to the transects. In September 2006, i.e. at the end of the dry season, we measured in each plot the soil water content [%] at 20 cm of soil depth by frequency-domain reflectometry (FDR, Theta-Probe ML2x, Delta-T, Cambridge, UK). In addition, during three flooding events in each rainy season, we visited the populations to record whether a population was flooded or not. Hemispherical photographs were taken above the *H. metallica* plants (c. 1.8 m height) with a camera with fisheye-converter (Nikon Coolpix 4500 with FC-E8 converter, Nikon, Tokyo, Japan), mounted on a levelled tripod in November 2004 and 2005, and the canopy openness in each plot was determined with the software Gap Light Analyzer 2.0 (Frazer et al. 1999).

Classification of population types by habitat conditions

We expected clear differences in the demography of populations of *H. metallica* between flooded and non-flooded and gap and non-gap sites. Therefore we distinguished four types of populations according to their habitat: (1) frequently flooded in gap (n = 3 populations), (2) frequently flooded in non-gap (n = 5), (3) non-flooded in gap (n = 3), and (4) non-flooded in non-gap (n = 5). The soil water content at 20 cm of soil depth was significantly higher in the frequently flooded than in the non-flooded populations at the end of the dry season (34.1% vs. 30.3%, $F_{1,14} = 6.6$, $p = 0.027$). The mean canopy openness in November 2004, measured above *H. metallica* ramets, was >4% in the six populations that were situated in and along the

margins of small canopy gaps (gap vs. non-gap: 4.8% vs. 3.5%, $F_{1,14} = 29.7$, $p < 0.001$). Populations of *H. metallica* were spatially more extended than the small canopy gaps and not all of the plots were strongly affected by the increase in canopy openness. Therefore, the means of the population maxima of canopy openness of gap and non-gap populations differed more strongly (gap vs. non-gap: 7.8% vs. 4.5%, $F_{1,14} = 30.0$, $p < 0.001$). The small canopy gaps closed rapidly due to the growth of pioneer trees in the gaps that shaded the ramets of *H. metallica* (mean canopy openness <4% in all gaps in November 2005), indicating a rapid transformation of gap to non-gap sites for *H. metallica* in about two years (see also Smith et al. 1992; Fraver et al. 1998).

Demographic field methods

During the initial census in October 2004, 2735 ramets of *H. metallica* were tagged with numbered green plastic strips in the permanent plots and the height and phenological state (vegetative, reproductive) of each ramet was recorded (123-211 ramets per population). Plots were revisited and plants measured four times at half year intervals to cover two rainy and two dry seasons in each population. Ramets whose above-ground parts were dead or vanished were considered dead. Each new ramet was marked and measured, and its mother ramet was determined by carefully following its rhizome to its origin. This was possible for 82% of the 3329 new ramets recorded during the study period. New seedlings could easily be distinguished from new ramets, but only 17 seedlings were found during the study period. Overall, the fates of 6081 ramets were recorded from 2004-2006 (1245-1740 ramets per population type).

Matrix model construction

We constructed size-based transition matrices to analyze the patterns of ramet stasis, ramet growth, clonal growth and seedling recruitment in each of the four types of populations situated in flooded or non-flooded, and gap or non-gap habitats. Demographic data from all permanent plots in a population type were pooled for the construction of transition matrices (see Horvitz & Schemske 1995). Because of the rarity of seedling recruitment in the established populations, we did not separate a distinct seedling stage and only distinguished three ramet stages, (1) small ramets ≤ 50 cm height, (2) large ramets > 50 cm height, and (3) reproductive ramets. Vegetative ramets could stay in their respective size class, could grow larger or could become reproductive within one time interval of six months. Regression of ramets into a smaller size class was not observed. The very few seedlings were treated as

small ramets that had been produced by reproductive ramets. To describe ramet stasis, ramet growth and fecundity, i.e. seedling recruitment, we constructed a matrix \mathbf{R} that included the corresponding life cycle transitions r_{ij} .

In addition, we constructed a matrix \mathbf{C} that included the observed transitions involving clonal growth c_{ij} (see transition matrices in Appendix A). New ramets formed by clonal propagation by ramets from all stages contributed to both vegetative size classes, but could not reach the flowering state within a time interval of six months. From the data on the mother ramet of each new ramet, we calculated to which proportion each stage class contributed to the production of small and large vegetative ramets. Using these proportions, we partitioned the new small and large vegetative ramets among the three ramets stages and then calculated the corresponding matrix elements c_{ij} of the matrix \mathbf{C} . To describe how ramets in each stage contributed to each stage during one time interval of six months, we then calculated the composite transition matrix \mathbf{B} given as $\mathbf{B} = \mathbf{R} + \mathbf{C}$ (Caswell 2001). Matrix elements were assigned to the different life cycle pathways of ramet stasis, ramet growth, fecundity and clonal growth (Silvertown et al. 1993). Life-cycle pathways that were overlapping in the composite transition matrix \mathbf{B} could be distinguished by the decomposition of matrix \mathbf{B} into its partial matrices of ramet stasis, ramet growth, and the rarely observed fecundity \mathbf{R} and that containing clonal growth \mathbf{C} , respectively (see transition matrices in Appendix A).

The periodic projection matrix model for the analysis was a time-varying model of the form $\mathbf{n}_{(t+1)} = \mathbf{B}_{\text{dry}} \cdot \mathbf{B}_{\text{wet}} \cdot \mathbf{n}_{(t)}$, where \mathbf{n} is a vector of the stage-classified ramets at times t and $t+1$, and \mathbf{B} is the 3 x 3 matrix of transition probabilities b_{ij} for wet and dry season, respectively. Hence, annual matrices for each study year starting with the wet season are given by $\mathbf{A}_y = \mathbf{B}_{\text{dry},y} \cdot \mathbf{B}_{\text{wet},y}$ (Smith et al. 2005). Separate transition matrices \mathbf{B} were constructed for each of the four types of populations and for all populations pooled (overall matrix weighed by the number of observations as suggested by Horvitz and Schemske 1995). Matrix calculations were carried out with R 2.4.1 (R Development Core Team 2006), and statistical analyses with SPSS 12.0.1 (SPSS Inc. 2003).

Spatiotemporal demographic variation

For each population and time interval, we calculated the overall survival of ramets, the probability of vegetative ramets to become reproductive, and the extent of clonal propagation (the number of new ramets per ramet). We used a hierarchical GLM to analyze the effects of population type (population as error term), and of season and year (adjusted for population) on survival, flowering probability and clonal propagation of *H. metallica* (Zar 1999).

Furthermore, we determined the density and proportion of small and large vegetative and reproductive ramets in each population in October 2004, 2005 and 2006, and compared the stage structure among the four types of populations. The homogeneity of variances and the distribution of residuals were checked for all studied variables.

In addition, we calculated the stable stage distribution as the right eigenvector of an arithmetic mean matrix of the two annual matrices for each population type (Colling & Matthies 2006), and measured the distance between the stable stage and the observed population stage structures by Keyfitz's Δ (Caswell 2001). From the mean annual matrix of each population type, excluding fecundity and clonal growth, we calculated the mean age of a ramet entering the reproductive state and the conditional total life span of large vegetative and reproductive ramets using equation 6 in Cochran and Ellner (1992) and subtracted one year from the estimated ages (as recommended by Ehrlén and Lehtilä 2002).

Finite rates of population growth

For each of the four types of populations and for all populations pooled, we calculated the finite rates of increase (λ) from the seasonal and annual matrices. To estimate sampling errors, we randomly sampled individual fates from the observed vector of fates for each time interval of six months with replacement and generated a bootstrap fate vector of the same sample size. Then, we calculated transition probabilities and λ for each time interval. Finally, we calculated an annual bootstrap matrix by matrix multiplication of the seasonal bootstrap matrices and determined its λ . We ran 10 000 bootstrap replications to calculate bias-corrected 95% confidence intervals around estimates of seasonal and annual λ (Caswell 2001).

To test for significant differences between flooded_(f) and non-flooded_(n) populations, separately for populations in gaps and non-gaps, we carried out two-tailed permutation tests with the null hypothesis that $\theta = |\lambda_f - \lambda_n| = 0$ (Caswell 2001; Colling & Matthies 2006). For each time interval, we randomly permuted individuals between population types and then constructed matrices for each population type to calculate the test statistic $\theta_{(i)}$ as the absolute difference between the projected growth rates of the respective population types (10 000 replications). Then, the probability p of obtaining a value of $\theta \geq \theta_{\text{observed}}$ was calculated as (Caswell 2001)

$$p[\theta \geq \theta_{\text{observed}} | H_0] = \frac{\#\{\theta_{(i)} \geq \theta_{\text{observed}}\} + 1}{10\,000 + 1}$$

Prospective analyses

For each of the four population types, classified by flooding^(f) and canopy openness^(c), sensitivities of the annual λ to the matrix elements of each of the two seasonal matrices, $\mathbf{B}_{(s=\text{wet,dry})}$, were calculated using equation 11 in Lesnoff et al. (2003), where the sensitivity matrices for the wet and dry season are given as

$$\mathbf{S}_{\text{wet}}^{(fc)} = \mathbf{B}_{\text{dry}}^{(fc)\text{T}} \cdot \mathbf{S}_{\text{year}}^{(fc)}, \text{ and } \mathbf{S}_{\text{dry}}^{(fc)} = \mathbf{S}_{\text{year}}^{(fc)} \cdot \mathbf{B}_{\text{wet}}^{(fc)\text{T}}$$

where $\mathbf{S}_{\text{year}}^{(fc)}$ is the sensitivity matrix of the annual matrix $\mathbf{A}_{\text{year}}^{(fc)}$ and ^T denotes the matrix transpose. To determine the relative importance of each element of the transition matrices for each annual λ , we used the two matrices of ramet stasis, ramet growth and fecundity ($\mathbf{R}_s^{(fc)}$), and of clonal growth ($\mathbf{C}_s^{(fc)}$) and calculated the elasticity of the annual λ to each element of these two matrices as (following equation 12 in Lesnoff et al. 2003)

$$\mathbf{E}_{s,R}^{(fc)} = \frac{1}{\lambda} \cdot \mathbf{R}_s^{(fc)} \circ \mathbf{S}_s^{(fc)}, \text{ and } \mathbf{E}_{s,C}^{(fc)} = \frac{1}{\lambda} \cdot \mathbf{C}_s^{(fc)} \circ \mathbf{S}_s^{(fc)}$$

where "o" denotes the element-by-element matrix product. The elasticities of the composite elasticity matrix $\mathbf{E}_s^{(fc)} = \mathbf{E}_{s,R}^{(fc)} + \mathbf{E}_{s,C}^{(fc)}$ sum to 1 for each time interval.

Retrospective analyses

In order to analyse which transitions contribute most to differences in growth rates among population types, we used life table response experiments (LTRE) as described by Caswell (2001) and for periodic matrix models by Smith et al. (2005). LTRE analyses decompose the effects of factors on population growth rates into the contribution of each vital rate to these effects. We used a fixed 2 x 2 factorial design with two types of flooding^(f=flooded,non-flooded) and two types of canopy openness^(c=gap,non-gap). We wrote a linear model for the projected annual growth rate $\lambda_y^{(fc)}$ as (following equation 7 in Smith et al. 2005)

$$\lambda_y^{(fc)} = \lambda_y^{(-)} + \alpha_{\text{wet},y}^{(f)} + \alpha_{\text{dry},y}^{(f)} + \beta_{\text{wet},y}^{(c)} + \beta_{\text{dry},y}^{(c)} + \alpha\beta_{\text{wet},y}^{(fc)} + \alpha\beta_{\text{dry},y}^{(fc)}$$

where y is a year index, and $\alpha_{s,y}^{(f)}$ is the sum of contributions of the main effect of flooding type f , $\beta_{s,y}^{(c)}$ of canopy openness type c , and $\alpha\beta_{s,y}^{(fc)}$ of the interaction effect during each wet and each dry season, respectively. The main effects of flooding and canopy openness were calculated by averaging the matrices including the respective factor level for each season, e.g. for the flooding effect as $\mathbf{B}_{s,y}^{(f\cdot)} = (\mathbf{B}_{s,y}^{(f,\text{gap})} + \mathbf{B}_{s,y}^{(f,\text{non-gap})}) / 2$ (Smith et al. 2005). Difference

matrices ($\mathbf{D}_{s,y}^{(fc)}$) were calculated for each of the four time intervals between the effect matrices for the main and interaction effects and the overall pooled matrix, e.g. for the main effect of flooding $\mathbf{D}_{s,y}^{(f)} = \mathbf{B}_{s,y}^{(f)} - \mathbf{B}_{s,y}^{(-)}$. We calculated midway matrices $\mathbf{B}_{M(s,y)}^{(fc)}$ as the arithmetic mean between the effect matrices and the overall matrix, e.g. for the main effect of flooding as $\mathbf{B}_{M(s,y)}^{(f)} = (\mathbf{B}_{s,y}^{(f)} + \mathbf{B}_{s,y}^{(-)})/2$, and calculated sensitivity matrices $\mathbf{S}_{M(s,y)}^{(fc)}$ for each midway matrix $\mathbf{B}_{M(s,y)}^{(fc)}$, using the method for seasonal matrices described above (Lesnoff et al. 2003). Finally, main and interaction effects on the annual growth rate λ were determined as the sum of contributions from each of the matrix elements during each time interval by decomposing the effect matrix into the matrix of ramet stasis, ramet growth and fecundity \mathbf{R} and of clonal growth \mathbf{C} as described above.

Then, the contributions of main and interaction effects during each season are given by (following Caswell 2001; Angert 2006),

$$\alpha_{s,y}^{(f)} = \alpha_{s,y,R}^{(f)} + \alpha_{s,y,C}^{(f)} = \mathbf{D}_{s,y,R}^{(f)} \circ \mathbf{S}_{M(s,y)}^{(f)} + \mathbf{D}_{s,y,C}^{(f)} \circ \mathbf{S}_{M(s,y)}^{(f)} = \lambda_{s,y}^{(f)} - \lambda_{s,y}^{(-)}$$

$$\beta_{s,y}^{(c)} = \beta_{s,y,R}^{(c)} + \beta_{s,y,C}^{(c)} = \mathbf{D}_{s,y,R}^{(c)} \circ \mathbf{S}_{M(s,y)}^{(c)} + \mathbf{D}_{s,y,C}^{(c)} \circ \mathbf{S}_{M(s,y)}^{(c)} = \lambda_{s,y}^{(c)} - \lambda_{s,y}^{(-)}$$

$$\alpha\beta_{s,y}^{(fc)} = \alpha\beta_{s,y,R}^{(fc)} + \alpha\beta_{s,y,C}^{(fc)} - \alpha_{s,y}^{(f)} - \beta_{s,y}^{(c)} = \lambda_{s,y}^{(fc)} - \lambda_{s,y}^{(-)} - \alpha_{s,y}^{(f)} - \beta_{s,y}^{(c)}$$

For each population type, the sums of the seasonal contribution matrices of main and interaction effects sum up to the observed difference in annual λ (see Smith et al. 2005).

Stochastic matrix models

We compared extinction risks between flooded and non-flooded populations and investigated the effects of gap formation on the extinction probability of these populations, using three different scenarios: (1) 0%, (2) 1%, and (3) 5% probability per year for the formation of a small canopy gap in a non-gap population. The second scenario is based on several studies in tropical forests that have found that c. 1% of the forest area is converted into treefall gaps during each year (Hartshorn 1990). However, the disturbance rate strongly depends on the definition of a canopy gap and small gaps that already affect *H. metallica* may be caused by tree and branch falls suggesting that the formation rate of small gaps may be higher than 1%.

To estimate extinction risks of flooded and non-flooded populations in the different scenarios, we simulated population development under stochastic fluctuations over 200 years using RAMAS[®]-Metapop (Akçakaya & Root 1998). First, we calculated an arithmetic mean matrix and a standard deviation matrix of flooded and non-flooded non-gap populations from

the observed annual matrices and incorporated these into the program. The program assigns during each time step to each transition rate a random value drawn from a normal or lognormal distribution whose mean and standard deviation are given by the empirical matrices. We chose a log-normal distribution for the stochastic simulations, because several elements of the stage matrices had small mean values, but large standard deviations (see Akçakaya & Root 1998). Demographic stochasticity was included by using the procedure implemented in RAMAS[®]-Metapop. For the case of gap formation, we presumed that the formation of small gaps affects an established population during three years of which two years can be considered as the gap phase and the third year as regression from the gap to the non-gap phase (see Smith et al. 1992; Fraver et al. 1998). In the model, if a gap was formed, we first sampled twice the gap matrix (flooded or non-flooded, respectively) observed in the first study year, i.e. during the gap phase, and then once the respective matrix of the second year, i.e. during the regression to the non-gap phase. For simulations in RAMAS[®]-Metapop, we summed up the gap cycle within a single transition matrix \mathbf{G} defined as (Caswell 2001)

$$\mathbf{G}^{(f,\text{gap})} = \mathbf{A}_{y=2}^{(f,\text{gap})} \cdot \mathbf{A}_{y=1}^{(f,\text{gap})} \cdot \mathbf{A}_{y=1}^{(f,\text{gap})}$$

where \mathbf{A} is the observed annual transition matrix, f is the type of flooding and y the year of observation. Then, to estimate the effect of gap formation on each transition probability in relation to the standard non-gap matrix, we calculated an effect matrix \mathbf{E} by element-by-element division as $\mathbf{E}^{(f)} = \mathbf{G}^{(f,\text{gap})} / \mathbf{A}_{\text{mean}}^{(f,\text{non-gap})}$, where \mathbf{A} is the mean matrix of each flooding type of the non-gap populations. The respective effect matrix \mathbf{E} was incorporated into RAMAS[®]-Metapop as a multiplier matrix and was sampled with a probability of 0%, 1% and 5% per year.

For the simulations, the initial population size was 250 ramets, which was a typical population size observed in the field, and the initial stage distribution was set to the stable stage of the respective type of non-gap population. We ran 10 000 replications of each model and determined extinction probabilities over time, defining extinction as the death of all ramets of a population, i.e. real extinction. Because the three year gap cycle of a population was modelled during a single time step, we corrected the estimates of the time to local extinction t according to the probability of gap formation in each scenario as $t_{\text{real}} = t + t \cdot p_{\text{gap}}$ (3-1), where p_{gap} is the probability of gap formation in the respective scenario. This approximate correction is assumed to be sufficiently exact due to the large number of replications run.

RESULTS

Spatiotemporal demographic variation

Ramet survival, flowering probability and clonal propagation strongly differed between seasons. Survival (70.2% vs. 67.8%, $F_{1,12} = 6.3$, $p = 0.028$) and clonal propagation (43.8% vs. 15.0%, $F_{1,12} = 169.9$, $p < 0.001$) of ramets were higher in the wet than in the dry season, whereas flowering probability (5.4% vs. 2.9%, $F_{1,12} = 23.1$, $p < 0.001$) was higher in the dry season. Survival (2005 vs. 2006: 70.6% vs. 67.4%, $F_{1,12} = 9.4$, $p = 0.010$) and flowering probability (6.2% vs. 2.0%, $F_{1,12} = 44.9$, $p < 0.001$) also differed between years, but not clonal propagation ($F_{1,12} = 0.1$, $p = 0.749$). Variation among habitat types was strong. Ramet survival was lower in gaps than in non-gaps (overall mean: 63.9% vs. 82.1%, $F_{1,12} = 10.3$, $p = 0.008$), but clonal propagation (0.34 vs. 0.27 new ramets per established ramets, $F_{1,12} = 12.5$, $p = 0.004$) and flowering probability (8.3% vs. 1.7%, $F_{1,12} = 45.5$, $p < 0.001$) were higher. Ramet survival was higher in flooded than in non-flooded populations (71.9% vs. 66.2%, $F_{1,12} = 5.3$, $p = 0.041$), but there were no differences in clonal propagation ($F_{1,12} = 0.3$, $p = 0.600$) and flowering probability ($F_{1,12} = 2.1$, $p = 0.172$).

The mean density of vegetative ramets did not differ among the four types of populations distinguished (flooding effect: $F_{1,12} = 0.02$, $p = 0.903$, gap effect: $F_{1,12} = 0.56$, $p = 0.467$). However, the density (3.5 vs. 0.8 reproductive ramets per 4 m², $F_{1,12} = 44.2$, $p < 0.001$) and the proportion of reproductive ramets (21.7% vs. 6.8% of reproductive ramets, $F_{1,12} = 37.1$, $p < 0.001$) were higher in gap than in non-gap populations.

The mean total life span of large vegetative and reproductive ramets was higher in non-gaps than in gaps (3.5 and 4.4 vs. 2.8 and 3.1 years), and slightly higher in flooded than in non-flooded populations (3.3 and 3.9 vs. 3.0 and 3.3 years). Ramets required a mean time of 1.7 years to flower in gaps and of 2.6 years in non-gaps. In gap populations, the observed and the stable stage distribution differed considerably (Keyfitz's Δ : gap vs. non-gap populations, 2004: 9.6% vs. 3.0%, 2006: 5.6% vs. 0.9%). In the non-gaps, the non-flooded populations differed more strongly from the stable stage than the flooded populations, but only at the beginning of the study period (Keyfitz's Δ : non-flooded vs. flooded populations, 2004: 4.8% vs. 1.3%, 2006: 0.5% vs. 1.2%). In response to canopy closure, the proportion of vegetative ramets that developed into reproductive ramets declined from the first to the second study year in gap populations (see the transition matrices in Appendix A), resulting in a strong decrease of the proportion of reproductive ramets from October 2004 to October 2006 (10.9% to 2.1%, $F_{1,10} = 20.7$, $p = 0.001$).

Finite rates of population growth

The finite rate of increase of all populations pooled was not significantly different from 1 in 2005 ($\lambda = 0.990$, 95% confidence interval 0.952-1.030), but less than 1 in 2006 ($\lambda = 0.910$, 0.873-0.949). In both years, populations increased during the wet ($\lambda = 1.154$, 1.121-1.186, and 1.131, 1.096-1.168), but decreased during the dry seasons ($\lambda = 0.839$, 0.816-0.862, and 0.797, 0.775-0.819). The finite rates of growth of the non-flooded populations were smaller than that of the flooded populations and were significantly <1 for all annual λ and the overall λ , calculated as the geometric mean of the two annual λ (Table 1). Only in flooded, non-gap populations annual λ were ≥ 1 in both years. Population growth rates did not vary between years in non-gaps (CV $< 1\%$), but strongly differed between the first and the second year in flooded gaps. There, populations increased during the first, but strongly decreased during the second year (Table 1). The decline during the dry seasons was mostly stronger in non-flooded than in flooded populations (Fig. 1). In non-gaps, λ did not differ between flooded and non-flooded populations during both wet seasons (permutation tests: $p = 0.490$ and $p = 0.718$, respectively), but was significantly smaller in non-flooded than in flooded populations during the dry seasons ($p = 0.003$ in both years). In gaps, λ was smaller in non-flooded than in flooded populations during the first year (wet: $p = 0.077$, dry: $p < 0.001$), but not during the second year (wet: $p = 0.781$, dry: $p = 0.308$).

Table 1. Finite rates of increase (λ) of four different types of populations of *H. metallica*. Populations that were regularly flooded were distinguished from those that were not, and populations situated in small gaps from those in non-gaps. Bias-corrected 95% confidence intervals obtained by bootstrapping are given in parenthesis. The overall λ from 2004-2006 was calculated as the geometric mean of the two annual λ . The coefficients of variation (CV) of the two annual λ are given.

	2005	2006	2004-2006	CV [%]
Flooded, gap	1.181 (1.074-1.291)	0.818 (0.751-0.891)	0.983 (0.922-1.046)	25.7
Non-flooded, gap	0.890 (0.799-0.987)	0.856 (0.752-0.978)	0.873 (0.801-0.949)	2.8
Flooded, non-gap	1.004 (0.936-1.070)	1.003 (0.931-1.073)	1.004 (0.953-1.051)	0.1
Non-flooded, non-gap	0.930 (0.865-0.995)	0.921 (0.853-0.988)	0.925 (0.879-0.971)	0.7

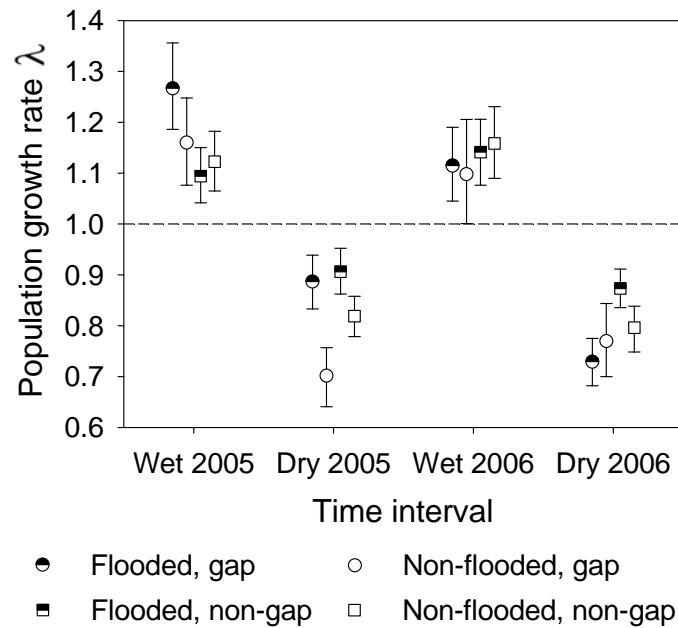


Figure 1. Finite rates of growth (λ) of four types of populations of *H. metallica* situated at flooded or non-flooded, and gap or non-gap sites in the wet and the dry season of 2005 and 2006. For each time interval, λ and its bias-corrected 95% confidence intervals are given. Note the reference line for stable population size ($\lambda = 1$).

Prospective analyses

Elasticity analysis revealed that transitions involving large vegetative ramets were most important for population growth (overall mean of contribution: 61.9%, see the elasticity matrices in Appendix A). In all population types, the stasis of vegetative ramets contributed most to the annual finite rate of increase (53.5%), whereas fecundity contributed very little to population growth (0.1%, Fig. 2). Stasis of vegetative ramets was more important during the dry than the wet season (62.5% vs. 44.5%), whereas clonal growth of vegetative ramets contributed more to λ during the wet than the dry season (32.7% vs. 16.2%). The contribution of stasis transitions to population growth was higher in non-gap than in gap populations (67.1% vs. 53.7%), whereas the contributions of clonal growth (32.1% vs. 24.6%) and of growth of vegetative ramets (13.9% vs. 8.3%) were higher in gap populations. Transitions involving reproductive ramets also contributed more to λ in gaps than in non-gaps (16.9% vs. 4.6%). In non-gap populations, patterns of elasticities were similar in both study years, whereas in the gap populations the importance of transitions involving reproductive ramets decreased from the first to the second year (24.1% vs. 9.7%), corresponding to an overall increase in the importance of the stasis of vegetative ramets (36.9% vs. 49.9%, Fig. 2). In contrast to the strong differences between gap and non-gap populations, the patterns of elasticities of flooded and non-flooded populations were similar throughout the study period.

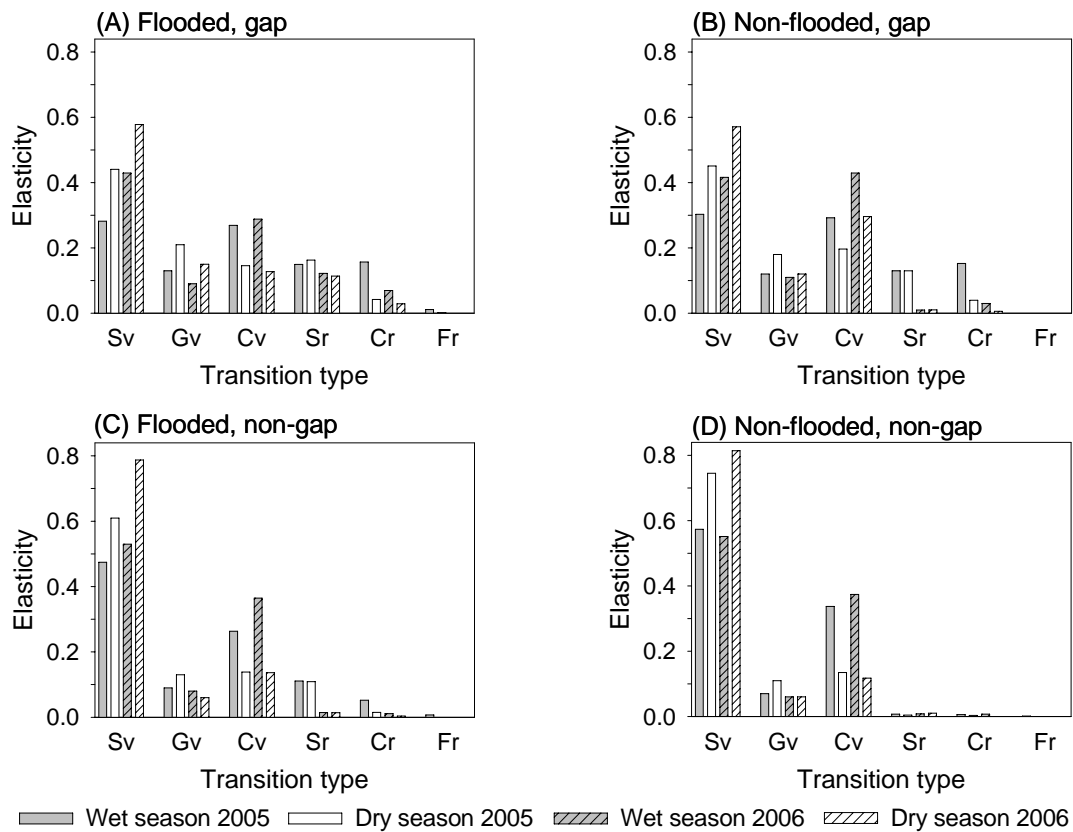


Figure 2. Elasticities of the annual growth rate, λ , to life-cycle transitions in four types of populations of *H. metallica* in the wet and the dry season of 2005 and 2006. Populations were situated at flooded (A, C) or non-flooded (B, D), and gap (A, B) or non-gap (C, D) sites. Transitions involving vegetative ramets are subdivided into stasis (Sv), growth (Gv), and clonal growth (Cv), and those involving reproductive ramets into stasis (Sr), clonal growth (Cr) and fecundity by seedling establishment (Fr). Fecundity elasticities were very small or zero.

Retrospective analyses

We carried out LTRE (life table response experiment) analyses to decompose the observed differences in λ among the four types of populations into the contributions of the life-cycle pathways ramet stasis, ramet growth, clonal growth and fecundity. Note that the sum of the contributions of ramet stasis and ramet growth equals the contribution of ramet survival. Interactions between flooding and canopy gaps were important for the effects on λ . Predictions of the annual λ by linear approximation including only the main effects of flooding and canopy type differed strongly from the observed effects on λ (mean deviation between observed and predicted effects: 96%), but were very accurate when interaction effects were included (0.01%). Therefore, we present for each population type and time interval the sum of the main and interaction contributions to the differences in λ in reference to the overall matrix of the respective study year.

Stasis transitions were most important for the differences in λ , in particular during the dry season (Fig. 3), whereas fecundity transitions did not contribute to differences in λ (in all cases <0.01 , data not shown). In gap populations, the probability of ramets to grow into another stage or to form new ramets by clonal propagation was higher, whereas the stasis of established ramets was lower than in non-gap populations. At non-flooded sites, ramet survival was much higher in non-gaps than in gaps. At flooded sites, the differences in ramet survival between gaps and non-gaps were much smaller, in particular during the first year. The magnitude of the flooding effects on the different life-cycle pathways were smaller than that of canopy gaps, but during the dry seasons flooding positively affected ramet survival in most cases. In gaps, flooding positively contributed to λ due to a higher probability of ramet survival, but only during the first year. In non-gap populations, the positive effect of flooding was stable (net contribution: $+0.08$ in both years), but only effective during the dry season (net contribution: $+0.10$ in the dry, but -0.02 in the wet season), when ramet survival and clonal growth positively contributed to λ (Fig. 3).

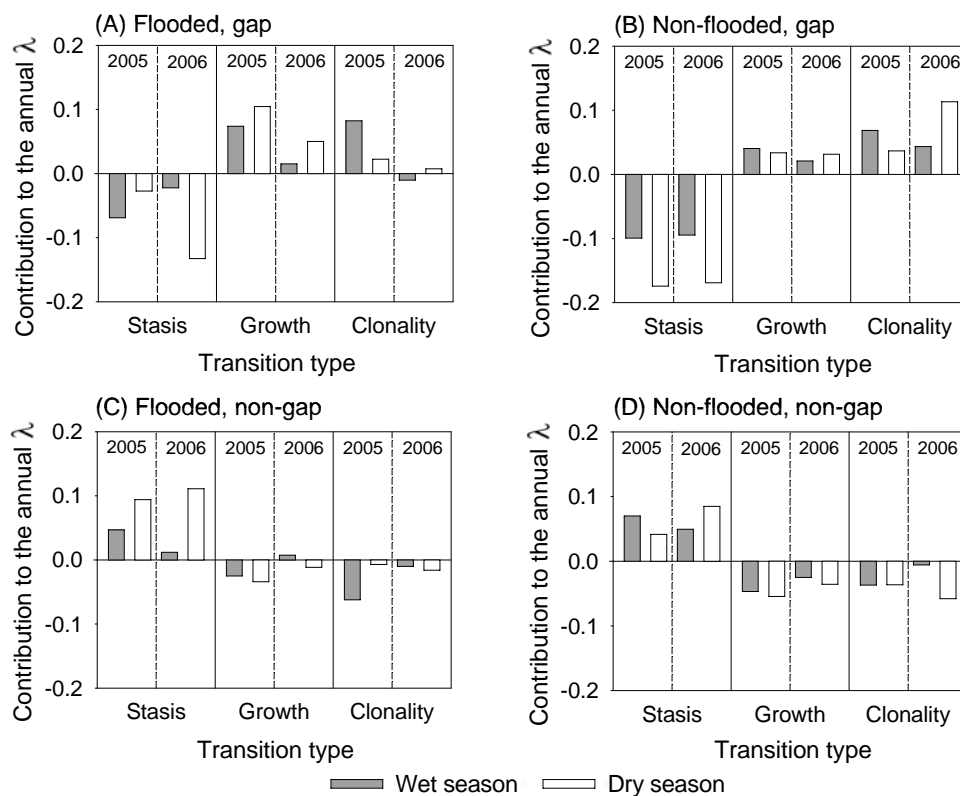


Figure 3. LTRE analyses of the main and interaction effects of flooding and canopy openness on the finite rates of increase (λ) of populations of *H. metallica*. Effects are shown as the sum of main and interaction contributions of stasis (S), growth (G), and clonal growth (C) during the wet and the dry season to the differences in annual λ between each of the four types of populations and the mean reference matrix for the years of 2005 and 2006, respectively. The overall λ was 0.990 in 2005 and 0.910 in 2006. Populations were situated at flooded (A, C) or non-flooded (B, D), and gap (A, B) or non-gap (C, D) sites. All contributions of the fecundity transition were <0.01 and are not shown.

Stochastic matrix models

Flooded and non-flooded populations strongly differed in their growth rate and extinction risk in stochastic simulations. Extinction risks of populations with an initial size of 250 ramets after 100 years were close to 100% at non-flooded and only c. 14% at flooded sites (Fig. 4). If the formation of small canopy gaps in established non-gap populations was incorporated into the stochastic simulations, extinction probabilities only changed considerably for populations at flooded sites. After 200 years, a 1% probability of gap formation decreased the extinction risk of a flooded population slightly from 50% to 44%, but a probability of 5% of gap formation would strongly decrease the extinction risk to 25% (Fig. 4).

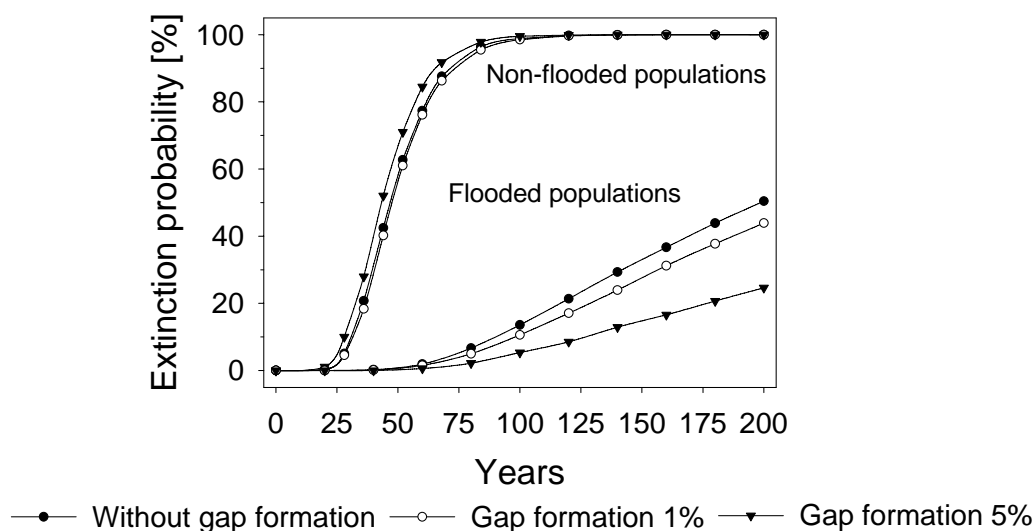


Figure 4. Extinction risks of populations of *H. metallica* in stochastic models of population dynamics. Extinction probabilities over time are given for populations at flooded and non-flooded sites with three different frequencies of gap formation: 0%, 1% and 5% per year.

DISCUSSION

The demography of *H. metallica*

The life history of *H. metallica* was dominated by transitions involving ramet survival and clonal growth. Elasticity analysis indicated that the stasis of vegetative ramets contributed most (54%) to the finite rate of growth (λ), and clonal growth a further 28%. Similar patterns have been found in the few previous studies of clonal understory plants (Nault & Gagnon 1993; Damman & Cain 1998), but the contribution of clonal growth in *H. metallica* was among the highest observed (Silvertown et al. 1993). Because of their clonal growth, the genets of *H. metallica*, like those of most clonal herbs, are potentially very long-lived (Inghe & Tamm 1985; Nicolè et al. 2005). However, the turnover of ramets of *H. metallica* was high and the mean total life span of a vegetative ramet was only slightly more than three years.

In contrast to clonal growth, the recruitment of seedlings did not contribute to the dynamics of established populations of *H. metallica*, but might be very important for the foundation of new populations. This type of clonal plant demography has been termed "the strategy of initial seedling establishment" by Eriksson (1989). The rarity of seedling recruitment in established populations might be due to light competition by the densely growing (up to 57 per 4 m²) and large clonal ramets of *H. metallica*, which strongly shade seedlings. It has been suggested that in the understory competition is generally low and that this contributes to species coexistence (Wright 2002). However, our observations strongly suggest that dense stands of clonal herbs like *Heliconia* spp. may locally exert strong competitive effects on other species in the understory of tropical forests.

The effects of flooding and drought

The climate of the Amazon rainforests is strongly seasonal (Myneni et al. 2007). Most of the precipitation falls during a rainy season when the lower parts of the floodplain are frequently inundated. The demography of *H. metallica* differed strongly between the wet and dry season. During the wet season, the mortality of ramets was lower and the clonal propagation of ramets was higher in both flooded and non-flooded populations, indicating that the populations were not sensitive to flooding. Populations of *H. metallica* increased in size during the wet, but decreased during the dry season. This is in contrast to the dynamics of the leaf area index (LAI) in Amazon rainforests that increases during the dry season (Myneni et al. 2007). Because changes in the LAI reflect changes in tree foliation, this suggests that the seasonal growth cycle of understory plants is out-of-phase with that of canopy and subcanopy trees. This may be due to a higher light availability in the forest understory during the wet season.

Flooding positively affected the projected growth rate (λ) of the populations of *H. metallica*. Over the study period, λ was very close to 1 in the lower, frequently flooded populations, but was significantly smaller than 1 in the higher, non-flooded populations due a strong decline of these populations during the dry season. The non-flooded populations may suffer from drought during the dry season, as we found a significantly higher soil water content in flooded than in non-flooded sites at the end of the dry season. *Heliconia metallica* may be sensitive to drought, because *Heliconia* spp. have a shallow root system (Skillman et al. 1999) and shade-tolerant plant species in general have little drought resistance (Coomes & Grubb 2000; Niinemets & Valladares 2006). Previous studies in Amazon rainforests have also found that water limitation during the dry season may strongly affect the population dynamics of plants in the forest understory (Bunker & Carson 2005). Similarly, Bruna et al. (2002) have

suggested that the dryer conditions in forest fragments are the main cause for the negative effects of forest fragmentation on the understory plant *Heliconia acuminata* in central Amazon rainforests.

The effects of canopy dynamics

The increase in light availability due to the formation of canopy gaps was rather small compared to that described in other studies (Smith et al. 1992; Fraver et al. 1998). However, because the populations of *H. metallica* were spatially more extended than the small gaps, we estimated the effect of gap formation at the population level by averaging the light availability in all plots, which resulted in relatively low values.

The structure and dynamics of populations of *H. metallica* in small canopy gaps were very different from those in non-gaps. While the density of vegetative ramets was similar, the density of reproductive ramets was fourfold higher in gap than in non-gap populations. The stage distribution of the gap populations differed from that in non-gaps, because ramets of *H. metallica* grew faster in gaps and required only 1.7 years to become reproductive in gaps, but 2.6 years in non-gaps. However, the dynamics of the gap populations were only transient. The observed and the stable stage distribution of gap populations differed considerably and during canopy closure in the second study year the proportion of flowering ramets decreased strongly. A higher reproduction in recently formed canopy gaps has been observed in other understory herbs (Horvitz & Schemske 1994; Valverde & Silvertown 1995), and gap duration was similarly brief for other understory herbs of tropical forests (Smith et al. 1992). The rapid closure of small gaps is due to the rapid growth of subcanopy trees that strongly shade understory herbs like *H. metallica* (Fraver et al. 1998). In contrast to most previous studies of understory herbs (Horvitz & Schemske 1995; Valverde & Silvertown 1998), population growth of *H. metallica* was not consistently higher in gaps, but depended on flooding. Non-flooded gap populations decreased throughout the study period, whereas flooded gap populations increased in recently opened gaps, but decreased during canopy closure in the second year.

Contributions of different life history processes to λ

The contribution of various life cycle transitions to λ can be analysed by both prospective and retrospective methods (Caswell 2001), but they can lead to contradictory results, because patterns of elasticities may vary with λ (Lehtilä et al. 2006). However, in our study, the results from the two methods were consistent. In prospective analyses, the stasis of vegetative ramets

during the dry season was the transition type with the highest contribution to λ , and in retrospective LTRE analyses differences in the stasis of ramets during the dry season contributed most to the differences in λ among population types. Moreover, although λ differed strongly between flooded and non-flooded populations, the patterns of elasticities were very similar for the two types of populations.

In LTRE analyses, the interacting effects of canopy openness and flooding were very important for the differences in λ among population types. Studies of plant demography that only focus on a single environmental gradient would miss such interaction effects that might be important for the demography of many plant species (see Elderd & Doak 2006). In the case of *H. metallica*, contributions to λ strongly differed between gap and non-gap populations and the effect of flooding depended on canopy openness. In recently formed gaps, flooding reduced ramet mortality, but the mortality of ramets during canopy closure in the second year was similarly high in flooded and non-flooded gaps. In contrast, the positive effect of flooding on the dynamics of the non-gap populations was very stable during the study period. In these populations, flooding had a slightly negative effect during the wet season, but increased ramet survival and clonal growth during the following dry season. For understory herbs like *H. metallica*, the survival of vegetative ramets and clonal propagation are the key life history processes that together can ensure population survival in a meristem bank of vegetative ramets in the forest understory.

Conclusions

The demography of *H. metallica* was strongly affected by the spatial and temporal environmental heterogeneity of its habitat. In stochastic models, the risk of extinction was low for flooded populations of *H. metallica*. In these populations, long phases of stability with some turnover of ramets but no change in population size may alternate with short phases of ramet growth, reproduction and clonal expansion in response to the formation of a gap. A higher frequency of gap formation considerably reduced the extinction risk of the flooded populations, suggesting that the plasticity of the ramets of *H. metallica* in response to light availability is important for the persistence of the populations (see Elderd & Doak 2006). The populations that can persist despite the variability in habitat conditions can provide reliable resources for animals and may be important components of their ecosystem (Eriksson 2000).

The annual growth rate of non-flooded populations of *H. metallica* was <1 in both study years and their extinction risk in the stochastic models was high, even if gaps were assumed to be frequently formed. To account for the presence of the non-flooded populations of

H. metallica, their growth rates must have been considerably higher in the past. The considerable difference between observed and stable stage distribution at the beginning of the study period in non-flooded populations suggests that their population dynamics may have been different in the recent past. The severe drought in Amazonia in 2005 (Aragão et al. 2007) might be an important reason for this change in the dynamics of the non-flooded populations. In contrast, in years with prolonged wet seasons, which occur irregularly in the study region (Terborgh 1990), annual population growth might be higher, because even the non-flooded populations increased in size during the wet seasons. As for other floodplain plants (Lytle & Merritt 2004; Smith et al. 2005), fluctuations in precipitation among years may therefore be important for the long-term dynamics of populations of *H. metallica*.

During the dry seasons, populations of *H. metallica* decreased even at frequently flooded sites. Over the past decades, changes in rainfall patterns and a prolongation of the dry season have been observed in parts of the tropics (Malhi & Wright 2002; Aragón et al. 2007) and are predicted to intensify as a consequence of forest fragmentation and global climate change (Hulme & Viner 1998; Betts et al. 2004). While seedlings of tropical forest trees are sensitive to drought (Engelbrecht et al. 2007), established trees appear to be less affected because of their deeper roots, indicating that Amazon forests may be more resilient than assumed (Saleska et al. 2007). However, our results suggest that the composition of the understory vegetation in Amazon forests might be altered as a consequence of the predicted changes in precipitation patterns. The clonal life form and plasticity of ramets, which are typical for many tropical understory herbs, are successful adaptations to variable light conditions, but may not be able to buffer the drought stress expected during longer dry seasons in the future.

ACKNOWLEDGEMENTS

PerúVerde provided us the opportunity to carry out this study in the forests close to Manu Wildlife Center. Logistical support by the staff of PerúVerde, InkaNatura and Manu Wildlife Center is gratefully acknowledged. Field assistance by J.G. Castillo, L.H. Zuñiga, M.T. Blanco and many others was invaluable, and organizational support from T. Becker, N. Salinas and R. Urrunaga very helpful. We thank the Amazon Conservation Association (ACA) for data on local climate and Madre de Dios River level. This study was supported by Ph.D.-scholarships of the German Academic Exchange Service (DAAD) and of Studienstiftung des deutschen Volkes. The research was authorized by the Institute for Natural Resources (INRENA) of the Peruvian government by authorization numbers 013-2005, 003-2006 and 131-2006-INRENA-IFFS-DCB.

APPENDIX A

Seasonal transition probabilities and the elasticities of the annual growth rate, λ , to the seasonal life-cycle transitions of the four types of populations of *H. metallica* for the wet and dry season of the years 2005 and 2006. Populations that were regularly flooded (A, C) were distinguished from those that were not (B, D), and populations situated in small gaps (A, B) from those in non-gaps (C, D). The transition and elasticity matrices of each time interval of six months are decomposed into a matrix **R** of ramet stasis, ramet growth and fecundity, and a matrix **C** of clonal growth. The dominant eigenvalue (λ) of the composite transition matrix **B** = **R** + **C** is also given for each time interval.

(A) Flooded, gap populations

Transition matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005 ($\lambda = 1.267$)						
Small vegetative	0.212	0	0.057	0.220	0.174	0.096
Large vegetative	0.436	0.589	0	0.253	0.3161	0.560
Reproductive	0.050	0.147	0.761	0	0	0
Dry season 2005 ($\lambda = 0.887$)						
Small vegetative	0.392	0	0.008	0.114	0.133	0.073
Large vegetative	0.287	0.590	0	0.015	0.072	0.098
Reproductive	0.042	0.207	0.575	0	0	0
Wet season 2006 ($\lambda = 1.115$)						
Small vegetative	0.270	0	0	0.176	0.196	0.215
Large vegetative	0.255	0.699	0	0.179	0.245	0.325
Reproductive	0	0.034	0.749	0	0	0
Dry season 2006 ($\lambda = 0.729$)						
Small vegetative	0.287	0	0	0.121	0.142	0.187
Large vegetative	0.210	0.551	0	0.008	0.009	0.040
Reproductive	0.012	0.067	0.555	0	0	0
Elasticity matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005						
Small vegetative	0.029	0	0.011	0.030	0.060	0.019
Large vegetative	0.074	0.253	0	0.043	0.136	0.138
Reproductive	0.007	0.051	0.150	0	0	0
Dry season 2005						
Small vegetative	0.066	0	0.002	0.019	0.078	0.017
Large vegetative	0.053	0.374	0	0.003	0.046	0.025
Reproductive	0.009	0.146	0.163	0	0	0
Wet season 2006						
Small vegetative	0.051	0	0	0.034	0.073	0.022
Large vegetative	0.071	0.378	0	0.050	0.132	0.048
Reproductive	0	0.021	0.122	0	0	0
Dry season 2006						
Small vegetative	0.068	0	0	0.029	0.087	0.022
Large vegetative	0.075	0.510	0	0.003	0.009	0.007
Reproductive	0.005	0.073	0.113	0	0	0

(B) Non-flooded, gap populations

Transition matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005 ($\lambda = 1.160$)						
Small vegetative	0.184	0	0	0.215	0.172	0.094
Large vegetative	0.388	0.534	0	0.205	0.345	0.482
Reproductive	0.020	0.112	0.718	0	0	0
Dry season 2005 ($\lambda = 0.702$)						
Small vegetative	0.220	0	0	0.131	0.133	0.081
Large vegetative	0.130	0.484	0	0.000	0.101	0.063
Reproductive	0.010	0.186	0.437	0	0	0
Wet season 2006 ($\lambda = 1.098$)						
Small vegetative	0.263	0	0	0.400	0.171	0.173
Large vegetative	0.274	0.597	0	0.107	0.320	0.315
Reproductive	0	0.038	0.535	0	0	0
Dry season 2006 ($\lambda = 0.770$)						
Small vegetative	0.349	0	0	0.169	0.216	0.051
Large vegetative	0.190	0.508	0	0.023	0.069	0.037
Reproductive	0	0.061	0.256	0	0	0
Elasticity matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005						
Small vegetative	0.019	0	0	0.022	0.043	0.013
Large vegetative	0.083	0.284	0	0.044	0.183	0.140
Reproductive	0.003	0.037	0.130	0	0	0
Dry season 2005						
Small vegetative	0.040	0	0	0.024	0.087	0.020
Large vegetative	0.031	0.411	0	0.000	0.086	0.020
Reproductive	0.002	0.150	0.130	0	0	0
Wet season 2006						
Small vegetative	0.087	0	0	0.132	0.078	0.009
Large vegetative	0.109	0.329	0	0.043	0.177	0.021
Reproductive	0	0.006	0.010	0	0	0
Dry season 2006						
Small vegetative	0.141	0	0	0.068	0.159	0.003
Large vegetative	0.088	0.430	0	0.011	0.058	0.003
Reproductive	0	0.030	0.010	0	0	0

(C) Flooded, non-gap populations

Transition matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005 ($\lambda = 1.094$)						
Small vegetative	0.396	0	0.068	0.231	0.180	0.131
Large vegetative	0.272	0.722	0	0.062	0.201	0.320
Reproductive	0.004	0.021	0.851	0	0	0
Dry season 2005 ($\lambda = 0.906$)						
Small vegetative	0.522	0	0	0.188	0.105	0.126
Large vegetative	0.204	0.699	0	0.024	0.034	0.017
Reproductive	0	0.071	0.676	0	0	0
Wet season 2006 ($\lambda = 1.141$)						
Small vegetative	0.442	0	0	0.329	0.151	0.083
Large vegetative	0.254	0.703	0	0.116	0.277	0.223
Reproductive	0	0.013	0.722	0	0	0
Dry season 2006 ($\lambda = 0.873$)						
Small vegetative	0.571	0	0.014	0.127	0.103	0.087
Large vegetative	0.129	0.765	0	0.013	0.016	0.016
Reproductive	0	0.024	0.606	0	0	0

Elasticity matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005						
Small vegetative	0.101	0	0.007	0.059	0.082	0.014
Large vegetative	0.079	0.373	0	0.018	0.104	0.038
Reproductive	0.001	0.012	0.111	0	0	0
Dry season 2005						
Small vegetative	0.139	0	0	0.050	0.057	0.013
Large vegetative	0.067	0.471	0	0.008	0.023	0.002
Reproductive	0	0.062	0.109	0	0	0
Wet season 2006						
Small vegetative	0.119	0	0	0.089	0.079	0.003
Large vegetative	0.076	0.411	0	0.035	0.162	0.008
Reproductive	0	0.004	0.015	0	0	0
Dry season 2006						
Small vegetative	0.195	0	0.001	0.044	0.076	0.003
Large vegetative	0.046	0.592	0	0.005	0.012	0.001
Reproductive	0	0.011	0.014	0	0	0

(D) Non-flooded, non-gap populations

Transition matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005 ($\lambda = 1.123$)						
Small vegetative	0.462	0	0.071	0.301	0.274	0.157
Large vegetative	0.199	0.755	0	0.038	0.184	0.098
Reproductive	0	0.004	0.750	0	0	0
Dry season 2005 ($\lambda = 0.819$)						
Small vegetative	0.504	0	0.023	0.122	0.095	0.129
Large vegetative	0.182	0.683	0	0.003	0.035	0.028
Reproductive	0	0.029	0.318	0	0	0
Wet season 2006 ($\lambda = 1.159$)						
Small vegetative	0.563	0	0	0.396	0.166	0.196
Large vegetative	0.158	0.713	0	0.082	0.239	0.320
Reproductive	0	0.007	0.621	0	0	0
Dry season 2006 ($\lambda = 0.796$)						
Small vegetative	0.580	0	0	0.104	0.068	0.056
Large vegetative	0.099	0.719	0	0	0.012	0
Reproductive	0	0.008	0.714	0	0	0

Elasticity matrices	Ramet stasis and growth, fecundity			Clonal growth		
	Small	Large	Reprod.	Small	Large	Reprod.
Wet season 2005						
Small vegetative	0.137	0	0.002	0.089	0.128	0.003
Large vegetative	0.074	0.437	0	0.014	0.106	0.003
Reproductive	0	0.001	0.007	0	0	0
Dry season 2005						
Small vegetative	0.206	0	0.001	0.050	0.055	0.003
Large vegetative	0.101	0.540	0	0.002	0.028	0.001
Reproductive	0	0.011	0.004	0	0	0
Wet season 2006						
Small vegetative	0.209	0	0	0.147	0.083	0.003
Large vegetative	0.056	0.342	0	0.029	0.115	0.005
Reproductive	0	0.003	0.008	0	0	0
Dry season 2006						
Small vegetative	0.331	0	0	0.059	0.050	0.001
Large vegetative	0.052	0.483	0	0	0.008	0
Reproductive	0	0.005	0.010	0	0	0

CHAPTER 5

Experimental assessment of factors
limiting seedling recruitment of
an Amazon understory herb

Submitted
with Vicky Huaman and Diethart Matthies

ABSTRACT

Clonal herbs are a typical component of tropical forests and can influence forest regeneration because of their local dominance. Due to their clonal life form, plants are long-lived, but seedling recruitment is crucial for the colonization of new, unoccupied sites. In a Peruvian floodplain forest, we studied the seed ecology of the widespread herb *Heliconia metallica* and tested the effects of the presence of mature plants and of disturbance in an experiment of seed addition and predator exclusion. Seed predation was high, but decreased with the openness of a site. After one year, most seeds had germinated or died, indicating that *H. metallica* does not form a long-lived seed bank. Seed addition increased the number of seedlings at both occupied and unoccupied sites. In contrast, the number of naturally recruited seedlings was higher in the vicinity of flowering plants of *H. metallica*, in particular at flooded sites. Due to competition with mature plants, seedling mortality was higher at occupied sites, although seedlings were more strongly damaged by herbivores at sites without *H. metallica*. In experimentally disturbed plots, light availability on the forest floor and as a consequence establishment, survival and size of seedlings were higher. In the disturbed plots, seedling establishment and size increased with canopy openness. We conclude that colonization is limited by insufficient dispersal of seeds to sites of higher light availability. A crucial process for the creation of such sites is flooding, and thus the regional dynamics of *H. metallica* are strongly influenced by river dynamics.

INTRODUCTION

Seedling recruitment is a crucial process in the dynamics of plant populations (Horvitz & Schemske 1994; Valverde & Silvertown 1995). While populations of short-lived species rapidly become extinct without frequent recruitment (Fischer & Stöcklin 1997; Matthies et al. 2004), populations of long-lived plants may survive for a long time without recruitment due to the longevity of established plants (Ehrlén & Lehtilä 2002). At a regional scale, dispersal of seeds and subsequent seedling establishment determine the frequency of colonization and thus the regional abundance of plants (Valverde & Silvertown 1997; Milden et al. 2006). Limitation of seed dispersal is thought to be a crucial mechanism for the maintenance of species diversity by slowing down competition (Schupp et al. 2002; Wright 2002).

Understory plants constitute an important component of forest plant diversity (Gentry 1990; Whigham 2004) and can affect tree regeneration (Denslow et al. 1991; George & Bazzaz 2003). Many understory plants are clonal and form dense patches that inhibit tree recruitment (Gonzalez et al. 2002; Griffiths et al. 2007). Established populations of clonal plants are usually buffered against fluctuations in habitat quality due to the plasticity of ramets and longevity of genets (Whigham 2004; Souza & Martins 2006). Hence, in many clonal plants, seedling recruitment is important during colonization, but rare in established populations (Eriksson 1989).

In tropical forests, processes in the understory are important for the dynamics of the forests and may contribute to the maintenance of species diversity (Wright 2002; Queenborough et al. 2007). Studies of the population dynamics of plants in the understory have mostly focussed on tree recruitment (Wright et al. 2003; Queenborough et al. 2007). The few studies of understory herbs have been constricted to non-clonal species (Horvitz & Schemske 1994; Bruna 2002), although most of these plants, e.g. in the genus *Heliconia*, are clonal (Berry & Kress 1991). Plants living in the understory of tropical lowland forests suffer from lack of light, as only 1-2% of the photosynthetically active radiation typically reaches the understory (Chazdon & Fetcher 1984). Variation in the openness of the forest canopy strongly influences light availability on the forest floor (Nicotra et al. 1999), and recruitment of many plants is higher in canopy gaps (Horvitz & Schemske 1994; Wright et al. 2003). However, differences in the cover of the understory vegetation may also affect light availability on the ground (Kabakoff & Chazdon 1996) and affect seedling recruitment (Montgomery & Chazdon 2002). In Amazon rainforests, an important cause of understory gaps may be disturbance by flooding, since c. 20% of Amazon forests are exposed to seasonal floods (Junk 1997). The micro-topography in tropical floodplains varies on a small spatial

scale (Terborgh 1990), and the patchiness of disturbance is important for the creation and distribution of suitable microsites for seedling recruitment (King 2003; Stevenson 2007).

Despite the availability of suitable microsites, seedling recruitment can fail because of seed limitation (Turnbull et al. 2000; Clark et al. 2007). In temperate herb communities, colonization is strongly limited by dispersal (Ehrlén & Eriksson 2000), but seeds of tropical plants are dispersed by frugivorous birds over larger distances (Muller-Landau & Hardesty 2005). However, seed limitation was shown to be strong in neotropical forests (Muller-Landau et al. 2002; Svenning & Wright 2005). In tropical forests, dispersal may be important to escape from the vicinity of the mother plant because of density and distance-dependent processes (Janzen 1970; Connell 1978). Recent studies of tropical plants have supported the Janzen-Connell hypothesis and demonstrated that seed predation and herbivory are often higher close to conspecific individuals (Massey et al. 2006; Norghauer et al. 2006; but see Hyatt et al. 2003). Moreover, competition by conspecific plants may also be higher in the vicinity of the mother plant (Weiner 1990), but this mechanism has received less attention in studies of tropical plants (but see Hubbell et al. 2001).

Here, we present the results of a two-year study of seedling recruitment of a clonal understory herb of Amazon floodplain forests (*Heliconia metallica* Planchon & Linden ex Hooker, Heliconiaceae). We combine observational and experimental data on seed predation, seedling establishment and survival to address the following questions: (1) Are seedling recruitment and colonization limited by seed availability and dispersal? (2) Are seedling establishment and survival affected by the presence of mature plants of *H. metallica*? (3) Is natural disturbance by flooding necessary for seedling recruitment of *H. metallica*?

METHODS

Study site and system

Field studies were carried out in a floodplain forest of the Madre de Dios River that grows on rich alluvial soils close to Manu Wildlife Centre in south-eastern Peru (270 m asl, 12°21'20"S, 70°42'44"W). The study area was a mature floodplain forest made up of a mosaic of different microhabitats of different canopy openness and relative elevation (maximum difference c. 6 m). The relief of the floodplain varies on a small spatial scale as a result of river and stream dynamics (Terborgh 1990). Annual precipitation in the study area is c. 2500 mm and strongly varies between a dry season from May to September and a rainy season from October to April (>80% of the precipitation). The river level fluctuates strongly within a year with

peak levels and occasional inundation of the floodplain between November and April (Amazon Conservation Association, unpublished data).

The more than 200 *Heliconia* spp. are important components of the understory of neotropical forests (Bruna & Kress 2002). *Heliconia metallica* is distributed from Honduras to Bolivia (Berry & Kress 1991) and is common in the floodplain of south-eastern Peru. The species is clonal and spreads laterally by rhizomes, which produce above-ground shoots (ramets) that form dense patches in the understory. Ramets of *H. metallica* reach a height of up to 3.5 m in canopy gaps where they produce a single terminal inflorescence and die after reproduction. During a 2-4 months period, each flowering ramet produces c. 40 flowers, which are a key nectar resource and are visited by at least seven species of hummingbirds. Most fruits are developed at the beginning of the rainy season and fruits contain up to three seeds of c. 70 mg each. Fruits of *Heliconia* spp. are eaten by frugivorous birds, but seeds are regurgitated and thus dispersed (Stiles 1979). Of the fruits of *H. metallica*, c. 65% is removed from the inflorescence by frugivores (M. Schleuning, unpublished data). Most seeds presented on the ground are removed within a single day by seed-predating rodents (*Dasyprocta variegata*) and birds (*Crypturellus undulatus*).

Natural recruitment of seedlings

In October 2005 within an area of 400 x 400 m, we randomly set up 140 plots of 5 x 5 m each that were marked with large metal nails to which strips of color tape were attached. In these plots, we recorded the cover of the understory vegetation and that of *H. metallica*, and whether flowering ramets of *H. metallica* were present or not. During a week without strong rainfall in October 2005, we measured the soil water content [%] by frequency-domain reflectometry at a depth of 6 cm at three random points in each plot (FDR, Theta-Probe ML2x, Delta-T, Cambridge, UK). During a flooding event in the rainy season of 2006, we recorded whether each plot was flooded or not. In addition, we took hemispherical photographs c. 1.8 m above the ground in October 2005 using a camera with fisheye-converter (Nikon Coolpix 4500 with FC-E8 converter, Nikon, Tokyo, Japan) mounted on a levelled tripod. We used the software Gap Light Analyzer 2.0 (Frazer et al. 1999) to determine the percentage of open sky in the photographs (canopy openness), which is a good measure of diffuse light (Chazdon & Field 1987).

In October 2005, April 2006 and October 2006, we carefully searched for naturally recruited seedlings of *H. metallica* in each plot and marked them. The cover of the understory vegetation, soil water content and canopy openness were compared between flooded and non-

flooded plots. We analyzed the effects of flooding, of the presence of flowering *H. metallica* ramets, of soil water content and of canopy openness on the probability of seedling recruitment by analysis of deviance using a logit-link and a binomial error distribution (Crawley 2007). Explanatory variables were removed stepwise from the model, if they did not explain a significant amount of the variation (backward elimination, $p > 0.05$).

Experiments of seed mortality and seedling establishment

In November 2004, we collected c. 2500 fruits from *H. metallica* plants that were growing at the opposite side of the river. Seeds were separated from the pulp by abrasion with a strainer and then bathed in a dilute bleach solution for 5 min to inhibit fungal pathogens. To keep seeds dry, they were stored until sowing in paper bags with peat moss that were placed in sealed plastic bags (Berry & Kress 1991). At the end of November 2004, we set up transects of c. 50 m length marked by wooden poles at 16 sites with and 9 without populations of *H. metallica* in 2 km² of floodplain forest. Study sites were chosen to cover a wide range of canopy openness, but sites with and without populations did not differ ($F_{1,23} = 1.3$, $p = 0.270$).

At each site with *H. metallica*, we set up 12 and at each site without the species 8 sowing plots of 20 x 20 cm each. In a distance of 1 m from each sowing plot, we marked an additional control plot. Plots were situated along the transects and were marked with large metal nails to which strips of color tape were attached. At four plots at each site, the understory vegetation up to a height of c. 2 m was completely removed in an area of 3 x 3 m around the plot to simulate disturbance by a scouring flood. The other plots were left untouched. In each sowing plot, 12 seeds of *H. metallica* were sown, the adjacent plot served as a control. To investigate seed removal and mortality, we buried two plastic cups filled with local soil on which four seeds had been placed adjacent to nine plots at sites with and six plots at sites without *H. metallica*. One of the two cups was covered with a fine mesh to prevent seed predation. In total, 4752 seeds of *H. metallica* were sown into plots and adjacent cups at the end of November 2004. We recorded seed survival and seedling establishment over a two year period after each rainy and each dry season (April 2005, October 2005, April 2006, October 2006).

During each visit, we first carefully excavated the buried cups. A few had been removed or damaged by ground-dwelling animals and were not considered further. We checked if any seedlings had established in the cups. If this was the case, we planted them into the adjacent plot and marked them individually using numbered cable tie. Most seedlings in the covered cups grew through the mesh without damage; the few that had been damaged were not

considered further. We carefully removed the mesh of covered cups and excluded cups with damaged meshes from the analyses. Then, we spread out the soil from each cup on a tarpaulin and carefully searched for the characteristic seeds of *H. metallica*. Hollow or broken seeds were considered dead, other seeds including those germinating viable. We refilled the plastic cups with local soil, put viable seeds back and in April 2005 covered half of the cups with a new mesh. From October 2005 on, only few viable seeds were left and surviving seeds were pooled in a single uncovered cup. As seed removal was due to seed-predating rodents and birds (M. Schleuning, unpublished data), we calculated seed mortality in a cup as the proportion of seeds that had disappeared or were dead excluding those seeds that had developed into a seedling. To compare seed mortality between covered and uncovered cups, we only included those plots in the analysis that contained both an undamaged covered and uncovered cup.

In each sowing and control plot, we recorded the number of established seedlings and marked them individually. We also recorded ramets that had been formed by clonal propagation by seedlings and marked them as daughter ramets belonging to the same genet. We measured the height and counted the number of leaves of all seedlings including their daughter ramets. During the first and second visit, we also estimated the proportion of leaf area removed by herbivores and calculated mean herbivorial damage over all leaves of a genet. During the visits from October 2005 on, we carefully searched for seedlings and daughter ramets that had been marked during the previous visit and those that had disappeared were considered to be dead. We calculated overall seedling establishment as the proportion of seeds that had developed into a seedling in each plot and in the two cups (if present) during the observation time of two years. The number of established seedlings was not corrected by the number of seedlings in the control plots, as only three seedlings established in all control plots throughout the study period. Seedling survival was calculated as genet survival to October 2006. For this calculation, we included all cohorts of seedlings, but not the four seedlings that just had become established in October 2006 to include only those that had survived at least one dry season. The same procedure was used to calculate establishment success after two years as the proportion of seeds that had developed into a seedling that survived until October 2006. To estimate the damage to the leaves of a seedling by herbivores, we used the data recorded in October 2005, unless the seedling had died before that date. If this was the case, data from April 2005 were used. To obtain estimates of seedling size in October 2006, we separately summed shoot length and number of leaves over all ramets belonging to the same genet.

To characterize the habitat conditions in each plot in October 2005, we measured the soil water content [%] during a week without strong rainfalls as described above, and took hemispherical photographs 40 cm above the ground and calculated canopy openness. Because these photographs were taken below the understory vegetation, they measure the overall openness at a site and estimate the availability of diffuse light at the forest floor. We compared the habitat conditions in the plots, i.e. overall openness and soil water content, between sites with and without *H. metallica* (only undisturbed plots) and between disturbed and undisturbed plots. Seed mortality was compared between covered and uncovered cups (adjusting for differences among plots) by analysis of deviance. To analyze patterns of natural seed mortality, we only included data from uncovered cups and tested the effects of the presence of a population of *H. metallica* and of experimental disturbance. The relationship between mean seed mortality at a site and overall openness was analyzed by linear regression.

Site and treatment effects on seedling establishment and mortality were analyzed by analysis of deviance, whereas effects on leaf damage by herbivores (angular-transformed) and seedling size two years after sowing (log shoot length, number of leaves) by ANOVA. In the analyses of the effects of the presence of a population of *H. metallica* on seedling establishment, survival and size, we used site as the error term and only included data from undisturbed plots, as we were only interested in the effect of natural differences between sites with and without mature plants of *H. metallica*. To analyze the effect of experimental disturbance, disturbance was tested against the site x disturbance interaction, because site was considered to be a random factor. We separately analyzed the influence of mean soil water content and canopy openness in addition to disturbance on mean seedling establishment, survival and size by linear regression (backward elimination, $p > 0.05$), using only data from experimentally disturbed plots. Statistical analyses were carried out with R 2.4.1 (R Development Core Team 2006).

RESULTS

Factors influencing natural seedling recruitment

Flowering shoots of *H. metallica* were present in 16% of the 5 x 5 m plots, and 34% of the plots were flooded. Soil water content was higher in flooded than in non-flooded plots (35.9% vs. 31.6%, $F_{1,139} = 14.3$, $p > 0.001$). Canopy openness measured 1.8 m above ground did not differ ($p > 0.9$), but the cover of the understory vegetation was reduced in flooded plots (after adjusting for the cover of *H. metallica*: 32.2% vs. 43.1%, $F_{1,138} = 20.8$, $p < 0.001$). From October 2005 to October 2006, we observed 31 seedlings of *H. metallica* in 23 of the 140

plots. 15 of these plots only contained a single seedling, the other plots two seedlings. The probability of seedling recruitment was higher in flooded plots (Quasi- $F_{1,137} = 26.5$, $p < 0.001$, Fig. 1), and also in plots with flowering ramets of *H. metallica* (Quasi- $F_{1,137} = 12.8$, $p < 0.001$, Fig. 1), whereas differences in soil water content and canopy openness did not explain a significant part of the variation.

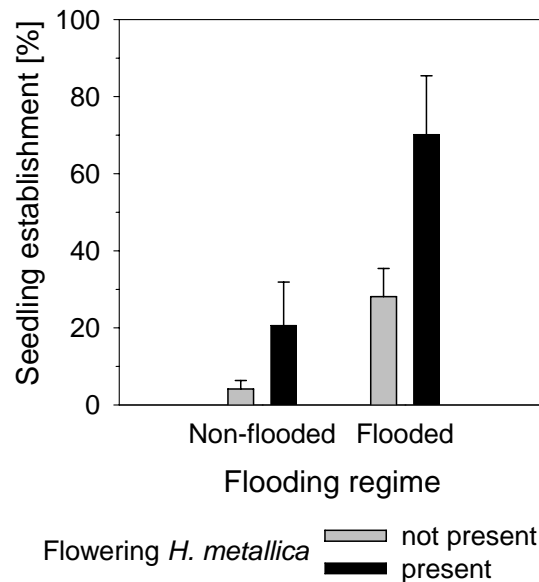


Figure 1. The effects of flooding and of the presence of flowering plants of *H. metallica* on the probability of natural seedling recruitment from October 2005 to October 2006. Data were obtained from 140 plots of 5 x 5 m situated in an area of 400 x 400 m. Given are means +1SE. Main effects were significant ($P < 0.001$), but not the interaction.

Factors influencing seed mortality

From November 2004 to April 2005, seed mortality was much higher in uncovered than in covered cups (41% vs. 16%, $F_{1,153} = 54.5$, $p < 0.001$), indicating considerable seed predation. In uncovered cups, seed mortality decreased with the overall openness at a site (Fig. 2). Seed mortality did not differ between sites with and without a population of *H. metallica* and between disturbed and undisturbed plots ($p > 0.8$ in both cases). During the following dry season, seed mortality was high both in uncovered and covered cups (90%) and was not influenced by site conditions. Most of the few remaining seeds died during the second wet season (77%), and of those remaining 86% during the following dry season. Of the seeds sown into plots and cups, 5.7% developed into a seedling during the first rainy season, but only a few more during the following time intervals (1.2%, 0.6% and 0.1%, respectively).

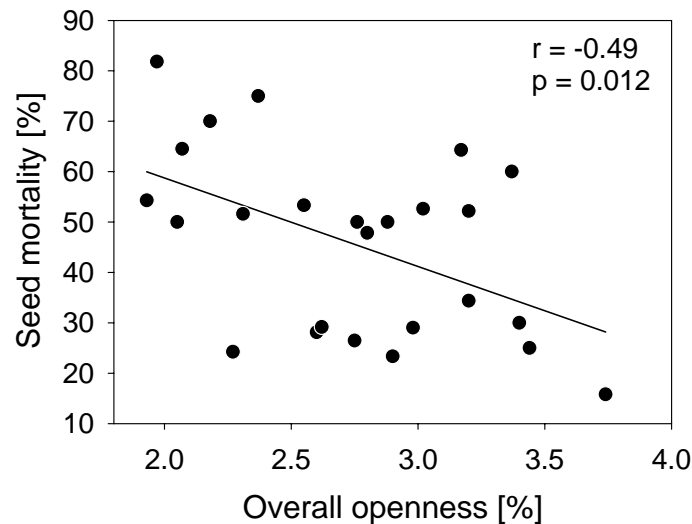


Figure 2. The relationship between the mortality of seeds of *H. metallica* during the first rainy season after sowing and the overall openness at 25 sites. Four seeds were sown into an uncovered plastic cup at 6-9 plots per site and their fate was followed. Overall openness was measured by hemispherical photographs taken in undisturbed plots 40 cm above ground.

Factors influencing seedling establishment

In the undisturbed plots, 5% of the seeds developed into a seedling during the two year study period and seedlings established at 24 of the 25 sowing sites. Two years after sowing, only 10% of the seedlings had survived and only nine sites contained established plants. Habitat conditions clearly differed between sites with and without a population of *H. metallica*. Light transmission to the forest floor estimated by overall openness was higher at sites without mature plants of *H. metallica* (3.1% vs. 2.6%, $F_{1,23} = 6.97$, $p = 0.015$), but soil water content was lower (36.7% vs. 39.4%, $F_{1,23} = 6.85$, $p = 0.015$). At eight of the nine sites without mature plants, seedlings developed after seed introduction into the undisturbed plots. Due to high seedling mortality, only four of those sites contained established plants two years after sowing. Overall seedling establishment did not differ between sites with and without mature plants of *H. metallica* (Fig. 3A), but survival of seedlings (Fig. 3B) and as a consequence establishment success after two years (Fig. 3C) were lower at sites with mature plants. In contrast, the leaves of seedlings were more strongly damaged by herbivores at sites without mature plants (13.1% vs. 4.3%, $F_{1,22} = 8.0$, $p = 0.010$). Two years after sowing, leaf number of the recruited plants was higher at sites without mature plants (Fig. 3D), but shoot length did not differ ($F_{1,11} = 0.6$, $p = 0.441$).

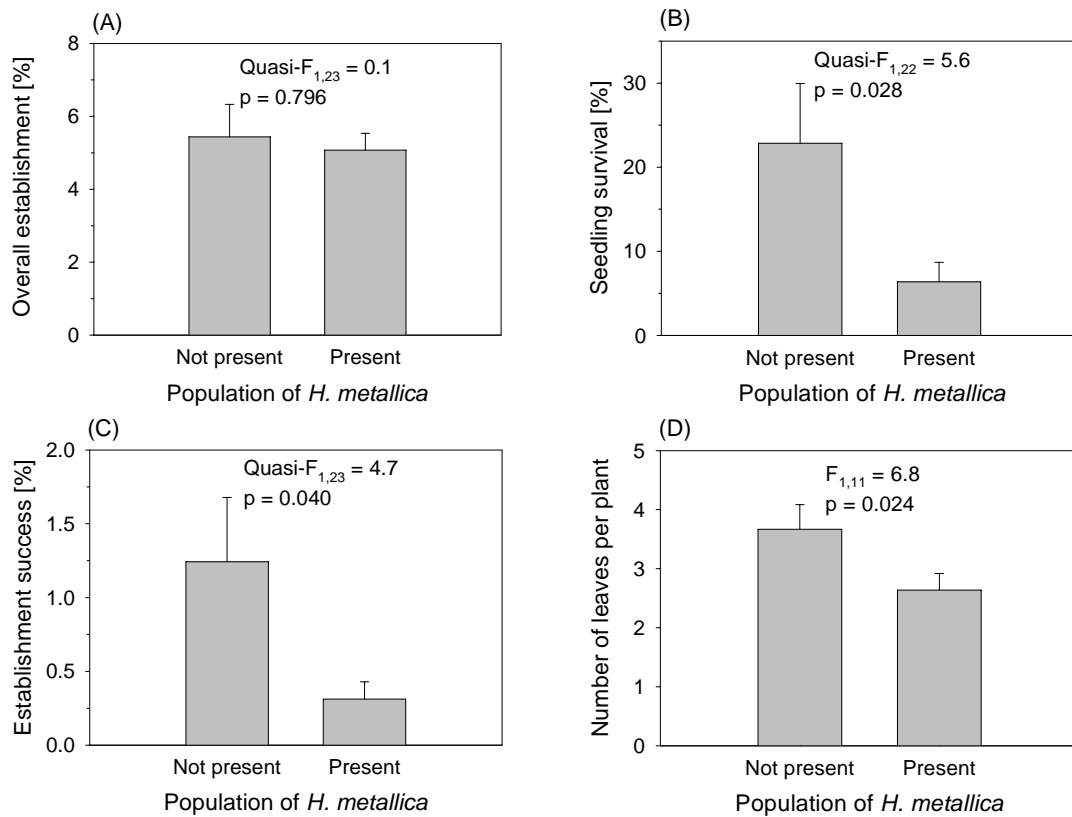


Figure 3. The effect of the presence of a population of *H. metallica* on (A) overall establishment, i.e. the proportion of seeds that developed into a seedling during the two year study period, (B) seedling survival, (C) establishment success after two years, and (D) seedling size in undisturbed plots. Data shown are from 16 sites with and 9 without a population of *H. metallica*. At each site, 4-8 undisturbed sowing plots had been set up. Error bars denote +1SE.

After experimental disturbance, seedlings developed at all sites, and plants were established two years after sowing at 20 sites of which seven previously had been unoccupied. Experimental disturbance increased light transmission to the forest floor (overall openness one year after disturbance: 3.0% vs. 2.7%, $F_{1,24} = 11.8$, $p = 0.002$), but did not affect soil water content (39.2% vs. 38.4%, $F_{1,24} = 1.6$, $p = 0.224$). Overall seedling establishment (Fig. 4A), survival (Fig. 4B), and establishment success (Fig. 4C) were much higher in experimentally disturbed than in undisturbed plots. In contrast, seedlings were more strongly damaged by herbivores in disturbed than in undisturbed plots (12.6% vs. 5.9%, $F_{1,23} = 6.5$, $p = 0.018$). Two years after sowing, both leaf number (Fig. 4D) and shoot length (17.5 cm vs. 8.5 cm, $F_{1,11} = 11.2$, $p = 0.007$) of the recruited plants were higher in disturbed plots. To analyze the effects of environmental factors on seedling performance in addition to that of disturbance, we separately analyzed data from disturbed plots only. Soil water content at a site did not affect establishment and seedling performance ($p > 0.4$ in all cases). With increasing canopy openness at a site, seedling establishment (Fig. 5A) and both shoot length (Fig. 5B) and leaf number ($r = 0.46$, $p = 0.043$) increased.

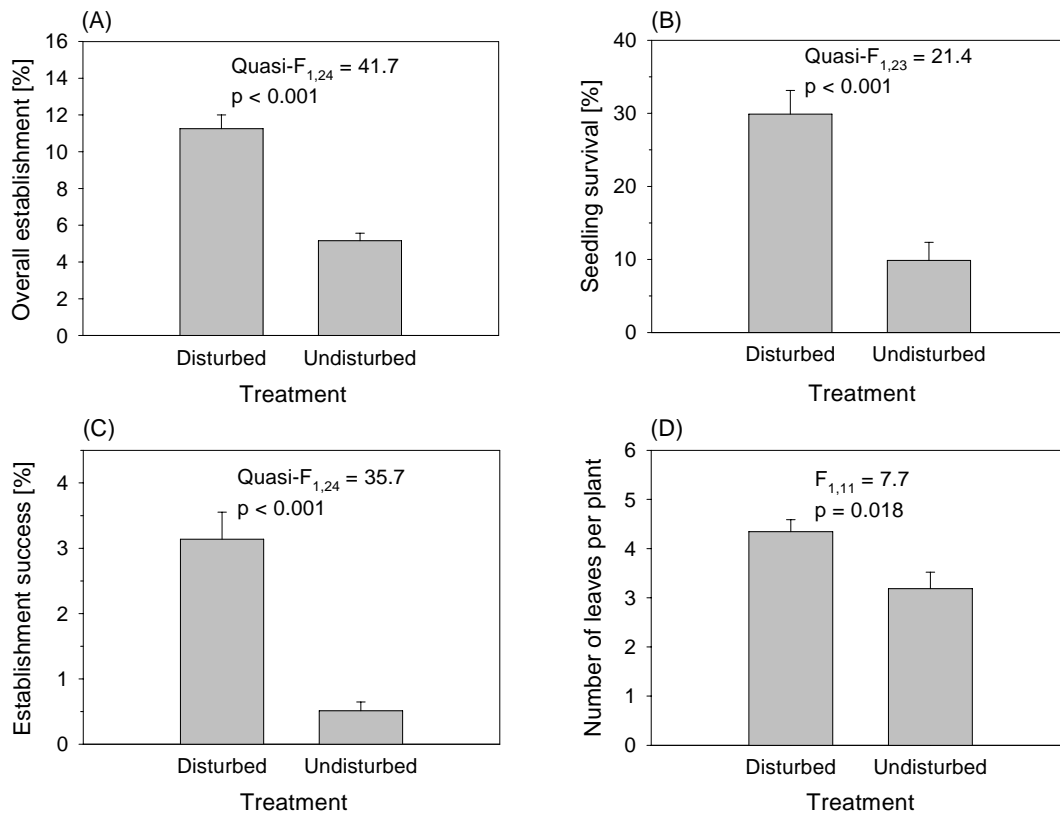


Figure 4. The effect of experimental disturbance on (A) overall establishment, i.e. the proportion of seeds that developed into a seedling during the two year study period, (B) seedling survival, (C) establishment success after two years, and (D) seedling size. Data shown are from 25 sites each with 4 disturbed and 4-8 undisturbed sowing plots. Error bars denote +1SE.

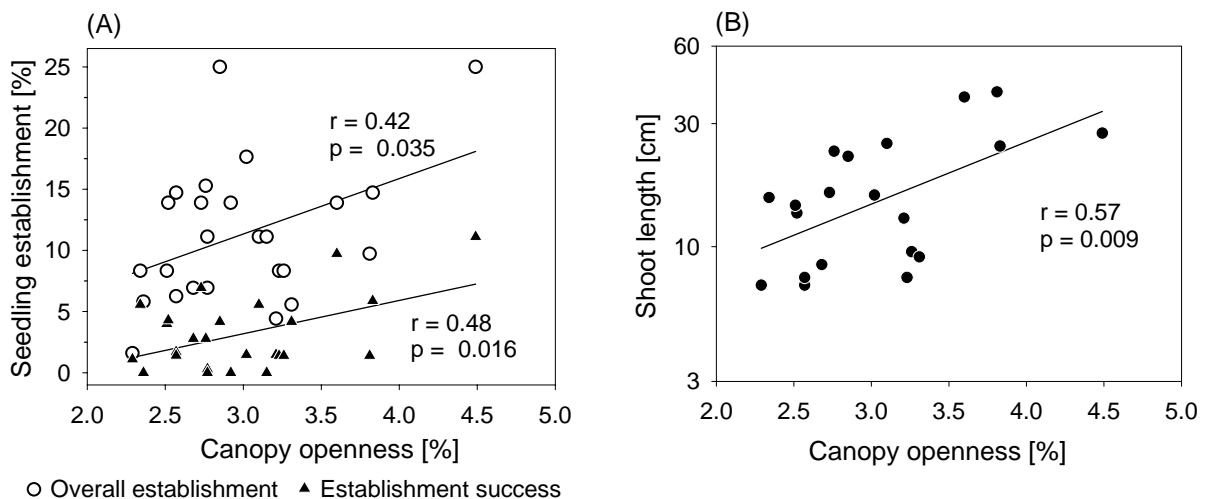


Figure 5. The influence of the mean canopy openness at 25 sites on (A) overall establishment, i.e. the proportion of seeds that developed into a seedling during the two year study period, and establishment success after two years, and on (B) shoot length of seedlings in disturbed plots. At each site, 4 disturbed sowing plots had been set up. Canopy openness was measured by hemispherical photographs.

DISCUSSION

Large clonal herbs are a typical component of tropical forests and form dense patches that can inhibit tree recruitment (Griffiths et al. 2007; Stevenson 2007), because they can shade out tree seedlings that are susceptible to light limitation (Nicotra et al. 1999; Montgomery & Chazdon 2002). Once established, these plants may form extensive clones that are long-lived (Whigham 2004; Souza & Martins 2006). However, the regional abundance of clonal herbs depends on the ability of seeds to colonize new sites (Eriksson 1989; Ehrlén & Eriksson 2000). In this study, we demonstrate that the colonization of new, unoccupied sites by the widespread tropical herb *H. metallica* is limited by seed dispersal and depends on natural disturbance.

Seed dispersal and predation

In many tropical plants, it is important for the descendants to escape from the home population (Wright 2002). Survival of seedlings of *H. metallica* was higher at sites without mature plants, and introduction of seeds strongly increased recruitment at most of the unoccupied sites. However, natural recruitment of seedlings was low at sites without a local seed source, indicating dispersal limitation. Similarly, seedling establishment of tropical pioneer trees is closely related to local seed rain (Dalling et al. 2002). In contrast, seed immigration into populations of the non-clonal herb *Heliconia acuminata* was substantial (Bruna 2003). Fruits of most tropical plants are dispersed by birds and mammals, and thus dispersal distances are expected to be rather long (Muller-Landau & Hardesty 2005). However, studies of the movement patterns of frugivorous birds have estimated low median dispersal distances of 30-60 m in the understory of tropical forests (Westcott & Graham 2000). Most fruits considered in these studies passed the gut of the birds, whereas seeds of *Heliconia* spp. are regurgitated (Stiles 1979), which shortens the time available for dispersal. Hence, long-distance dispersal may be rare, and colonization may typically occur close to an established population of *H. metallica*. This may explain why only c. 60% of the flooded sites in the study area were occupied by *H. metallica* (M. Schleuning, unpublished data), although numerous seedlings established after seed introduction into disturbed, unoccupied sites, and populations once established are long-lived.

Another potentially important factor influencing the regional dynamics of plants is the presence of a long-lived seed bank (Fornara & Dalling 2005). In tropical forests, seed banks are rare (Vázquez-Yanes & Orozco-Segovia 1993), but seed dormancy was shown to be important for the population dynamics of the tropical herb *Calathea ovandensis* (Horvitz &

Schemske 1994). However, seeds of *H. metallica* were short-lived. In contrast to low predation rates found in other tropical herbs (Horvitz & Schemske 1994; Bruna 2002), we observed that rodents and birds rapidly removed seeds of *H. metallica* from the ground and frequently found damaged seeds close to our plots. Hence, we assume that most of the removed seeds had been destroyed. Seed predation may strongly reduce the availability of seeds of *H. metallica*, although rodents can also hoard seeds in caches and thereby contribute to dispersal (Forget et al. 2000). However, in *H. metallica* germination of seeds from caches may not be important, because we never observed more than two naturally recruited seedlings together. Predation of seeds did not differ between sites with and without mature plants of *H. metallica*, although seed predation is supposed to be higher in the vicinity of conspecific plants in tropical forests (Wyatt & Silman 2004; Norghauer et al. 2006). However, predation of seeds of *H. metallica* increased with the overall vegetation density at a site. Previous studies in tropical forests have found inconsistent effects of microhabitat differences on seed predation (Wenny 2000; Fleury & Galetti 2006). In the case of *H. metallica*, lower predation of seeds at disturbed sites with an open understory may contribute to higher seedling establishment in these microhabitats.

Seedling establishment and survival

Seed addition considerably increased the number of established seedlings of *H. metallica*. The effect was stronger in experimentally disturbed plots, suggesting that recruitment was limited by the availability of seeds at microsites of low competition. Seed limitation is typical for large-seeded species inhabiting successional habitats (Turnbull et al. 2000; Moles & Westoby 2002; Clark et al. 2007) and is known to be strong in other tropical plants (Muller-Landau et al. 2002; Svenning & Wright 2005).

It has been suggested that the colonization of new sites by forest herbs is a two-stage process in which initial seedling establishment is determined by the availability of seeds and in which environmental sorting occurs during later seedling growth into a mature plant (Verheyen et al. 2003). Indeed, the environmental conditions during the development of a seedling into a mature plant are known to be an important filter affecting colonization (Turnbull et al. 2000). In line with that, competition by the established vegetation strongly affected both survival and growth of the newly recruited plants of *H. metallica*. In contrast to high survival in the non-clonal herb *H. acuminata* (Bruna 2002), most newly recruited plants of *H. metallica* died during the two-year study period, in particular at sites with strong competition. However, once a mature plant of *H. metallica* has established, it may further

colonize a site by clonal propagation. This type of demography is known from other clonal plants and has been termed "the strategy of initial seedling establishment" (Eriksson 1989).

Seedlings were more strongly damaged by herbivores at sites without mature plants of *H. metallica*. This is in contrast to the results of studies of herbivory in tropical tree seedlings (Massey et al. 2006; Norgauer et al. 2006) and might be due to a lack of herbivores specialized on leaves of *Heliconia* spp. (Bruna et al. 2002). Despite higher herbivory, seedling mortality was lower at sites without mature plants. This indicates that competition by larger, clonally propagated ramets was more important than herbivory. Strong resource competition between seedlings and adult plants is considered to be an important barrier to successful establishment in temperate systems (Turnbull et al. 2000), and may be so in the understory of tropical forests (see Hubbell et al. 2001).

Higher seedling survival at sites without mature plants of *H. metallica* and at experimentally disturbed sites is probably due to higher light availability at the forest floor. Below-ground competition is not a likely explanation for these differences. Water might be a limiting factor during the dry seasons, e.g. in the very dry study year 2005 (Aragão et al. 2007), but soil water content did not differ between disturbed and undisturbed plots and was even higher at sites with *H. metallica*. Nutrient availability is also not likely to be a limiting factor in the floodplain forest that grows on rich alluvial soils (Terborgh 1990). Similarly, the results of other studies indicate that recruitment of rainforest plants is limited by the low amount of light reaching the forest floor (Nicotra et al. 1999; King 2003). Even a slightly higher light availability in the understory can strongly increase growth and survival of tropical tree seedlings (Montgomery & Chazdon 2002). Spatial differences in light availability may often be due to differences in the cover of the understory vegetation (Kabakoff & Chazdon 1996). Understory gaps, e.g. because of the absence of large understory herbs, might thus be important for plant recruitment in tropical forests (see Griffiths et al. 2007), and competition among understory plants for light may be more important than previously suggested (see Wright 2002).

Natural recruitment of *H. metallica* was higher at flooded sites. Because many plants do not survive periodic flooding (Stevenson 2007), at flooded sites the cover of the understory vegetation was lower and thus light availability at the forest floor higher. This favours recruitment of *H. metallica* and has similar effects on other floodplain plants not susceptible to periodic flooding (King 2003). In the disturbed plots, we recorded an additional positive effect of tree canopy openness on establishment success and seedling size of *H. metallica*,

indicating that growth of newly recruited plants and thus potentially also further colonization by clonal growth are more rapid in small canopy gaps.

We conclude that the colonization of unoccupied sites is a critical phase in the regional dynamics of clonal herbs in tropical forests, because seeds are poorly dispersed and seedlings are outcompeted by established plants at undisturbed sites. This strongly suggests that low colonization ability limits site occupancy and regional abundance of clonal herbs, which in turn may reduce the competitive exclusion of tree seedlings in the understory and increase species diversity (see Wright 2002). Moreover, our results suggest that the regional dynamics of clonal herbs are strongly influenced by river dynamics. Over the past decades, rainfall patterns have changed in the tropics (Aragão et al. 2007), and these changes are predicted to intensify as a consequence of climate change (Hulme & Viner 1998; Betts et al. 2004). This may influence the frequency and timing of flooding and thereby alter the plant community of Amazon floodplain forests.

ACKNOWLEDGEMENTS

PerúVerde provided us the opportunity to carry out this study in the surroundings of Manu Wildlife Center. Logistical support by the staff of PerúVerde, InkaNatura and Manu Wildlife Center is gratefully acknowledged. Field assistance by J.G. Castillo, L.H. Zuñiga, M.T. Blanco and many others was invaluable, and organizational support from T. Becker, N. Salinas and R. Urrunaga very helpful. This study was supported by Ph.D.-scholarships of the German Academic Exchange Service (DAAD) and of Studienstiftung des deutschen Volkes. The research was authorized by the Institute for Natural Resources (INRENA) of the Peruvian government by authorization numbers 013-2005, 003-2006 and 131-2006-INRENA-IFFS-DCB.

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SUMMARY

A MAJOR GOAL OF ECOLOGICAL RESEARCH is to understand how plant populations respond to spatial and temporal variation in environmental conditions. To disentangle the complex relationship between the demography of perennial plants and the environmental variation in their habitats, I analyzed the effects of varying habitat conditions on the population dynamics of two herbaceous perennials. One of the plants, *Trifolium montanum*, grows in nutrient-poor grasslands in a semi-natural landscape of central Europe, while the other plant, *Heliconia metallica*, grows in lowland rainforests in a natural landscape of Amazonian Peru. I studied the various demographic processes in the life cycle of the two perennial model species over several years and in numerous populations. Using matrix population models, I decomposed differences in population growth rates into the contributions of the different demographic processes and projected population development into the future taking into account the effects of environmental stochasticity. I demonstrate which processes are particularly important in the life cycle of perennial plants and how deterministic and stochastic components of environmental variation influence the viability of populations of perennial plants.

During the last decades, changes in land use have resulted in a considerable loss of nutrient-poor grasslands in central Europe, and in the remnant sites plant diversity has decreased. Short-lived species rapidly respond to changes in habitat conditions, but little is known about the effects on the population dynamics of long-lived plants. I studied the effects of habitat degradation and fragmentation on stage structure, recruitment, reproduction and offspring performance in populations of the declining perennial plant *Trifolium montanum* L. in central Germany, and used demographic data from nine sites and four years to analyze the effect of habitat degradation on the population dynamics of *T. montanum* using matrix models. To assess the habitat quality in a site, I measured the leaf area index (LAI) above *T. montanum* plants as an estimate of light competition. Density and survival of juvenile plants decreased with LAI, resulting in aged populations with few juvenile plants in unmanaged sites with higher LAI. The finite growth rate of a population strongly decreased with LAI. In unmanaged sites, population growth was <1 , which was mostly due to lower survival and flowering of large plants. Simulated management by clipping rapidly increased population growth because of higher survival and flowering of large plants.

In contrast to flowering probability, the number of seeds per fruithead was not related to LAI, but increased with local density, suggesting pollinator limitation in populations with a low density of flowering *T. montanum* plants. In a common garden experiment, the seed production of the sown offspring decreased with isolation, and in strong contrast to previous studies, also decreased with size and density of the population of origin. This might be due to

increased inbreeding because of pollination between closely related neighboring plants in dense and large populations. The contrasting effects of habitat fragmentation on reproduction and offspring performance indicate that the effects of population size, density and isolation on plant fitness and population viability may be complex. However, in the short term cessation of management which results in an increase in light competition affects populations of the perennial plant *T. montanum* more strongly than habitat fragmentation.

Due to its perennial life history, even in small populations of *T. montanum* the process of extinction may take a long time. In stochastic simulations, the median time to extinction of unmanaged populations of 100 flowering plants was still about 50 years. However, because of the effects of environmental stochasticity, small populations though managed and presumably stable in size were threatened by stochastic extinction and required a minimum number of 60 flowering plants to survive with 95% probability over the next 100 years. However, most populations of *T. montanum* in central Germany consist of less than 50 flowering plants.

Due to the enormous reduction in the area of nutrient-poor grasslands, the regional dynamics of plant species restricted to these grasslands have been disrupted in central Europe. Today, the probability of colonization of unoccupied sites is very low, and the regional viability of these species mostly depends on the survival of the remnant populations. However, the example of *T. montanum* shows that the combined effects of deterministic and stochastic factors will drive many of the extant populations to extinction in the long term. Many populations of other perennial plants of semi-natural grasslands might also be doomed because of the low quality of their habitats and their small size. However, the results indicate that the extinction process may take a long time in perennial plants like *T. montanum*, resulting in an extinction debt. The actual plant diversity of the remnant sites might thus be a misleading indicator of their conservation status.

In contrast to the semi-natural landscape in central Europe, large areas of tropical rainforests are still shaped mainly by natural processes. Natural disturbance by flooding and treefalls are the crucial processes shaping the environmental conditions in the understory of many Amazon forests. Clonal herbs are an important component of these forests and influence forest regeneration because of their local dominance in the understory. However, very little is known about the demographic response of these herbs to the varying habitat conditions in the forest understory.

In a Peruvian floodplain forest, I analyzed the influence of seasonal and spatial environmental variation on the population dynamics of the clonal herb *Heliconia metallica* Planchon & Linden ex Hooker over two wet and two dry seasons and carried out an

experiment of seed addition and predator exclusion to assess the role of seed ecology for the local and regional population dynamics. The life history of *H. metallica* was dominated by clonal growth and ramet survival. Only in recently formed canopy gaps, growth and clonal expansion of the ramets were rapid and reproduction was frequent. Predation of seeds of *H. metallica* was high and after one year nearly all sown seeds had either germinated or died. Due to strong light competition with mature plants, seedling mortality was very high in established populations of *H. metallica*, and seedling recruitment contributed very little to local population dynamics.

I analyzed in a factorial design the interacting effects of flooding and canopy gaps on the population dynamics of *H. metallica* using periodic matrix models. All populations increased in size during the wet and decreased during the dry season. Finite annual growth rates of non-flooded populations were <1 both in gaps and non-gaps. In contrast, growth rates of flooded populations were ≈ 1 in non-gaps and significantly >1 in recently formed gaps. The lower growth rate at non-flooded sites was mainly due to the lower survival of ramets during the dry season. In stochastic simulations, the extinction risk of the non-flooded populations of *H. metallica* was high even if gaps were assumed to be formed in 5% of the years, whereas that of flooded populations was low and decreased with the frequency of gap formation. These populations may persist for a long time in the flooded understory.

In a regional inventory of natural recruitment, seedlings of *H. metallica* were more numerous at flooded sites and in the vicinity of flowering plants of *H. metallica*. Seed addition in unoccupied sites strongly increased seedling recruitment, indicating dispersal limitation. The effect of seed addition was stronger in plots that had been disturbed experimentally, because light availability on the forest floor and as a consequence seedling establishment and survival were higher in disturbed than in undisturbed plots. In the disturbed plots, a greater canopy openness positively affected seedling establishment and size, and thus the success of colonization.

The results indicate that the local and regional population dynamics of *H. metallica* are shaped by the interacting effects of seasonal flooding and of transient canopy gaps. Ramet survival and clonal growth are crucial for the persistence of populations of *H. metallica* in the forest understory, while the colonization of unoccupied sites is limited by insufficient dispersal of seeds to sites of higher light availability. Currently, the regional abundance of *H. metallica* in the floodplain is rather limited by colonization than by local extinction. The environmental differences between the wet and dry season strongly affected the populations of *H. metallica*, and all populations decreased in size during the dry season. However, an

increase in the length of the dry season has been observed in Amazon rainforests during the last decades. The results of this study suggest that the clonal life form of *H. metallica* enables populations to persist under variable light conditions, but might not be able to buffer the effects of drought stress during longer dry seasons. Climate change might cause a decrease in the regional abundance of the widespread clonal understory herbs of Amazon rainforests.

I found that populations of perennial plants strongly respond to the spatial and temporal environmental variation in their habitats. However, the response of the different life-cycle phases varied strongly. Seedling recruitment of *T. montanum* declined with increasing light competition, while the probability of flowering and seedling recruitment of *H. metallica* were limited by the light availability in the understory. However, in both species these life-cycle transitions, which showed the strongest response to environmental variation, did not account for the observed differences in population growth among habitats, which in contrast were survival and flowering of large plants of *T. montanum*, and survival of ramets of *H. metallica* during the dry season. Studies that focus on single life-cycle components should be interpreted with caution and should not be used to draw conclusions at the population level.

The combined effects of deterministic and stochastic environmental factors play an important role in plant population dynamics. In both the semi-natural and natural system, deterministic environmental change was the main driver of population extinction, while disturbance by grazing or flooding was crucial to maintain habitat quality and a stable population size. I conclude that the effects of stochastic environmental variation on the population dynamics of perennial plants are intricate. While strong fluctuations in habitat conditions may drive small populations to extinction, stochastic events of disturbance, as exemplified by grazing in *T. montanum* and by flooding in *H. metallica*, may provide the only opportunity for colonization in closed habitats. However, the probability of colonization of unoccupied grasslands by *T. montanum* is very low in the fragmented European landscape. In contrast, the colonization of new sites by *H. metallica* in the continuous Amazon floodplain forests is more frequent and reduces the risk of regional extinction.

Due to increasing human impact, strong changes in the environmental conditions have occurred in many ecosystems during the last decades and are predicted to intensify in the future. Populations of perennial plants, which depend on specific environmental conditions like *T. montanum* and *H. metallica*, are strongly affected by the environmental changes in their habitats and are increasingly prone to extinction. However, the extinction process may take a long time in perennial plant species, and the current distribution of these species may not reflect the viability of their populations.

ZUSAMMENFASSUNG

EIN WICHTIGES ZIEL ÖKOLOGISCHER FORSCHUNG ist zu verstehen, wie Pflanzenpopulationen auf die räumliche und zeitliche Variabilität ihrer Umwelt reagieren. Um die komplexe Beziehung zwischen der Demographie langlebiger Pflanzenarten und der Variabilität ihrer Habitate zu entschlüsseln, untersuchte ich die Effekte unterschiedlicher Habitatbedingungen auf die Populationsdynamik von zwei krautigen, ausdauernden Pflanzenarten. Eine Art, *Trifolium montanum*, wächst in Kalkmagerrasen der mitteleuropäischen Kulturlandschaft und die andere Art, *Heliconia metallica*, im Tieflandregenwald einer Naturlandschaft in Peru. Ich untersuchte die verschiedenen demographischen Prozesse im Lebenszyklus der beiden Modellarten über mehrere Jahre und in zahlreichen Populationen. Mit Hilfe von Matrix-Modellen zerlegte ich die Unterschiede in den Wachstumsraten der Populationen in die Beiträge der verschiedenen demographischen Prozesse und simulierte die zukünftige Entwicklung der Populationen unter Berücksichtigung zufälliger Schwankungen in den Umweltbedingungen. Auf diese Weise wird gezeigt, welche Prozesse im Lebenszyklus der beiden ausdauernden Arten besonders wichtig sind und wie deterministische und stochastische Komponenten der Umweltvariabilität das Überleben von Populationen ausdauernder Pflanzen beeinflussen.

Während der letzten Jahrzehnte haben Veränderungen in der Landnutzung zu einem beträchtlichen Verlust von Magerrasen in der Kulturlandschaft Mitteleuropas geführt, und in den verbliebenen Magerrasen ist die Pflanzenvielfalt zurückgegangen. Kurzlebige Arten reagieren schnell auf die Veränderungen in den Habitatbedingungen. Über die Auswirkungen auf die Populationsdynamik der langlebigen Arten ist aber nur wenig bekannt. In Populationen der seltenen Kleeart *Trifolium montanum* L. untersuchte ich die Effekte von verminderter Qualität und zunehmender Fragmentierung der Habitate auf die Stadienstruktur, Keimlingsrekrutierung und Reproduktion sowie die Fitness der Nachkommen in Kalkmagerrasen in Nordhessen und Südniedersachsen. Die Effekte verminderter Habitatqualität auf die Populationsdynamik von *T. montanum* analysierte ich in einem Matrix-Modell mit demographischen Daten aus neun Populationen und vier Jahren. Um die Habitatqualität in den verschiedenen Populationen zu beurteilen, wurde der Blattflächenindex (LAI) oberhalb von *T. montanum*-Pflanzen als ein Maß für die Stärke der Lichtkonkurrenz gemessen. Die Dichte und das Überleben der jungen Pflanzen nahmen mit zunehmender Lichtkonkurrenz ab. Dies führte zur Bildung von überalterten Populationen mit wenigen Jungpflanzen an Orten ohne regelmäßige Nutzung und höherem LAI. Die spezifische Wachstumsrate der Populationen nahm mit zunehmender Lichtkonkurrenz ab. An Orten ohne Nutzung war das Populationswachstum kleiner als 1. Der Rückgang dieser Populationen war vor allem durch eine höhere

Mortalität und eine geringere Blühwahrscheinlichkeit der großen Pflanzen bedingt. Experimentelle, kleinflächige Mahd führte rasch zu einem höheren Populationswachstum, weil das Überleben und die Blühwahrscheinlichkeit der großen Pflanzen erhöht waren.

Im Gegensatz zur Blühwahrscheinlichkeit der *T. montanum*-Pflanzen wurde die Anzahl der Samen pro Blühköpfchen nicht von der Lichtkonkurrenz beeinflusst, nahm aber stark mit der lokalen Dichte der blühenden *T. montanum*-Pflanzen zu, wahrscheinlich bedingt durch eine geringere Bestäubung in Populationen geringer Blühdichte. In einem Anzuchtexperiment in einem Botanischen Garten nahm die Samenproduktion der angesäten Pflanzen mit der Isolation, und im Gegensatz zu früheren Studien, auch mit der Größe und Dichte der Ursprungspopulation ab. Dieses Ergebnis war vermutlich die Folge von Inzuchteffekten aufgrund häufiger Bestäubung zwischen benachbarten und nahe verwandten Individuen in großen und dichten Populationen von *T. montanum*. Die gegensätzlichen Auswirkungen der Habitatfragmentierung auf die Reproduktion und Fitness der Nachkommen zeigen, dass die Effekte von Größe, Dichte und Isolation der Populationen auf die Fitness von Pflanzen und das Überleben von Populationen komplex sein können. Zumindest kurzfristig beeinflusst die stärkere Lichtkonkurrenz in brachliegenden Magerrasen die Populationen von *T. montanum* stärker als die Habitatfragmentierung.

Aufgrund des mehrjährigen Lebenszyklus von *T. montanum* ist der Aussterbeprozess selbst kleiner Populationen von langer Dauer. In Simulationsmodellen von brachliegenden Populationen mit 100 blühenden Pflanzen dauerte es im Mittel noch etwa 50 Jahre, bis die Populationen ausstarben. Allerdings war aufgrund zufälliger Umweltschwankungen das Aussterberisiko selbst von Populationen, die regelmäßig genutzt wurden und eine scheinbar stabile Populationsgröße hatten, erheblich. Diese Populationen benötigten mindestens 60 blühende Pflanzen, um mit einer Wahrscheinlichkeit von 95% die nächsten 100 Jahre zu überleben. In Niedersachsen bestehen aber die meisten Populationen von *T. montanum* aus weniger als 50 blühenden Pflanzen.

Wegen des starken Flächenrückgangs von Kalkmagerrasen in Mitteleuropa ist die Besiedlung neuer Orte heute sehr selten, weshalb das regionale Überleben der Pflanzenarten, die nur auf Kalkmagerrasen vorkommen, fast ausschließlich vom Überleben der verbliebenen Populationen abhängt. Allerdings zeigt die hier präsentierte Studie, dass die gemeinsamen Effekte deterministischer und stochastischer Einflussfaktoren langfristig zu einem Aussterben von vielen verbliebenen Populationen führen werden. Viele Populationen auch von anderen langlebigen Arten dürften wegen der geringen Habitatqualität und ihrer geringen Größe zum Aussterben verurteilt sein. Allerdings zeigen die Ergebnisse meiner Arbeiten auch, dass das

Aussterben einer Population bei langlebigen Pflanzenarten wie *T. montanum* eine lange Zeit dauert. Die aktuelle Pflanzenvielfalt der verbliebenen Magerrasen ist daher nicht im Gleichgewicht mit der Habitatqualität und kann bei der Bewertung der naturschutzfachlichen Qualität eines Magerrasens ein irreführender Indikator sein.

Im Gegensatz zur mitteleuropäischen Kulturlandschaft werden große Gebiete tropischer Regenwälder auch heute noch vor allem durch natürliche Prozesse geprägt. Hier bestimmen natürliche Störungen, z.B. durch Überschwemmung oder das Umstürzen großer Bäume, die Umweltbedingungen im Unterwuchs des Waldes. Krautige, klonale Pflanzen sind wichtige Bestandteile des Unterwuchses dieser Wälder, die wiederum wegen ihrer Dominanz die Verjüngung des Waldes beeinflussen. Allerdings ist kaum etwas über die Populationsdynamik dieser Unterwuchspflanzen in Abhängigkeit der veränderlichen Habitatbedingungen bekannt.

Ich untersuchte den Einfluss von saisonaler und räumlicher Umweltvariabilität auf die Populationsdynamik der klonalen Pflanzenart *Heliconia metallica* Planchon & Linden ex Hooker während zwei Regen- und zwei Trockenzeiten in einem peruanischen Tieflandregenwald. Außerdem führte ich ein Aussaatexperiment mit Ausschluss von Samenprädatoren durch, um die Rolle der Samen und der Etablierung von Keimlingen in der lokalen und regionalen Dynamik der Populationen zu untersuchen. Die Lebensgeschichte von *H. metallica* war von klonalem Wachstum und dem Überleben der Sprossindividuen dominiert. Nur im Bereich jüngerer Kronenlücken wuchsen die Sprosse schnell, breiteten sich durch klonales Wachstum rasch aus, und reproduzierten häufig. Die Prädation der Samen von *H. metallica* war hoch, und nach einem Jahr waren fast alle Samen entweder gekeimt oder gestorben. Aufgrund der starken Beschattung durch die ausgewachsenen Pflanzen war die Mortalität der Keimlinge in etablierten Populationen von *H. metallica* sehr hoch, und die Rekrutierung von Keimlingen trug daher nur sehr wenig zur lokalen Dynamik der Populationen bei.

Ich untersuchte in einem faktoriellen Design die interagierenden Effekte von Überschwemmung und Kronenlücken auf die Populationsdynamik von *H. metallica* und erstellte dazu periodische Matrix-Modelle. Alle Populationen nahmen während der Regenzeit zu und während der Trockenzeit ab. Die spezifische jährliche Zuwachsrate der nicht-überfluteten Populationen war kleiner als 1 sowohl in den Kronenlücken als auch unter einem geschlossenen Kronendach. Im Gegensatz dazu betrug das Populationswachstum an überfluteten Orten etwa 1 unter einem geschlossenen Kronendach und war größer als 1 in den jungen Kronenlücken. Die niedrigere Wachstumsrate an Orten ohne Überflutung war vor allem durch ein geringeres Überleben der Sprossindividuen während der Trockenzeit verursacht. In stochastischen Simulationsmodellen war das Aussterberisiko von *H. metallica*-

Populationen an Orten ohne Überschwemmung hoch, und zwar selbst wenn an einem Ort in 5% der Jahre eine Kronenlücke gebildet wurde. Im Gegensatz dazu war das Aussterberisiko der Populationen an überfluteten Orten gering und nahm mit der Frequenz der Bildung von Kronenlücken ab. Offensichtlich können die Populationen an regelmäßig überfluteten Orten lange Zeiträume überleben.

In einer regionalen Erfassung der natürlichen Keimlingsrekrutierung waren Keimlinge von *H. metallica* an überfluteten Orten und in der Nähe blühender *H. metallica*-Pflanzen zahlreicher. Das Ausbringen von Samen an unbesiedelte Orte erhöhte die Keimlingsetablierung von *H. metallica* deutlich. Die erfolgreiche Etablierung an diesen Orten deutet auf eine Limitierung der Samenausbreitung hin. Die Etablierung und das Überleben der Keimlinge waren höher in Flächen, die zuvor experimentell gestört worden waren und in denen daher mehr Licht den Boden erreichte. In den gestörten Flächen wirkte sich eine offene Baumkrone positiv auf die Etablierung und Größe der Keimlinge, und damit auf den Besiedlungserfolg aus.

Die Ergebnisse zeigen, dass die lokale und regionale Populationsdynamik von *H. metallica* stark von der saisonalen Überflutung und von der Bildung temporärer Kronenlücken beeinflusst werden. Die Auswirkungen dieser beiden Umweltfaktoren auf die Populationsdynamik interagieren zudem stark. Das klonale Wachstum und das Überleben der Sprossindividuen waren entscheidend für das Überdauern der Populationen von *H. metallica* im Unterwuchs des Waldes, und die Besiedlung neuer Orte war durch die Ausbreitung von Samen an gestörte, helle Orte limitiert. Somit ist die regionale Häufigkeit von *H. metallica* gegenwärtig vor allem durch eine limitierte Ausbreitung und nicht durch das Aussterben etablierter Populationen begrenzt. Der saisonale Wandel zwischen Regen- und Trockenzeit beeinflusste die Populationen von *H. metallica* stark, und alle Populationen nahmen während der Trockenzeit ab. Allerdings wurde während der letzten Jahrzehnte eine zunehmende Länge der Trockenzeit in amazonischen Regenwäldern beobachtet, und eine weitere Zunahme der Häufigkeit von Trockenperioden wird vorhergesagt. Die Ergebnisse der vorliegenden Studie deuten daraufhin, dass die klonale Lebensstrategie von *H. metallica* in Habitaten variierender Lichtverfügbarkeit erfolgreich ist, dass diese Strategie aber weniger geeignet erscheint, um längere Trockenperioden zu überdauern. Es ist daher möglich, dass die klimatischen Veränderungen zu einer Abnahme der regionalen Häufigkeit der weit verbreiteten klonalen Unterwuchspflanzen in Amazonien führen.

Mit meinen Untersuchungen konnte ich zeigen, dass Populationen ausdauernder Pflanzenarten stark auf die räumliche und zeitliche Variabilität ihrer Habitatbedingungen

reagieren. Allerdings variierte die Reaktion der verschiedenen Teile des Lebenszyklus stark. Die Rekrutierung von Keimlingen von *T. montanum* nahm mit zunehmender Lichtkonkurrenz ab, und sowohl die Keimlingsetablierung als auch die Blühwahrscheinlichkeit etablierter Sprosse von *H. metallica* waren von der Lichtverfügbarkeit im Unterwuchs limitiert. Bei beiden Arten erklärten allerdings diese demographischen Übergänge, die am stärksten von der Umweltvariabilität beeinflusst wurden, nicht die beobachteten Unterschiede im Populationswachstum zwischen den verschiedenen Habitaten. Bei *T. montanum* waren hierfür vor allem das Überleben und die Blühwahrscheinlichkeit der großen Pflanzen, und bei *H. metallica* das Überleben der Sprosse während der Trockenzeit verantwortlich. Studien, die nur einen Teil des Lebenszyklus betrachten, sollten daher vorsichtig interpretiert werden und nicht dazu genutzt werden, um Schlussfolgerungen auf Populationsniveau zu ziehen.

Deterministische und stochastische Umweltfaktoren spielen eine wichtige Rolle in der Dynamik von Pflanzenpopulationen. In beiden Modellsystemen, in der Kultur- und der Naturlandschaft, war der deterministische Wandel der Habitatbedingungen die wichtigste Ursache für das Aussterben von Populationen, wohingegen sich Störung durch Beweidung oder durch Überflutung positiv auf die Habitatqualität und das Populationswachstum auswirkten. Die Auswirkungen stochastischer Umweltschwankungen auf die Populationsdynamik langlebiger Pflanzenarten können komplex sein. Während starke Schwankungen der Umweltbedingungen zum Aussterben kleiner Populationen beitragen, sind stochastische Störungsereignisse, wie Beweidung bei *T. montanum* und Überflutung bei *H. metallica*, häufig der einzige Mechanismus, der geeignete Bedingungen für die Kolonisierung neuer Orte schafft. Die Kolonisierung unbesiedelter Magerrasen durch *T. montanum* ist in der fragmentierten, mitteleuropäischen Kulturlandschaft ein sehr seltenes Ereignis. Im Gegensatz dazu ist die Kolonisierung neuer Orte durch *H. metallica* in den zusammenhängenden amazonischen Tieflandregenwäldern häufiger und führt zu einer Verringerung des regionalen Aussterberisikos.

Außerdem einer Zunahme der anthropogenen Einflüsse hat in vielen Ökosystemen in den letzten Jahrzehnten ein starker Wandel der Umweltbedingungen stattgefunden, der in Zukunft weiter voranschreiten wird. Populationen von Pflanzenarten, die wie *T. montanum* und *H. metallica* auf spezifische Umweltbedingungen angewiesen sind, werden von den Veränderungen in ihren Habitaten stark beeinflusst und sind daher in zunehmender Weise vom Aussterben bedroht. Allerdings kann das Aussterben einer Population bei ausdauernden Pflanzenarten eine lange Zeit dauern. Die aktuelle Verbreitung dieser Arten ist daher kein geeignetes Maß, um die Gefährdung ausdauernder Pflanzenarten abzuschätzen.

ACKNOWLEDGEMENTS

I am grateful to all the people who accompanied me during these last three years of delightful and sometimes exhausting research: Thanks to all of you who diverted and encouraged me and to all who contributed to the success of this project with time, enthusiasm and ideas.

Diethart Matthies formed my scientific skills during the last years and guided me through this wondrous world of deviances, eigenvalues and elasticities. Thank you for supporting me on whatever continent, for all your valuable ideas during the studies and for the very helpful comments on the manuscripts. I also thank Thomas Becker, who supervised parts of my Peruvian research, helped in various ways and proof-read parts of this thesis. I am grateful to Roland Brandl for being co-referee of this thesis and for his recommendation during scholarship application. Thank you Birgit Ziegenhagen and Volker Grimm for your participation in the disputation committee, and Georg Miede and Katrin Böhning-Gaese for scholarship recommendations. Without financial support from the German Academic Exchange Service (DAAD) and from Studienstiftung des Deutschen Volkes this dissertation would not have been possible. I really appreciate this funding and hope that many other scholarship holders will have the opportunity to follow their scientific ideas, although they may not be scientific mainstream. I thank Dirk Kaesler who was my Studienstiftung's tutor for supporting me even when I was far from Marburg.

Trifolium research would not have been possible without the friendly collaboration with Ute Becker, Marc Niggemann and initially Henrik Berg. Thank you Ute and Marc for sharing study sites, collecting seeds and growing plants. And thanks Marc for always attending me in whatever conversation though not on conservation. I am grateful to Rainer Peilstöcker, who took care of the plants in Marburg and who helped in a lot of logistical details. Thanks to all other members of the working group for sharing coffee/tea breaks and for having a good time. I am grateful to all grassland users and owners for their astonished understanding. And thanks to Julia and Keram for housing me in Marburg during transitional visits.

Crossing the ocean: Indeed, I am grateful to Iberia Airlines for allowing me extra luggage though it may not arrive on the spot, but all these flights were professional anyway. Thanks to Alvan for always awaiting me at Lima airport and making me feel like coming home. I am very grateful to Norma Salinas and Rosa Urrunaga from the University of Cuzco and to Mery L. Suni and Giovana P. Vadillo from the University of San Marcos in Lima for helping me with their experience in conducting scientific projects in Peru. I thank Karina Ramirez (INRENA) for advice on research permits. In a very special way, I like to thank Tropical Nature and PerúVerde, and in particular Charles Munn and Daniel Blanco, for giving

me the opportunity to work in the superb rainforest around Manu Wildlife Center. Thank you Daniel for supporting my project from the beginning to the end: All the best for your conservation work! Every moment in these forests pays your efforts back. Thanks a lot to Juan Carlos Cardenas, Nidia Torres and all the other people in InkaNatura Selva for taking me and my people into the forest and getting us out on whatever date. Sorry for the extra work - I'll try to pay it back in German chocolate. I also thank Elizabeth Valverde for thoroughly coordinating our many stays in Manu Wildlife Center.

Getting into the Manu forest is nothing but easy: Thanks to all pilots easily approaching this tiny landing strip and to Guillermo for calmly driving the winding roads to Atalaya. Thanks to all boat-drivers for taking us down the wild river waters: Dionisio, Nestor, Daniel, Rufino, Wilson, Ritmer, Benito, Moises and many others. Without my Diploma students Gabrielle Lohß and Mathias Templin lots of aspects of the secret life of *Heliconia* would still be hidden – thanks to Markus Fischer for supervising their theses. I like to thank all the students, who contributed with their enthusiastic field work to the *Heliconia* project: Maria T. Blanco, Nina Holstein, Alida Kossack, Juliane Steckel, Matthias Dehling, Juliane Wunderlich and Christine Bohn. This work would not have been possible without my Peruvian counterpart: Vicky Huaman from the University of Cuzco accompanied the complete field work and really made a great job. Muchas gracias! Thanks to all those who assisted in the field: Esteban, Carlos, Nicolas, Vicente, Neydu, Abel, Wilson, Ronaldo and many others. Your enthusiasm, L. Hebert Zuñiga, was really invaluable, when you joined those exhausted people at the end of the project – thank you, Hebert! And last but not least thanks to my native genius José G. Castillo. You learned me a lot about your forest and about living down there on the other side. That's more valuable than the scientific details in this thesis: Lo mejor para ti, Isaura y los enanos – hasta la proxima! There were many more people who made Manu easy and unforgettable: Thanks to all guides for having such a good time, gracias Julio Oviedo and Julian Gray for lodging support, gracias Anselmo for best Lemon pie, Leandro for roof-topping, Yolinda for trying the undryable, Victor for smiling at 5 am and thanks to all the rest of you in Cedro and Isla for your hospitality. I will be back on a soccer Sunday.

I thank my parents who always encouraged me and who have taught me to discover the beautiful and special in the creatures out there. Thanks to Julio, Marita and Tatiana for accommodating me in your family with so much affection. Someone left? You have been in the beginning and you are still: Thank you, Monika, for your faith and for shedding light on the winding rivers, trails and trampling paths in Amazon lowlands and German grasslands. This is really exceptional!

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ERKLÄRUNG

Ich versichere, dass ich meine Dissertation

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selbständig, ohne unerlaubte Hilfe angefertigt und mich dabei keiner anderen als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe.

Die Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg (Lahn), den 17.12.2007

Matthias Schleuning