## RESEARCH PROJECT

# Does habitat fragmentation reduce the long-term survival of isolated populations of dominant plants? A field design

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## Summary

1 This paper describes relevant theory and a novel research approach to evaluate the responses of plant populations to habitat fragmentation. We propose a hierarchical spatial design of fen systems, consisting of large islands with adjacent and remote small islands, with explicit distance and size criteria, to study the effects of habitat fragmentation and isolation.

2 Contrary to earlier studies conducted on small and isolated populations of rare species, our focus is on abundant species. We want to test whether spatially isolated, dominant species have reduced vitality and vigor and thus are more susceptible to extinction, as suggested by recent modelling. If so, ecosystem functioning and in turn the persistence of rare plant and animal species could be impaired.

3 The vegetation types studied are the highly fragmented and diverse pre-alpine fens (Caricion davallianae) of Switzerland. Nearly 50% of all the threatened plant species in Switzerland occur in these semi-natural wetlands.

4 We are examining the demographic composition of the populations, the growth, reproduction and survival of marked individuals, and the genetic structure of populations in relation to geographical isolation. Our specific research questions and the experimental protocol are presented in this paper.

Keywords: calcareous fens, demography, genetic variability, population viability, reciprocal transplants, reproduction

## Theoretical background

### METAPOPULATIONS AND HABITAT FRAGMENTATION

Many plants and animals live in habitats that are becoming increasingly rare due to human activity. Such habitats are often reduced and fragmented into isolated patches with different levels of interconnectedness. Fragmentation might have a larger influence on species persistence than processes within populations, occurring at smaller spatial scale (Hanski & Gilpin 1991; Eriksson 1996).

Metapopulation dynamics, following classic colonization-extinction models (MacArthur & Wilson 1967; Levins 1969, 1970) have been a major focus in conservation and biogeography in recent years. In these models, populations in well-defined habitat fragments are interconnected by a regular migration of individuals. Long-term persistence is maintained via a continuous colonization and extinction of habitat fragments.

The metapopulation concept has mainly been applied to animal populations. Its application to plants is more difficult (Silvertown 1991). Many plants resist extinction for a considerable period of time via a long life span, clonal growth or a persistent seed bank, even in situations where only a part of the life cycle can be maintained (Eriksson 1996). Plants also have a more restricted dispersal capacity than animals (Ouborg 1993), which makes the traditional idea of interconnected populations questionable. Furthermore, high variability among remnant fragments can complicate the interpretation of statistical relationships between fragment and plant community attributes (Jules 1998), for example with regard to fragment size (Ouborg 1993) or vegetation type (Oostermeijer et al. 1994a). Consequently, metapopulation models, and more importantly empirical studies to test these models, are almost absent for plants (Husband & Barett 1996). It is apparent that these models certainly cannot be used in their rudimental form.

Two theoretical modelling approaches easing the translation of metapopulation theory to plant population dynamics in fragmented or isolated habitats are the source-sink model (Pulliam 1988; Gosselin 1996; Loreau & DeAngelis 1997) and the mainland-island model (Gotelli 1991; Harrison & Hastings 1996). In the source-sink model, the sink population is unable to compensate local

mortality via reproduction; nevertheless, populations may persist in such habitats, due to the continued immigration from the more productive source populations nearby (Pulliam 1988). In contrast, in mainland-island models populations on the small or distant islands still maintain sufficient reproduction, but may suffer from genetic drift and inbreeding. Immigration counteracts and homogenizes the reduction in gene frequencies, and decreases inbreeding coefficients (Harrison & Hastings 1996). Dispersal of either pollen or seeds from the larger sites to the isolated or marginal sites thus may be crucial for the long-term survival of populations in smaller fragments.

## ISOLATION AND EXTINCTION IN PLANT COMMUNITIES

Recent studies of plant populations in fragmented habitats show that geographical isolation and small population size can ultimately lead to the extinction of populations (Ellstrand & Elam 1993). Reduced pollination and seed dispersal within and among fragmented habitats cause reduced reproduction (Fischer & Matthies 1997, 1998). Genetic characteristics of large populations can be regarded as intact, with regard to random mating and the maintenance of a genetic equilibrium (Harrison & Hastings 1996). Small populations, however, are subject to increased genetic drift with unpredictable fluctuations in allele frequencies and possible fixation of deleterious alleles. In addition, increased mating between closely related individuals within populations, i.e. inbreeding, can cause an increase in the frequency of homozygous genotypes. Often these have more variable and reduced fitness than do heterozygous genotypes (Ellstrand & Elam 1993; Oostermeijer et al. 1994b, 1995). This can lead to "senile" populations consisting only of

flowering and vegetative adults, but lacking juvenile plants and seedlings (Oostermeijer *et al.* 1994a). Recent field studies have provided evidence for a correlation between the loss of genetic variability and fitness loss in populations (Oostermeijer *et al.* 1994b, 1995; Koelewijn 1998). Populations with reduced fitness cannot easily respond to a changing environment and stochastic effects, and thus have a higher risk of extinction (Menges 1990; Ellstrand 1992a; Fischer & Matthies 1997; Berge *et al.* 1998).

### THE ROLE OF GENE FLOW

The negative effects of fragmentation mentioned above can be counteracted by gene flow through either seeds or pollen from neighbouring populations. Gene flow is crucial for the maintenance of high levels of genetic variation in small and isolated populations (Levin 1988; Ellstrand 1992a). The extent of gene flow varies largely among species (Ellstrand 1992a) and is mostly dependent on breeding and mating systems of the different species (Berge *et al.* 1998). Normally outcrossing species might be more susceptible to a reduction in vitality and vigor due to a increased selfing and inbreeding with close relatives in isolated populations, compared to species with a high incidence of selfing and inbreeding (Fischer & Matthies 1997). Irrespective, the importance of gene flow and its rapid reduction with increasing distance is undisputed, but an estimate for the maximum dispersal distance of single propagules is difficult to arrive at (Ellstrand 1992a). The likelihood of reduced gene flow over larger distance leads us to focus on the relationship between geographical isolation and population structure, fitness and genetic variability of populations.

We also include the seed bank in our study, because it is thought that dormant seeds in the soil can compensate for the lack of gene flow. Seeds of other genotypes than those present in the vegetation can be stored in the seed bank for a long time. However, the exact contribution of the seed bank in counterbalancing the effects of habitat fragmentation is still unclear (Husband & Barrett 1996).

### DOMINANT SPECIES

The focus of research on the consequences of habitat fragmentation has mainly been on rare, attractive, sparsely distributed or endangered plant species such as *Gentianella germanica* (Fischer & Matthies 1997, 1998), *Salvia pratensis, Scabiosa columbaria* (Ouborg *et al.* 1991; van Treuren *et al.* 1991, 1993; Ouborg & van Treuren 1994) and *Gentiana pneumonanthe* (Oostermeijer *et al.* 1992, 1994a,b, 1995). However, the severe effects of habitat fragmentation need not to be restricted to rare species only. Abundant species can be subject to similar effects, although mechanisms involved may differ (Eriksson 1996). Recent models by Tilman and co-workers (Tilman *et al.* 1994, 1997) indicate that dominant or abundant species should be among the first species to suffer from extinction through habitat destruction and fragmentation. Their main rationale is that dominant species are good competitors but among the poorest dispersers. The latter trait reduces their chances of gene flow and establishment following fragmentation and habitat destruction. This conclusion contrasts with the view that extinction risk is greatest in rare species.

Tilman's model has not yet been tested in the field and has been challenged on several grounds. According to Loehle & Li (1996), the model is very dependent on the individual mortality rate and is limited to cases in which the scale of habitat destruction is comparable to the patch size and the dispersal distances of individuals. Irrespective of the outcome of

this controversy, the decline of dominant species will influence the functioning of the total community, leading to a destabilization and a potential loss of the ecosystem functioning akin to the "keystone effect", as defined by Power et al. (1996). Dominant species form the matrix of the community and may support and shelter other organisms. Therefore, a serious decline in dominant species may lead to the subsequent extinction of rare and endangered species. In addition the loss of dominant species will permanently alter a given community and its associated flora and fauna. Since most of the studies on the keystone effect were again done with animals, application of the results to plants is difficult.

EXPERIMENTAL APPROACHES

Generally spoken there are two different types of approaches in habitat fragmentation research, which make use of geographical distances between fragments. The first is an experimental approach employing artificially created fragments with strictly regulated, but small distances between patches and relatively small and regulated patch sizes (e.g. Holt et al. 1995; Baur et al. 1996). The second is a comparative approach making use of isolated natural populations without explicit distance and size criteria (e.g. Ouborg 1993; Kadmon & Pulliam 1993, 1995; Giles & Goudet 1997; Groom 1998).

(1) The experimental approach employs artificial fragments of different sizes, created by regular mowing between fragments (Holt et al. 1995; Baur et al. 1996). Distances between fragments are relatively small and the sizes of the fragments differ by several orders of magnitude. In Baur et al.'s study (1996) isolation distances of 5 m between fragments were used, with fragment sizes of 0.25–20.25 m². Holt et al.

(1995) used isolation distances of 15 m and fragment sizes of 32–5,000 m². This last size is comparable with that of the smallest habitat fragments in our design. Both studies share the disadvantages of very small isolation distances and a limited period of isolation, which is too short for genetic effects to become detectable. Nevertheless, Holt et al. (1995) observed a distinct decline in species richness as fragment size decreased.

(2) In the comparative approach, natural populations dispersed more-or-less randomly throughout the landscape are compared. Ouborg (1993) resampled natural populations of 15 species and calculated extinction rates based on historical records. The distance to the nearest occupied site (0.5–35 km) served as an explanatory variable. Using the metapopulation approach, Ouborg found that some species were clearly influenced by isolation. The classical island biogeography approach (MacArthur & Wilson 1967) did not reveal this influence. This lead Ouborg (1993) to conclude that the metapopulation approach, relating extinction probability to the distance to nearest occupied sites, is a more powerful tool in analyzing isolation effects than is the island biogeography approach. Groom (1998) examined natural populations of *Clarkia concinna* with isolation distances of tens of meters among populations. She found a severe reduction in gene flow among populations, although according to Levin (1988) these distances do not preclude gene flow. Kadmon & Pulliam (1993, 1995) monitored plant colonization and extinction on natural islands in a lake formed in 1954. The distance range to the mainland (=shoreline) was 20–816 m (av-

erage 268 m), with island sizes of 0.28–0.84 ha. Species richness of disturbed islands was negatively related to the degree of isolation, whereas species identity was dependent on dispersal properties. Similar to Kadmon & Pulliam (1993, 1995), Giles & Goudet (1997) surveyed 52 newly created island in the Gulf of Bothnia, formed by land uplift. They studied genetical differentiation of *Silene dioica* between islands related to island age and included isolation by distance in a subsample of islands. More isolated islands were genetically more differentiated, caused by a lack of seed and pollen flow.

In relation to the experimental approach (1), the comparative approach (2) has the advantage that it incorporates both a historical component and actual isolation effects in the landscape. The disadvantage is, however, that there is no uniformity in isolation distances and that they may be confounded with other unmeasured variables.

Unfortunately, the majority of conservation-oriented studies on the effects of habitat fragmentation on plant population dynamics have focussed on population size, rather than on isolation (Ellstrand & Elam 1993), or they have addressed isolation indirectly (cf. Fischer & Stöcklin 1997). A notable exception was the study of Goodell *et al.* (1997), who separated the effects of population size and isolation in experimentally established populations of *Raphanus*. They were able to show that both factors regulated the gene flow.

## Perspectives for research

So far we outlined the potential consequences of habitat fragmentation on plant populations, namely reduced reproductive output and

growth, as well as inbreeding and genetic drift, which can eventually lead to population extinction. These effects are reasonably well described for rare plants, but not for abundant species. Yet these species may be among the first to suffer extinction, which could destabilizes the whole community (Tilman *et al.* 1994, 1997). Consequently, our main research objective aimed at addressing these deficits can be stated as: *Does geographical isolation due to habitat fragmentation significantly reduce the possibilities of long-term survival of isolated populations of dominant plant species?*

An experimental design, making use of the metapopulation approach, is preferable to the classical island biogeography models for detecting isolation effects (Ouborg 1993). However, the prerequisites for metapopulation dynamics, the extinction and colonization of sites, are unrealistic for dominant species, as the extinction of keystone species is usually associated with the loss of colonizable habitats. Our experimental design therefore resorts to an intermediate approach, containing elements of both metapopulation dynamics and island biogeography, namely mainland-island models (Wright 1943; Gotelli 1991; Harrison & Hastings 1996) in a hierarchical, spatially controlled field design, consisting of large islands with adjacent and remote small islands, based on explicit distance and size criteria.

## The study system

### VEGETATION TYPE

The vegetation type we chose are the highly fragmented calcareous pre-alpine fens (Caricion davallianae) of Switzerland. Since 1850, about 90% of all Swiss wetlands have disappeared due to human activities. Nearly 50% of all the threatened plant species of Switzerland occur

in fens (BUWAL 1990). In addition, fens harbor a number of rare and endangered specialist insect species (e.g. grasshoppers and butterflies, Wettstein 1998). Although most large areas are now protected, many small sites are not, and they are thus subject to continued fragmentation and degradation due to agricultural activities. With our study, we want to contribute to a better understanding of the possible consequences of this ongoing deterioration of wetlands. Our aim is to develop better management instruments for protecting the small islands with sustainable populations. We use a hierarchical spatial design (fen systems) with large and small fens, as habitat islands in the landscape to study the effects of geographical isolation on four dominant species.

FEN SYSTEMS

In our approach, fragmented pre-alpine fens are viewed as a field representation of the mainland-island model (Wright 1943; Gotelli 1991; Harrison & Hastings 1996). In these models, the dispersal of both seeds and pollen from large to small sites (islands) insures the long-term survival of local populations (Eriksson 1996), and losses in genetic variation due to genetic drift and inbreeding may be compensated. In cases where dispersal among populations is severely hampered due to fragmentation, an isolated population on a small habitat island may be on its way to extinction (Harrison & Hastings 1996). According to published data (Levin 1988), gene flow through either seeds or pollen becomes extremely rare at distances >1,000 m and can be significantly reduced at distances of several tens of meters (Primack & Miao 1992; Morris 1993; Williams 1994; Groom 1998). However, there have also been some reports of sporadic gene flow into islands separated by thousands of meters (Ellstrand 1992b).
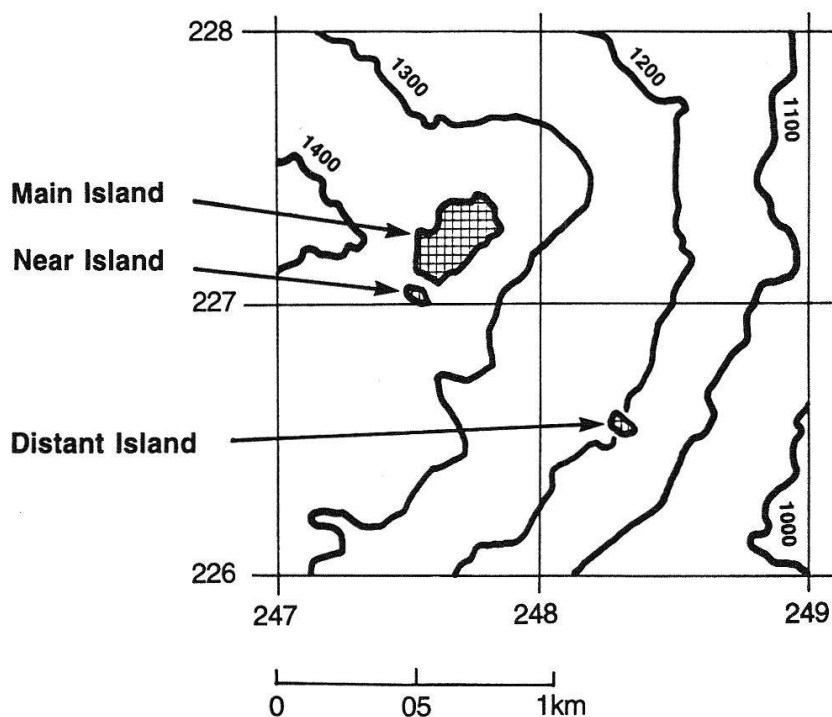


Fig. 1. The fen system Grabs (Canton St.Gallen), with its "mainland", "near" and "distant" islands. Fen sites are directly drawn on the map. Except for altitudinal markers all other map attributes are erased. Cutout of the Swiss map 1: 25'000, no. 1135; reproduced by permission of the Swiss Federal Office of Topography, 25 March 1999.

*Table 1.* Name, island size and isolation distances of the small islands to the mainland of the six study sites in the research project

| Site (Canton) | Code (see Fig. 2) | Island type | Island size (ha) | Distance to mainland (m) |
|---|---|---|---|---|
| Ebnat-Kappel (SG) | EK | Main | 4.28 | – |
| | | Near | 0.54 | 106 |
| | | Distant | 0.20 | 750 |
| Nesslau (SG) | NE | Main | 5.00 | – |
| | | Near | 0.30 | 52 |
| | | Distant | 0.20 | 800 |
| Grabs (SG) | GR | Main | 5.73 | – |
| | | Near | 0.20 | 45 |
| | | Distant | 0.45 | 800 |
| Wildhaus (SG) | WH | Main | 5.45 | – |
| | | Near | 0.57 | 40 |
| | | Distant | 0.52 | 925 |
| Alpthal (SZ) | AT | Main | 7.47 | – |
| | | Near | 0.20 | 44 |
| | | Distant | 0.87 | 1825 |
| Sattel (SZ) | SA | Mainland | 6.68 | – |
| | | Near | 0.22 | 60 |
| | | Distant | 0.57 | 800 |

Keeping those gene flow distances in mind, we selected a total of six systems of fens in NE-Switzerland, each containing three "natural" habitat islands. The "main" island (mainland) in all systems is a large fen, usually larger than 5 ha. Two selected islands surround this main island. They are preferably smaller than 0.5 ha and have two different levels of geographical isolation. The first island is located at 25–100 m distance from its main island and is termed "near". It is assumed to have a reduced but still sporadic gene flow from the main island. The second island, termed "distant", is located approximately 1,000 m from the main island. We assumed that the distant island had no seed and pollen flow from either the main island or other (more distant) sites, and was thus most liable to a reduction of population fitness and decreased genetic variability. Most sites were separated by either pastures or (planted) forest strips. A summary of the sizes and the extent of geographical isolation of the six fen systems is contained in Table 1. Given the strict spatial requirements we imposed, i.e. the distance between islands and the size of the islands, this number is the maximum number of suitable fen systems we found in the study area. One of these systems is depicted in Fig. 1.

All fens are mown once a year (mostly around mid September) and not grazed. The altitudinal range was restricted to 900–1400 m a.s.l., coinciding with the center of distribution of these wetlands. To allow analysis of regional effects, we assigned pairs of fen systems to three different areas of NE-Switzerland as can be seen in Fig. 2. Within each of the islands all experiments will be carried out on five randomly selected plots (1 m x 5 m).

## STATISTICAL ANALYSIS

The described set-up enables us to analyze fragmentation effects over several spatial scales, i.e. from the plot and the (fen) system

level to the regional level. We include a skeleton ANOVA model of our hierarchical design similar to Fischer & Stöcklin (1997) and Fischer & Matthies (1997) in Table 2. Regions, systems and island types (degree of isolation: main, near or distant islands) are seen as fixed factors. Island types are considered to represent different treatments with six replicates and are thus not nested within the systems. This factor can be decomposed into two contrasts, each with one degree of freedom, namely (1) main *versus* near and distant islands and (2) a within small island contrast (near *versus* distant sites – not included in Table 2). The plot level can be tested if individual plants, located in plots, are added to the analysis (not included in the skeleton ANOVA). In addition, suitable covariables can be incorporated in the analysis, of which population size is the most obvious choice, since island sizes need not be proportional to population sizes of a given species. Furthermore, we will attempt to find out the history

of the different sites with regard to the isolation period, which can be incorporated as an additional covariable.

## TARGET SPECIES

The species we work with are abundant in Swiss calcareous fens and for the most part also common throughout Switzerland (Table 3). The four target species are: *Carex davalliana* SM. (Cyperaceae), *Succisa pratensis* Moench. (Dipsacaceae), *Swertia perennis* L. (Gentianaceae) and *Tofieldia calyculata* Wahlenb. (Liliaceae); nomenclature follows Binz & Heitz (1990).

*Carex davalliana* is the dominant and characteristic graminoid species of these calcareous fens. Like in other clonal Cyperaceae, *C. davalliana* has low seedling establishment (Maas 1988) resembling the K-strategy at the genet level (Schmid 1984, 1986). *Carex davalliana* is diecious with individual tillers attaining about 10–30 cm in height. Flowering occurs in April–May, just after melting of the
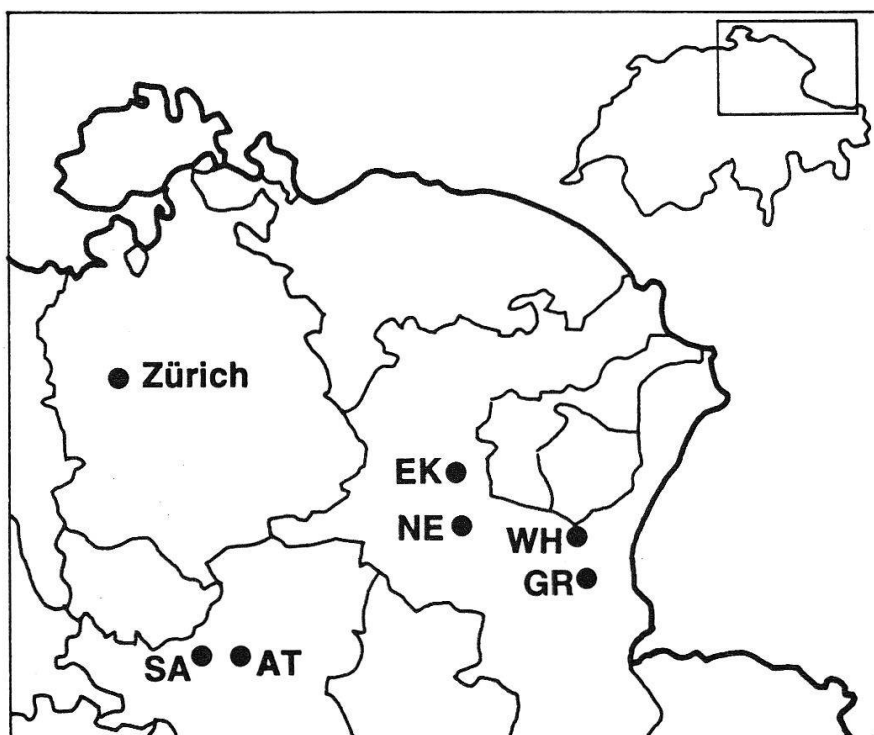


*Fig. 2. Location of the six fen systems in NE-Switzerland. For explanation of the symbols see Table 1.*

***Table 2.*** *Skeleton ANOVA model for testing the effects of isolation on demographic, survival and establishment characteristics (factors in normal format,* covariables in italics*)*

| Source of variation | df | Mean squares | F |
|---|---|---|---|
| Region (R) | 2 | $M_r$ | $M_r/M_s$ |
| System (nested in region) (S) | 3 | $M_s$ | $M_s/M_{sit}$ |
| *Population size (PZ)* | 1 | $M_{pz}$ | $M_{pz}/M_{sit}$ |
| Island type (IT) | 2 | $M_{it}$ | $M_{it}/M_{sit}$ |
| R x IT | 4 | $M_{rit}$ | $M_{rit}/M_{sit}$ |
| S (nested in R) x IT (= population) | 6 | $M_{sit}$ | $M_{sit}/M_{res}$ |
| Residual (RES) (= plots) | N-19 | $M_{res}$ | |

***Table 3.*** *Brief overview of differences between the four study species, regarding life form, plant height, seed maturation time and distribution in Swiss fens (Binz & Heitz 1990) and throughout Switzerland (Lauber & Wagner 1998)*

| | Life form | Inflorescence height | Seed maturation * | Seed output † | Distribution | |
|---|---|---|---|---|---|---|
| | | | | | Swiss fens | Switzerland |
| *Carex davalliana* | Graminoid | 10–30 cm | VI–VII | 5–20 | Abundant | 68% |
| *Succisa pratensis* | Forb | 20–80 cm | IX–X | 40–150 | Abundant | 48% |
| *Tofieldia calyculata* | Lily | 10–30 cm | VII–VIII | >500 | Abundant | 72% |
| *Swertia perennis* | Forb | 15–50 cm | IX | >500 | Locally abundant, overall rare | 11% |

* Calendar month; † seeds per inflorescence, own observations in 1998.

snow cover. Tillers exist probably for 2–3 years in a vegetative state and die after reproduction, as typical for *Carex* (Schmid 1984).

*Succisa pratensis* is a long-lived forb with occasional clonal growth (daughter ramets are formed at the base of the rosette), well known from previous studies (e.g. Adams 1955; Pegtel 1986). Aside from fens, *S. pratensis* also occurs in heaths and other nutrient-poor habitats. In our fens it is the dominant forb species. With a height of about 20–80 cm its bright purple flower heads form the upper canopy. *Succisa pratensis* is a keystone species for phytophagous insects (Di Giulio 1996). Because of the late flowering (August–September), recruitment of this species can be hampered when fens are mown before seed maturation.

*Tofieldia calyculata* is a subdominant clonal lily with appressed rosettes. It occurs primarily in fens and wet grasslands. The flower stalks with alternate leaves reach a height of about 10–30 cm and have light-yellow inflorescences. In our fens flowering occurred in June–July in 1998.

*Swertia perennis* is a rare but locally abundant long-lived forb with a very distinct regional distribution from NE- to SW-Switzerland (Welten & Sutter 1982; Table 3). It grows in calcareous fens and very wet grasslands. The vegetative adult stage with leaves in a rosette, can occasionally initiate daughter ramets.

Flowering plants reach a height of about 15–50 cm and produce very distinct purple, star-like flowers in a thyrse. The flowering period is around July–August. As in *S. pratensis,* early mowing can prevent recruitment of *S. perennis* because of late seed maturation.

All investigations described below will be carried out with the first three species, whereas only the descriptive ones will be conducted with *S. perennis,* because it did not occur in all fens and is not a consistently dominant species (Table 3). Since differences in species strategies can result in large differences in the reaction to fragmentation (Berge *et al.* 1998), we will record several aspects of the life strategy of the species. In addition, we will attempt to discern the breeding and mating systems of the different species and the type of seed bank they have. Table 3 gives a brief overview of the differences among the four species regarding life form, inflorescence height, seed output, maturation and distribution in fens and throughout Switzerland.

Throughout this study a plant population is defined as all individuals of a species occurring in a habitat island. Because every species occurs on each island, 18 populations exist for each of the four species, except for *S. perennis,* which grows in 17 out of the 18 sites. However, because plant densities vary among islands, population sizes are not strictly proportional to island sizes. This fact needs to be taken into account in the data analysis, e.g. by using population size as a covariable.

RESEARCH QUESTIONS AND EXPERIMEN-
TAL OUTLINE

We will examine the effects of habitat fragmentation on long-term persistence of the target species by focussing on three topics associated with population dynamics (demography, seed bank composition, experimental

seedling establishment) and a fourth one dealing with genetic characteristics of populations. Leading questions (in italics) and experimental protocols are briefly summarized below.

(1) Effects of isolation on demographic traits and population structure.
*Do establishment, growth and survival of individual plants within a population decline with increasing isolation?*
*Does geographical isolation have a significant effect on the life-stage structure within a population and the transition rates between these stages?*
We monitor the demographic structure of populations and observe randomly selected individuals for survival and life stage transitions over a 3-yr period. Other measures include population size, seed production and seed viability, which will be incorporated into transition matrices and population models.

(2) Effects of isolation on the seed bank and its buffering capacity.
*Does the quantity of viable seeds in the seed bank change in response to isolation?*
*Is the seed bank able to store genotypes other than those present in the standing vegetation?*
To address these questions, 25 soil samples were taken per site (*c.* 125 cm$^3$ per sample). We monitor the number of emerging seedlings, as an estimate of the number of viable seeds in the soil, over a 2-yr period in a common garden. A subsample of seedlings can be used to conduct allozyme electrophoresis to test for genotypic differences between seed bank and standing vegetation. This comparison will define the role of the seed bank in storing genotypes not present in the vegetation.

(3) Effects of isolation on experimental establishment of seedlings.

*Do seeds and seedlings from isolated sites have a lower establishment potential than seeds from main islands as a result of inbreeding?*

Two approaches will be utilized here to examine two critical life history stages, namely seed germination and establishment. First, we reciprocally transplanted seeds in and among islands within systems, into plots of 400 cm². The seedlings emerging in these plots are counted and followed to test whether seeds from main islands have higher fitness with respect to germination and establishment. Secondly, seedlings will be transplanted reciprocally among sites within a system. Establishment, survival, growth and fecundity will be examined over a 2-yr period. We assume that this artificial gene flow will not influence the population genetic structure within the limited time-span of the experiment. In addition, seeds and seedlings of all fen sites will be planted in a common garden, without competition from other plants. We will measure the same parameters as in the field sites to examine regional and site-specific (genotypic) differences in plant performance.

(4) Effects of isolation on genetic characteristics.

*Does genetic variation decline in populations on small islands compared with large populations on main islands?*

*Do inbreeding level and inbreeding depression increase with increasing distance from the main island?*

*Is there a correlation between the genetic structure and fitness as measured by the demographic variables at the population level?*

The level of heterozygosity, the proportion of polymorphic loci and the number of alleles per locus are being evaluated with allozyme electrophoresis (*T. calyculata* and *S. perennis*) and microsatellite analyses (*C. davalliana* and possibly *S. pratensis*) on a selection of 30 plants per population. These genetic characteristics will be correlated with the results of the studies on growth, reproduction and survival of individuals in established populations (topic 1) and of transplanted seeds and seedlings (topics 2–3).

In summary, the results of observations and experiments, focussing on the population dynamics and genetic characteristics of contiguous and isolated populations, will provide an understanding of how geographical isolation affects long-term survival of dominant fen species. We believe that the use of a hierarchical spatial design in the natural landscape, as proposed here, is particularly important, since it combines the advantages of both experimental and comparative approaches to habitat fragmentation. Our study is based on an experimental design with relevant isolation distances, which is novel for comparative studies. The landscape setting incorporates historical effects of isolation, which are manifested in the demographic and genetic characteristics of populations, not contained in strictly experimental approaches (cf. Holt *et al.* 1995; Baur *et al.* 1996).

The effects of habitat fragmentation have so far not been examined specifically with dominant species. In light of the "keystone effect" (Power *et al.* 1996), our study addresses an unknown, yet vital question in habitat fragmentation research: Are populations of dominant or abundant species with the capacity for clonal growth impaired by geographical isolation? Furthermore, ele-

ments of Tilman's prediction, that dominant species may be among the first to suffer from habitat disturbances, can be tested with four species, which differ in physiognomic and reproductive traits.

Finally, our study touches on a real-life conservation issue, namely whether dominant plant populations in small, highly isolated fens are self-sustainable in the long-term or not. In the latter case, it is likely that these communities will ultimately cease to exist. Information on establishment success of experimentally introduced seeds and seedlings may help to provide a possible management tool to improve and maintain the genetic diversity and fitness of isolated populations, thereby alleviating the adverse effects of habitat fragmentation.

## Acknowledgments

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