2012

Process-based long-term evaluation of an ecological network of calcareous grasslands

Post-print/Accepted manuscript

Helene H. Wagner

Henry Lehnert

Yessica Rico

Hans Juergen Boehmer

Wagner, H. H., Rico, Y., Lehnert, H. and Boehmer, H. J. (2013), Process-based long-term evaluation of an ecological network of calcareous grasslands connected by sheep herding. *Ecography*, 36: 374–382. doi:10.1111/j.1600-0587.2012.07463.x

This is the peer reviewed version of the following article: Wagner, H. H., Rico, Y., Lehnert, H. and Boehmer, H. J. (2013), Process-based long-term evaluation of an ecological network of calcareous grasslands connected by sheep herding. *Ecography*, 36: 374–382, which has been published in final form at [doi:10.1111/j.1600-0587.2012.07463.x](https://doi.org/10.1111/j.1600-0587.2012.07463.x) This article may be used for non-commercial purposes in accordance with [Wiley Terms and Conditions for Self-Archiving](#).

HOW TO CITE TSPACE ITEMS

Always cite the published version, so the author(s) will receive recognition through services that track citation counts, e.g. Scopus. If you need to cite the page number of the TSpace version (original manuscript or accepted manuscript) because you cannot access the published version, then cite the TSpace version **in addition to** the published version using the permanent URI (handle) found on the record page.

**Process-based long-term evaluation of an ecological network of
calcareous grasslands**

Helene H. Wagner (corresponding author), University of Toronto, Department of Ecology and
Evolutionary Biology, 3359 Mississauga Road, Mississauga, Ontario L5L 1C6, Canada. Phone:
+1-905-569-4702, fax: +1-905-828-3792, email: helene.wagner@utoronto.ca

Henry Lehnert, University of Bonn, Interdisciplinary Latin America Center (ILZ), Walter-Flex-
Str. 3, D-53113 Bonn, Germany. Phone: +49-228-734900, fax: +49-228-731789, email:
lehnert@uni-bonn.de

Yessica Rico, University of Toronto, Department of Ecology and Evolutionary Biology, 3359
Mississauga Road, Mississauga, Ontario L5L 1C6, Canada. Phone: +1-905-569-4696, fax: +1-
905-828-3792, email: yessica.rico@utoronto.ca

Hans Juergen Boehmer, University of Bonn, Interdisciplinary Latin America Center (ILZ),
Walter-Flex-Str. 3, D-53113 Bonn, Germany, and Technical University of Munich, Department
of Ecology and Ecosystem Management, Landscape Ecology (LOEK), Emil-Ramann-Strasse 6,
D-85350 Freising-Weihenstephan, Germany. Phone: +49-228-734901, fax: +49-228-731789,
email: HJ.Boehmer@uni-bonn.de

Abstract

This paper evaluates the long-term effect of an ecological network of calcareous grasslands, a habitat type that experienced dramatic habitat loss and fragmentation during the 20th century. Calcareous grasslands are of special conservation concern as the habitat type with the highest diversity in plant and invertebrate species in Central Europe. A baseline survey in 1989 established complete vascular plant species lists for all 62 previously abandoned calcareous grassland patches in the study area and assessed the presence of 48 habitat specialist plant species. An ecological network was initiated in 1989 to reconnect these patches with existing core areas through large flock sheep herding where feasible, as sheep are thought to be the primary dispersal vectors for calcareous grassland plants. An evaluation survey in 2009 showed significant increase in species richness of habitat specialist plants in patches reconnected by sheep herding, indicating successful colonizations by habitat specialist plant species, while ungrazed patches showed no significant change. Baseline species richness after abandonment was associated with patch area and vegetation type, suggesting that extinction delays depended on asymmetry of competition with later seral species, whereas subsequent increase in species richness was related to connectivity by sheep herding and the presence of a diversity of structural elements providing microsites for establishment. The implementation of this ecological network represents a long-term ‘natural experiment’ with baseline data, manipulation, and evaluation of hypothesized effects on a clearly defined target variable. It thus provides much needed empirical evidence that species loss in fragmented calcareous grassland communities can be counteracted by restoring functional connectivity among remnant patches.

42 **Keywords**

43 Biodiversity, colonization, connectivity, extinction, fragmentation, Franconian Alb, Germany,
44 grazing, habitat loss, natural experiment.

Introduction

The promotion of ecological networks for conservation management in human altered landscapes relies on the assumption that corridors and stepping stone habitats increase the exchange of target species among local populations, thus facilitating the persistence of metapopulations and preserving biodiversity at a landscape scale (Bennett and Wit 2001, Opdam et al. 2006, Boitani et al. 2007). While habitat networks are aimed at a single target species, ecological networks target ecosystems and their ecological communities, and thus have been defined as “*a set of ecosystems of one type, linked into a spatially coherent system through flows of organisms, and interacting with the landscape matrix in which it is embedded*” (Opdam et al. 2006, p 324). Using ecological networks as a conservation management strategy thus implies that functional connectivity among patches in terms of the exchange of individuals of many target species is a key determinant of biodiversity, and that connectivity may depend not only on the physical distance between patches but on how well organisms are able to traverse the intervening matrix (Taylor et al. 2006, Fahrig 2003).

Ecological networks aim to counteract negative effects of habitat fragmentation on biodiversity. Habitat fragmentation typically results in smaller and more isolated patches (Fahrig 2003). Theoretical expectations of the effects of habitat fragmentation on biodiversity and species persistence are often derived from island models (Haila 2002), which predict that equilibrium species richness of local communities depends on patch size and patch isolation, where larger patches are expected to have lower extinction rates (area effect) and more isolated patches lower immigration rates (isolation effect) as observed at the levels of either species (MacArthur and Wilson 1967) or individuals (Hubbell 2001). Theoretical and empirical results from spatially

explicit metapopulation theory suggest that extinction rate of local populations is a function of patch area, whereas the rate of colonization of empty patches of suitable habitat is proportional to patch connectivity (Hanski and Ovaskainen 2003).

Economic or social constraints often preclude biodiversity management by increasing habitat area or changing habitat spatial configuration (Taylor et al. 2006). Alternative conservation management strategies should recognize the limitations of theoretical predictions from island models for complex heterogeneous landscapes and focus on the suite of ecological processes that maintain biodiversity in the landscape (Taylor et al. 2006). As summarized above, ecological theory identifies extinction and immigration / colonization as key processes, but the equilibrium assumption may rarely hold in cultural landscapes that are dominated by human land use. Empirical studies of fragmentation effects thus need to accommodate transient dynamics related to delays in extinction or colonization. Similarly, the intervening matrix cannot be assumed homogeneous but likely contains different cover types, which will affect movement behavior and dispersal rates of organisms. Hence, functional connectivity may also be increased by managing the matrix (Taylor et al. 2006).

The empirical base regarding fragmentation effects on biodiversity is strongly biased towards mammals and birds (Fischer and Lindenmayer 2007). True experiments that test the effect of habitat fragmentation on vegetation are rare (Debinski and Holt 2000), and such experiments often are limited to spatial scales too small to inform real-world resource management and conservation (Lindenmayer 2009). Ecological networks represent long-term ‘natural experiments’, where habitat fragmentation is manipulated but is not fully controlled by the researcher. A lack of randomization may introduce bias related to confounding variables, and

the scientific evaluation of ecological networks is often limited by the lack of baseline data, empirically testable targets and hypothesized effects because evaluation was not anticipated at the time of establishment (Wagner et al. 2007). Paradoxically, governments and conservation agencies are investing major resources in maintaining or enhancing landscape connectivity, but it is rare that actual connectivity in terms of colonization events or dispersal patterns is evaluated after ecological networks have been established (Boitani et al. 2007, Kareiva 2006).

In recent decades, cultural landscape change in Europe led to a widespread loss of calcareous grasslands (Poschlod and WallisDeVries 2002). Calcareous grasslands typically are nutrient poor, unfertilized and free of herbicide or pesticide application and thus provide important refugia for plant and animal species in an otherwise intensively used agricultural landscape (Green 1972). Abandonment of calcareous grasslands, followed by shrub encroachment and natural reforestation (Hakes 1987), results in a grave loss of diversity of flora and fauna (Butaye et al. 2005). In many landscapes, formerly widespread calcareous grasslands are reduced to small and isolated fragments (e.g. Boehmer 1994, Beinlich and Plachter 1995, Bender et al. 2005).

Here we evaluate the long-term effect of an ecological network, which was initiated in 1989 to restore calcareous grassland connectivity by large-flock sheep herding, on the species richness of habitat specialist plants, based on a baseline survey in 1989 and an evaluation survey in 2009. Empirical comparison of alternative connectivity models for this data set showed strong support for sheep herding as the main seed dispersal vector (Rico et al. 2011). We hypothesize that the effect of abandonment, i.e., baseline species richness in previously abandoned patches, is primarily related to patch area and to factors delaying extinction, whereas the effect of the

ecological network, i.e., net change in species richness between the two surveys, is primarily related to patch geographic isolation, connectivity by sheep as dispersal vectors, and factors promoting establishment of propagules. We test for potential bias introduced by non-random assignment of grazing treatments. We thus use this ecological network as a ‘natural experiment’ to assess whether species loss in calcareous grassland communities can be counteracted by restoring functional connectivity among remnant patches.

Materials and methods

Study area

The study area of approx. 10 x 15 km is located in the southern Franconian Alb near Weissenburg, Bavaria, Germany (see Appendix S1 in Supporting Information). Altitude varies between 410 m (lower Jurassic valleys) – 630 m (upper Jurassic limestone plateaus), with a mean annual precipitation of 665 mm and mean annual temperature of 8.1 °C measured at Weissenburg.

Forest cover in the Franconian Alb increased between 1900 and 1960 from 18% to about 40%. Reforestation by natural succession mostly occurred on abandoned pastures, which declined from 15% to about 1% today (Bender et al. 2005). In the study area, this caused a dramatic loss of 67 % of calcareous grassland habitat from 970 ha in 1830 to 302 ha in 1989 (Dolek and Geyer 2002).

Ecological network established since 1989

In 1989, a pilot project was initiated in the study area to create an ecological network with a system of corridors to re-connect many of the previously abandoned grassland patches with remaining core areas in three non-overlapping transhumant sheep herding systems (Appendix S1), as sheep are thought to be the primary dispersal vectors of calcareous grassland plants (Fischer et al. 1996). Each sheep herding system includes up to 140 ha of calcareous grasslands, which are grazed 3 – 5 times per year, typically for not more than a day at a time, throughout the vegetation period. Each of the present-day sheep herding systems, with sheep herding routes of up to 55 km, spans across several municipalities that historically used to have their own smaller-scale herding systems. Herd sizes range from 400 to 800 ewes (approx. 1000 including lambs), and two of the three herds contain 5 % goats to prevent shrub encroachment.

Baseline and evaluation field surveys

As a basis for the establishment of this ecological network, Boehmer et al. (1990) conducted a baseline survey of all existing pastures ('core areas') or previously abandoned calcareous grasslands ('abandoned patches') in the study area (Appendix S1), including any area of at least 25 m² with remnants of *Gentiano-Koelerietum pyramidatae* vegetation, the typical plant community of grazed calcareous grassland in the Franconian Alb region (gentian-hairgrass turf; Oberdorfer 1978). For all 62 previously abandoned patches, they assessed several patch characteristics that were included in the present analysis as follows (Fig. 1, Appendix S2): (i) Patch area (*PatchArea*) was recorded in five size classes: 1 = < 25 m², 2 = 25 – 100 m², 3 = 100 – 400 m², 4 = 400 – 2500 m², and 5 = > 2500 m². (ii) The baseline survey classified patches into seven sub-types of calcareous grassland vegetation representing alternative facies during early

stages of secondary succession following abandonment: A = grass dominated, B = with tall herb components, C = with forest edge components, D = with xeric components, E = with wetland components, F = with eutrophic components, and A/C = open pine groves. We used *VegetationType* as a proxy for strength of competition with later seral species that may moderate extinction rates (Fig. 1). Type E contained a single patch (A55) and had to be dropped from some analyses. (iii) We defined *Elements*₁₉₈₉ as the number of dynamic structural elements present that provide microsites for the establishment of habitat specialist plant species and thus may increase colonization rates: rock debris, erosion, anthills, and small mammal burrows.

From a complete list of vascular plant species with Braun-Blanquet abundance information collected for each previously abandoned patch during at least three visits in summer and fall of 1989 and spring of 1990, Boehmer et al. (1990) assessed the number of habitat specialist plant species present (*Richness*₁₉₈₉). The list of 48 habitat specialist species (see Appendix S2) was based on the vegetation classification system for Central Europe (Oberdorfer 1978) and verified by a survey of 11 core areas. Baseline data for the core areas are preserved only in terms of the frequency of occurrence of each species among the 11 sampled core areas.

For the evaluation survey, the 62 previously abandoned patches included in the baseline survey were revisited at least three times during summer 2008 and spring and fall 2009 to assess the occurrence and population size of each of the 48 habitat specialist species. Change in species richness of habitat specialist plants was expressed as $RelativeChange = (Richness_{2009} - Richness_{1989}) / (48 - Richness_{1989})$ so as to scale the observed net number of colonizations by the maximum possible net number of colonizations for each patch. Structural elements were recorded

again in the field in 2009 and *Elements*₂₀₀₉ was defined analogous to *Elements*₁₉₈₉. Patches were digitized from orthophotos in ArcGIS 9.3.

With the exception of *Euphrasia stricta*, the habitat specialists plants considered here (Appendix S3) are perennial, and most are known to lack a persistent seed bank (Thompson 1997, Poschlod et al. 2003). Repeated visits by different observers suggested that all species could be reliably detected and identified even vegetatively, except for *Allium oleraceum*. Consistency between surveys was high, as both surveys were carried out by the same scientist (all visits in the baseline survey and at least one of the visits of each patch in the evaluation survey). However, baseline summer surveys were carried out in late summer 1989, which may have decreased detection probability of species that flower in early summer, specifically, *Ajuga genevensis*, *Leontodon hispidus*, *Linum catharticum* and *Ranunculus bulbosus*. We assessed sensitivity to assumptions on seed bank and detectability by repeating analyses without species with potential issues as listed above.

Grazing treatments 1989 – 2009

Grazing management 1989 – 2009 and sheep herding routes were reconstructed for each patch based on archive records, detailed maps of sheep grazing systems, and shepherd interviews. Out of the 62 previously abandoned patches, 26 were ‘consistently grazed’ since the initiation of the ecological network in 1989 and 23 remained ‘ungrazed’ (Appendices 1, 2). The remaining 13 patches were ‘intermittently grazed’, which means that they were only grazed for a few years or only later in the season after crops have been harvested. According to the archive records, shrub clearing occurred on five of the ‘intermittently grazed’ patches, but only on one of the

‘consistently grazed’ and two of the ‘ungrazed’ patches (Appendix S2), representing very small proportions in these groups. Hence clearing was not considered separately in subsequent analysis.

Patch isolation and sheep herding connectivity

Patch isolation was quantified for each patch i with ArcGIS using connectivity index S_i (Hanski 1994) defined as:

$$PatchIsolation = \sum e^{-\alpha d_{ij}} p_j,$$

where α is a constant scaling parameter with value $\alpha = 0.2$ based on optimization in (Rico et al. 2011), d_{ij} is the Euclidean distance (in km, center to center) from focal patch i to any previously abandoned source patch or core area $j \neq i$, and p_j is the mean patch occupancy of source patch j for the 48 habitat specialist species, i.e., $Richness_{1989} / 48$. Note that high values of S_i indicate low isolation. We included all core areas and previously abandoned patches as potential sources, as the species richness of some patches was comparable to core areas. Preliminary analysis showed that when source patch area A_j was included in the calculation of *PatchIsolation*, model performance decreased, hence we did not include A_j .

Sheep herding connectivity *SheepConnectivity* = $\sum e^{-\alpha d_{ij}} p_j$ was quantified based on the best model identified in (Rico et al. 2011), using the same formula as for *PatchIsolation* but defining distance d_{ij} as the number of patches that the sheep would traverse on their route from source patch j to focal patch i , counting both ‘consistently’ and ‘intermittently’ grazed patches.

Data analysis

We expected that *PatchArea* is primarily related to ecological drift (Hubbell 2001), that *VegetationType* is related to delays in extinction e.g. due to reduced competitive advantage of

later seral species, and that both affect extinction rates of habitat specialist species (Fig. 1). Another set of factors was expected to affect the rate of colonization by habitat specialist species, either through propagule immigration (*PatchIsolation*, *SheepConnectivity*) or the availability of microsites for establishment (*Elements*, and *GrazingTreatment* through changes of habitat quality and gap creation). As patch species richness results from the combination of extinction and colonization rates, both sets of predictors were included to predict *Richness*₁₉₈₉ and *RelativeChange*. Hence, we fitted two full linear models:

Note that both full models include an area and an isolation effect. For each model, we used multi-model inference with the R (R Development Core Team 2010) library ‘MuMIn’ (Barton 2009) by fitting all subsets of the full model. The relative importance of each predictor was assessed by the sum of Akaike model weights w_i over all models that included the predictor (Burnham and Anderson 2002) based on a subset of models with cumulative weight of 0.95. For the best-ranked model, we performed residual analysis to check regression assumptions, assessed model fit with adjusted R^2 , and performed significance tests for regression coefficients.

In order to check for potential bias in terms of which patches were included in the ecological network, we used one-way ANOVA to test for a difference in mean *Richness*₁₉₈₉ among the three groups of patches defined by *GrazingTreatment*. Analysis was repeated for *PatchArea*, *PatchIsolation* and *Elements*₁₉₈₉. The association between *GrazingTreatment* and *VegetationType* was tested with Fisher’s exact test, a small sample alternative to the chi-square test of independence.

Results

Effect of abandonment

In the baseline survey, the 62 previously abandoned patches varied tremendously in *Richness*₁₉₈₉, with 3 – 37 of the 48 habitat specialist species present (mean = 18.8, SE = 0.8). The best ranked model (lowest AICc) contained the predictors *VegetationType* and *PatchArea*. Based on this model, the number of habitat specialist species present in 1989 increased significantly with patch size, whereas patches with eutrophic elements (Type F) or with forest edge elements (Type C) contained almost 9 habitat specialist species less on average than the reference group of grass-dominated sites (Type A; Appendix S4). Patches with xeric elements (Type D) tended to have higher *Richness*₁₉₈₉ (with almost 4 species more than Type A on average), though this effect was not significant possibly due to small sample size for this vegetation type (n = 5). For further analysis, we thus reclassified *VegetationType* into a new variable *VegetationType2* with ‘low patch quality types’ (C, F) and ‘high patch quality types’ (A, A/C, B, D).

The most important factors for explaining *Richness*₁₉₈₉ were *VegetationType2* (relative importance = 1.0) and *PatchArea* (1.0), followed by *Elements*₁₉₈₉ (0.43) and *PatchIsolation* (0.40). The best model (AICc = 385, *w* = 0.35) with predictors *VegetationType2* and *PatchArea* explained adj. $R^2 = 0.28$ of the variation in *Richness*₁₉₈₉. The residuals showed no major problems.

Interestingly, *PatchArea* had no significant effect on *Richness*₁₉₈₉ (p-value = 0.143, adj. $R^2 = 0.019$) in univariate analysis, but after accounting for *VegetationType2*, *PatchArea* was significant and increased model fit from adj. $R^2 = 0.18$ to 0.28 compared to a model with

VegetationType2 only (Fig. 2). *PatchIsolation* was not statistically significant in either univariate or multivariate analysis.

Overall effect of ecological network

Relative change in species richness, which indicates net colonization rate between baseline and evaluation surveys, differed significantly among the three grazing treatments (Fig. 3; one-way ANOVA, $df = 2$, $F = 16.5$, $p\text{-value} < 0.001$). ‘Ungrazed’ patches showed lower mean *RelativeChange* than previously abandoned patches that, after 1989, were ‘consistently grazed’ ($p\text{-value} < 0.001$) or ‘intermittently grazed’ ($p\text{-value} = 0.006$ Tukey’s test with family-wise $\alpha = 0.05$). Overall, ‘ungrazed’ patches did not show a significant change in species richness, i.e., mean *RelativeChange* was not significantly different from zero (one-sample t -test, $df = 22$, $t = 0.68$, $p\text{-value} = 0.501$).

Inclusion of previously abandoned patches into the ecological network was based on practical considerations rather than randomization, therefore we tested *a posteriori* for potential bias in terms of systematic differences between grazing treatments in baseline species richness or other patch characteristics (Appendix S5). Overall, grazing treatments differed significantly in *PatchArea* (one-way ANOVA, $df = 2$, $F = 3.84$, $p\text{-value} = 0.027$) and in *PatchIsolation* (one-way ANOVA, $df = 2$, $F = 6.96$, $p\text{-value} = 0.002$). Pairwise comparisons indicated that compared to ‘continuously grazed’ patches, ‘ungrazed’ patches were significantly smaller ($p\text{-value} = 0.042$), but showed clearly no significant differences in patch isolation ($p\text{-value} = 0.99$) (Tukey’s test with family-wise significance levels of $\alpha = 0.05$, Appendix S5). There was no significant association between grazing treatments and *Richness*₁₉₈₉ (one-way ANOVA, $df = 2$, $F = 2.12$, $p\text{-value} = 0.129$), *Elements*₁₉₈₉ (one-way ANOVA, $df = 2$, $F = 0.309$, $p\text{-value} = 0.735$), or

VegetationType2 (Fisher's exact test, p-value = 0.594; Appendix S5). Patch isolation was not correlated with any other predictor, but *VegetationType2* was positively associated with *PatchArea* and *Elements*₁₉₈₉ (Appendix S6), where low quality patches (Types C and F) were larger on average and had fewer structural elements than high quality patches.

Determinants of changes in species richness since 1989

The most important variables for explaining *RelativeChange* were *Elements*₂₀₀₉ (relative importance = 1.0), and *SheepConnectivity* (0.82), followed by *GrazingTreatment* (0.26), *PatchArea* (0.24), *VegetationType2* (0.23) and *PatchIsolation* (0.07). The best model (AIC = -45.3, $w = 0.42$) contained the predictors *Elements*₂₀₀₉ and *SheepConnectivity* and explained $\text{adj.}R^2 = 0.49$ of the variation in *RelativeChange* (Table 1), with well-behaved residuals. Repeating the analysis without eight species that may form a long-term persistent seed bank (Appendices 2 and 3), or without the five species with potential issues of detectability (*Allium oleraceum*) or consistency of detectability between surveys (*Ajuga genevensis*, *Leontodon hispidus*, *Linum catharticum* and *Ranunculus bulbosus*), did not change the nature or statistical significance of the results (Table 1).

Discussion

Effect of abandonment

In the first part, we compared species richness of habitat specialist plant species among 62 previously abandoned patches, which were abandoned at least since 1960 (Dolek and Geyer 2002). These data need to be interpreted with caution, as we cannot establish whether patches had comparable species richness of habitat specialist species before abandonment, nor whether all

patches were abandoned at roughly the same time. Time of abandonment is likely correlated within the realm of historic sheep herding systems, as grazing was not managed at the patch level but relied on traditional sheep herding routes, so that entire groups of patches likely were abandoned at the same time. The vegetation types used to classify different facies of beginning secondary succession should not be interpreted as seral stages of a single successional pathway. Rather, they represent alternative successional pathways (Hakes 1987, Boehmer 1994) that are not necessarily correlated with time since abandonment. This interpretation was supported by the lack of association between isolation and vegetation type and by the fact that patch types with low vegetation quality (Types C and F) were significantly larger on average than patch types with high vegetation quality (Types A, A/C, B, D). While further research could provide a detailed spatially explicit reconstruction of historic sheep herding systems and grazing intensity at different points in time (Bender et al. 2005), the lack of spatially explicit species distribution data is a typical limitation of empirical studies on long-term fragmentation effects (Kuussaari et al. 2009).

Extinction debt (Tilman et al. 1994) has been proposed to explain the absence of pure area effects following habitat fragmentation in calcareous grasslands (Butaye et al. 2005, Cousins 2009, Kuussaari et al. 2009, Krauss et al. 2004, Krauss et al. 2010). In communities of long-lived perennial plants, many of which propagate clonally, equilibrium species richness may not have been reached after historic habitat fragmentation. Simulations suggest that competitive exclusion may be delayed by longevity of the inferior competitor, or if competition is not completely asymmetric, i.e., if the superior competitor experiences some competition from the inferior competitor and does not always win competitive interaction (Higgins and Cain 2002).

In the present study, the remaining species richness of habitat specialist plants in previously abandoned patches, before the implementation of the ecological network, was related to patch size and vegetation type, which characterizes alternative facies of early secondary succession after abandonment. Within groups of patches of the same vegetation type, patch area had a strong and statistically significant effect on species richness, whereas this effect could not be detected without accounting for vegetation type. Adriaens et al. (2006), who related richness of specialist species in grass-dominated (corresponding to Type A vegetation in our study) calcareous grassland fragments in Belgium to present and historic patch area and connectivity, found that richness was explained by present patch area and thus showed no extinction debt. Observational studies that did not find patch area effects (related to ecological drift) may have failed to account for important factors (e.g., related to competitive exclusion) that moderate extinction rate.

During secondary succession following abandonment of calcareous grasslands, habitat specialist species are likely outcompeted by taller growing species (Hakes 1987, Dzwonko and Loster 2007). Competition in calcareous grasslands is largely driven by nutrient availability, which naturally increases during secondary succession and may be elevated by the presence of shrubs, whereas xeric conditions may reduce competition (Green 1972). Our observation of the lowest mean values of baseline species richness of habitat specialist plants for Type F (with eutrophic elements) and Type C (with forest edge elements), and a trend for the highest values in Type D (with xeric elements), is thus compatible with the hypothesis that extinction delay may depend on the asymmetry of competition with later seral species.

Patch isolation and the number of dynamic structural elements in 1989 were not related to baseline species richness. This supports the interpretation that species richness of specialist species after abandonment is governed primarily by extinction. While (Piessens et al. 2005) found that patch isolation was the most important factor determining the occurrence of heathland plants, empirical results for calcareous grasslands are mixed. For instance, Adriaens et al. (2006) found that isolated fragments had fewer specialist species, whereas Krauss et al. (2004) and Bisteau and Mahy (2005) did not find such an effect. A lack of isolation effect however does not necessarily mean that connectivity is not a crucial factor, as functional connectivity in terms of colonization rates may depend on factors such as the presence of sheep as dispersal vectors rather than pure geographic distance between patches (Rico et al. 2011). While it is conceivable that the micro-habitat diversity related to the presence of dynamic structural elements could affect competitive interactions and thus extinction rate, we found no evidence for such an effect.

Effect of ecological network

Since the establishment of the ecological network, newly grazed patches were re-connected by sheep herding within three non-overlapping grazing systems with the goal of promoting seed dispersal by sheep. In this ‘natural experiment’, ungrazed patches acting as pseudo-controls showed no significant change in species richness of habitat specialist plants between baseline and evaluation surveys, whereas the species richness of grazed patches increased significantly irrespective of the type of grazing (continuous or intermittent), reflecting net colonizations by habitat specialist species. While patches were not randomly assigned to grazing treatment, we found no bias with respect to vegetation type (high or low quality types) or isolation, and there was no significant difference in baseline species richness between

‘consistently grazed’ and ‘ungrazed’ patches. The only bias we could detect was related to patch area, where ‘ungrazed’ patches were on average smaller than ‘consistently grazed’ ones.

To account for the confounding of sheep herding connectivity with grazing per se, we included both terms in the analysis. Multi-model inference clearly identified sheep herding connectivity as the more important factor than grazing treatment, with relative importance values of 0.82 and 0.26, respectively. While grazing may affect vegetation in various ways, colonization requires propagule immigration, and a strong association between sheep herding connectivity and colonization thus suggests that sheep connect patches by transporting propagules. Although we cannot rule out that some species re-established from the seed bank (Blanckenhagen and Poschlod 2005), this is unlikely to explain our findings as the results were unaffected by the exclusion of eight species that reportedly may form a long-term persistent seed bank. Furthermore, increase in species richness of habitat specialist plants could not be explained by patch isolation as a function of geographic distance to nearby patches. Our results thus confirm the pivotal role of sheep herding for maintaining and improving diversity in calcareous grasslands. Sheep have been suggested as key dispersal vectors for calcareous grassland plants (Fischer et al. 1996, Poschlod et al. 1998). In two studies without baseline data, Schrautzer et al. (2009) and Piqueray et al. (2011) found that species richness of habitat specialist species in restored calcareous grasslands depended on the time of subsequent sheep herding.

Jackson and Sax (2010) argue that as both extinction and colonization may be delayed, their assessment requires long time spans, and it is often difficult to attribute specific extinctions or colonizations to previous forcing events. Delayed colonization may be related to a lack of propagule immigration, which depends not only on distance from source populations but also on

dispersal mechanisms and seed production in source populations, failure in local establishment of propagules, which often depends on suitable microsite conditions, or failure to survive and reproduce (Jackson and Sax 2010). Maintenance of calcareous grassland plant diversity may depend not only on dispersal vectors but also on the availability of diverse types of regeneration niches (Rusch and Fernandez-Palacios 1995, Willems and Bik 1998). The number of different dynamic structural elements present (i.e., rock debris, erosion, ant hills, small mammal burrows) was linearly related to increase in species richness between baseline and evaluation surveys. This confirms that propagule immigration is not sufficient to maintain or increase biodiversity of calcareous grasslands in the absence of diverse regeneration niches. Further gaps may have been created by sheep trampling or occasional shrub clearing (Blanckenhagen and Poschlod 2005). The high proportion of variance in relative change in species richness explained by sheep herding connectivity and the number of dynamic structural elements alone (adj. $R^2 = 49\%$) and a normal distribution of residuals suggest however that no major factor was missing from the model.

Notably, patch size and vegetation type had no significant effect on change in species richness between baseline and evaluation surveys. This underscores that the restoration of impoverished grasslands is likely driven primarily by propagule influx and establishment, and less so by factors related to ecological drift and competition. Although it is conceivable that area would affect colonization rate e.g. by increasing the probability of deposition of wind- or animal-dispersed propagules, we did not find any indication of such an effect. This is consistent with empirical results from spatially explicit metapopulation theory, where single-species extinction rates were found to depend strongly on patch area and colonization rates on connectivity (Ovaskainen and Hanski 2004). Furthermore, the absence of a patch size effect suggests that the

initial difference in patch size between ‘consistently grazed’ and ‘ungrazed’ patches cannot explain the difference in increase in species richness between baseline and evaluation surveys.

Conclusions

The ecological network evaluated here 20 years after its inception represents a long-term ‘natural experiment’ with exceptionally detailed and extensive baseline data. Data consistency was unusually high as the same person was in charge of both surveys. The data set provides evidence that this ecological network was successful at restoring functional connectivity of previously abandoned patches at a community level, and for the pivotal role of sheep as dispersal vectors. More detailed analysis at the level of species groups is needed to assess whether certain species remain at risk depending on specific traits, their degree of habitat specificity or baseline population size. Analysis of species-level extinction and colonization dynamics in grazed and ungrazed patches may provide insight into the relative importance of deterministic and stochastic changes in plant species composition of grassland fragments.

The availability of extensive baseline data, with species lists for each patch rather than fixed-size permanent plots, is a prerequisite for disentangling colonization and extinction processes at a landscape scale. These processes cannot be understood without explicit consideration of factors modifying the rates of extinction and colonization, such as strength of competition with later seral species, seed dispersal vectors and their interaction with the matrix, and the presence of a variety of microsites facilitating establishment. A process-based perspective on fragmentation effects may help resolve the current debate around the existence of extinction debt in fragmented semi-natural grasslands (Adriaens et al. 2006, Butaye et al. 2005, Cousins 2009, Kuussaari et al. 2009, Krauss et al. 2010).

The evaluation of ecological network projects in terms of measuring actual dispersal and colonization events is not an unnecessary expense (Kareiva 2006). Rather, funding agencies should require an *a priori* plan for definition of target variables, baseline data collection and statistical evaluation of long-term effects before investing major resources in maintaining or enhancing landscape connectivity. This is likely the most feasible and cost effective way to obtain the empirical evidence needed to justify such investment and to assess its effectiveness.

Acknowledgments

The baseline survey was funded by the Government of Central Franconia. The present research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant, H. W.), the National Council on Science and Technology of Mexico (CONACYT; Y. R.), and the German Academic Exchange Service (DAAD; Y. R.). We thank Karlheinz Dadrich, Doris Baumgartner, Bernd Raab, Stefanie Haacke, Jens Sachteleben, Erich Beil, Erich Neulinger, Alfred Grimm, Bernhard Spachmueller and Christian Haeberling for valuable information and support, and two anonymous reviewers for helpful comments on an earlier version of the manuscript.

References

- Adriaens, D., Honnay, O. and Hermy, M. 2006. No evidence of a plant extinction debt in highly fragmented calcareous grasslands in Belgium. - Biol Conserv 133: 212-224.
- Barton, K. 2009. MuMIn: Multi-model inference. R package version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>.
- Beinlich, B. and Plachter, H. 1995. Ein Naturschutzkonzept für die Kalkmagerrasen der Mittleren Schwäbischen Alb (Baden-Württemberg) : Schutz, Nutzung und Entwicklung. - Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 83, 520pp.

- 456 Bender, O., Boehmer, H. J., Jens, D. and Schumacher, K. P. 2005. Analysis of land-use change in
457 a sector of Upper Franconia (Bavaria, Germany) since 1850 using land register records. -
458 Landscape Ecol 20: 149-163.
- 459 Bennett, G. and Wit, P. 2001. The development and application of ecological networks, a review
460 of proposals, plans and programmes. International Union for Conservation of Nature and
461 Natural Resources (IUCN), Gland, Switzerland.
- 462 Bisteau, E. and Mahy, G. 2005. A landscape approach for the study of calcareous grassland plant
463 communities. - Biotechnol Agron Soc Environ 9: 93-99.
- 464 Blanckenhagen, B. v. and Poschlod, P. 2005. Restoration of calcareous grasslands: the role of the
465 soil seed bank and seed dispersal for recolonisation processes. - Biotechnol Agron Soc
466 Environ 9: 143-149.
- 467 Boehmer, H. J. 1994. Die Halbtrockenrasen der Fränkischen Alb - Strukturen, Prozesse,
468 Erhaltung. - Mitteilungen der Fränkischen Geographischen Gesellschaft 41: 323-343.
- 469 Boehmer, H. J., Janeck, L., Steidler, S. and Raab, B. 1990. Verbundsystem Halbtrockenrasen.
470 Trittstein- und Refugialbiotope im östlichen Landkreis Weißenburg-Gunzenhausen.
471 Bayerisches Landesamt für Umweltschutz, LfU, Munich.
- 472 Boitani, L., Falcucci, A. and Maiorano, L. 2007. Ecological Networks as Conceptual Frameworks
473 or Operational Tools in Conservation. - Conserv Biol 21: 1414-1422.
- 474 Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: A
475 practical information-theoretic approach. - Springer.
- 476 Butaye, J., Adriaens, D. and Honnay, O. 2005. Conservation and restoration of calcareous
477 grasslands: a concise review of the effects of fragmentation and management on plant
478 species. - Biotechnol Agron Soc Environ 9: 111-118.
- 479 Cousins, S. A. O. 2009. Extinction debt in fragmented grasslands: paid or not? - Journal of
480 Vegetation Science 20: 3-7.
- 481 Debinski, D. M. and Holt, R. D. 2000. A survey and overview of habitat fragmentation
482 experiments. - Conserv Biol 14: 342-355.
- 483 Dolek, M. and Geyer, A. 2002. Conserving biodiversity on calcareous grasslands in the
484 Franconian Jura by grazing: a comprehensive approach. - Biol Conserv 104: 351-360.
- 485 Dzwonko, Z. and Loster, S. 2007. A functional analysis of vegetation dynamics in abandoned and
486 restored limestone grasslands. - J Veg Sci 18: 203-212.
- 487 Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. - Annual Review of Ecology
488 34: 487-515.
- 489 Fischer, J. and Lindenmayer, D. B. 2007. Landscape modification and habitat fragmentation: a
490 synthesis. - Global Ecol Biogeogr 16: 265-280.
- 491 Fischer, S., Poschlod, P. and Beinlich, B. 1996. Experimental studies on the dispersal of plants
492 and animals on sheep in calcareous grasslands. - J Appl Ecol 33: 1206-1222.

- 493 Green, B. H. 1972. The relevance of seral eutrophication and plant competition to the
494 management of successional communities. - *Biol Conserv* 4: 378-384.
- 495 Haila, Y. 2002. A conceptual genealogy of fragmentation research: From island biogeography to
496 landscape ecology. - *Ecological Applications* 12: 321-334.
- 497 Hakes, W. 1987. Einfluß von Wiederbewaldungsvorgängen in Kalkmagerrasen auf die
498 floristische Artenvielfalt und Möglichkeiten der Steuerung durch Pflegemaßnahmen. -
499 *Dissertationes Botanicae* 109, 151pp.
- 500 Hanski, I. 1994. A practical model of metapopulation dynamics. - *J Anim Ecol* 63: 151-162.
- 501 Hanski, I. and Ovaskainen, O. 2003. Metapopulation theory for fragmented landscapes. - *Theor*
502 *Popul Biol* 64: 119-127.
- 503 Higgins, S. I. and Cain, M. L. 2002. Spatially realistic plant metapopulation models and the
504 colonization–competition trade-off. - *J Ecol* 90: 616-626.
- 505 Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. - *Monographs*
506 *in Population Biology* 32: 1-375.
- 507 Jackson, S. T. and Sax, D. F. 2010. Balancing biodiversity in a changing environment: extinction
508 debt, immigration credit and species turnover. - *Trends Ecol Evol* 25: 153-160.
- 509 Kareiva, P. 2006. Introduction: Evaluation and quantifying the conservation dividends of
510 connectivity. - In: Crooks, K. R. and Sanjayan, M. A. (eds.), *Connectivity conservation*.
511 Cambridge University Press, pp. 293-295.
- 512 Krauss, J., Klein, A. M., Steffan-Dewenter, I. and Tschardt, T. 2004. Effects of habitat area,
513 isolation, and landscape diversity on plant species richness of calcareous grasslands. -
514 *Biodiversity and Conservation* 13: 1427-1439.
- 515 Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., Lindborg,
516 R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K. M., Sang, A., Stefanescu, C.,
517 Teder, T., Zobel, M. and Steffan-Dewenter, I. 2010. Habitat fragmentation causes immediate
518 and time-delayed biodiversity loss at different trophic levels. - *Ecol Lett* 13: 597-605.
- 519 Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger,
520 E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M. and Steffan-Dewenter,
521 I. 2009. Extinction debt: a challenge for biodiversity conservation. - *Trends in Ecology &*
522 *Evolution* 24: 564-571.
- 523 Lindenmayer, D. 2009. Large-scale landscape experiments : lessons from Tumut. - Cambridge
524 University Press.
- 525 MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. - Princeton
526 University Press.
- 527 Oberdorfer, E. 1978. *Süddeutsche Pflanzengesellschaften*, vol. 2. – Gustav Fischer Verlag.
- 528 Opdam, P., Steingrover, E. and Rooij, S. v. 2006. Ecological networks: A spatial concept for
529 multi-actor planning of sustainable landscapes. - *Landscape Urban Plann* 75: 322-332.

- 530 Ovaskainen, O. and Hanski, I. 2004. Metapopulation dynamics in highly fragmented landscapes.
531 - In: Hanski, I. and GAGGIOTTI, O. E. (eds.), Ecology, Genetics, and Evolution in
532 Metapopulations. Academic Press, pp. 73-103.
- 533 Piessens, K., Honnay, O. and Hermy, M. 2005. The role of fragment area and isolation in the
534 conservation of heathland species. - *Biol Conserv* 122: 61-69.
- 535 Piqueray, J., Bottin, G., Delescaille, L., Bisteau, E., Colinet, G. and Mahy, G. 2011. Rapid
536 restoration of a species-rich ecosystem assessed from soil and vegetation indicators: The case
537 of calcareous grasslands restored from forest stands. - *Ecol Ind* 11: 724-733.
- 538 Poschlod, P., Kiefer, S., Tränkle, U., Fischer, S. and Bonn, S. 1998. Plant Species Richness in
539 Calcareous Grasslands as Affected by Dispersability in Space and Time. - *Applied*
540 *Vegetation Science* 1: 75-90.
- 541 Poschlod, P., Kleyer, M., Jackel, A. K., Dannemann, A. and Tackenberg, O. 2003. BIOPOP - a
542 database of plant traits and Internet application for nature conservation. - *Folia Geobotanica*
543 38: 263-271.
- 544 Poschlod, P. and WallisDeVries, M. F. 2002. The historical and socioeconomic perspective of
545 calcareous grasslands—lessons from the distant and recent past. - *Biol Conserv* 104: 361-
546 376.
- 547 R Development Core Team 2010. R: A language and environment for statistical computing. R
548 Foundation for Statistical Computin, Vienna, Austria. ISBN 3-900051-07-0, URL
549 <http://www.R-project.org>.
- 550 Rico, Y., Boehmer, H. J. and Wagner, H. H. 2011. Determinants of actual functional connectivity
551 for calcareous grassland communities linked by rotational sheep grazing. - *Landscape*
552 *Ecology*. Doi: 10.1007/s10980-011-9648-5.
- 553 Rusch, G. and Fernandez-Palacios, J. M. 1995. The influence of spatial heterogeneity on
554 regeneration by seed in a limestone grassland. - *Journal of Vegetation Science* 6: 417-426.
- 555 Schrautzer, J., Jansen, D., Breuer, M. and Nelle, O. 2009. Succession and management of
556 calcareous dry grasslands in the Northern Franconian Jura, Germany. - *Tuexenia* 29: 339-
557 351.
- 558 Taylor, P. D., Fahrig, L. and With, K. A. 2006. Landscape connectivity: a return to the basics. -
559 In: Crooks, K. R. and Sanjayan, M. A. (eds.), *Connectivity conservation*. Cambridge
560 University Press, pp. 31-43.
- 561 Thompson, K. 1997. The soil seed banks of north west Europe : methodology, density and
562 longevity. - Cambridge University Press.
- 563 Tilman, D., May, R. M. and Lehman, C. L. 1994. Habitat destruction and the extinction debt. -
564 *Nature* 371: 65-66.
- 565 Wagner, H. H., Jedicke, E., Retzer, V. and Boehmer, H. J. 2007. Turning landscape conservation
566 projects into biodiversity experiments. - In: Bunce, R. G. H., Jongman, R. H. G., Hojas, L.
567 and Weel, S. (eds.), *25 years of Landscape Ecology: Scientific Principles in Practice*.
568 International Association of Landscape Ecology, pp. 670-671.

569 Willems, J. H. and Bik, L. P. M. 1998. Restoration of high species density in calcareous
570 grassland: the role of seed rain and soil seed bank. - Applied Vegetation Science 1: 91-100.
571

572

Tables

Table 1: Best model explaining relative change in species richness between baseline and evaluation surveys (*RelativeChange*). Model results are given for all 48 habitat specialist species. In addition, p-values are provided for a model with 43 species, excluding five species with potential issues of detectability, and for a model with 40 species, excluding eight species that may form a long-term persistent seed bank (Appendix S3). Patch A51 was excluded due to missing data for *RelativeChange*.

<i>Parameter</i>	<i>N</i>	<i>DF</i>	<i>Coefficient</i>	<i>SE</i>	<i>t-value</i>	<i>P-value</i>	<i>P-value</i>	<i>P-value</i>
						<i>48 species</i>	<i>43 species</i>	<i>40 species</i>
Intercept	62	1	-0.085	0.043	-1.99	0.052	0.026	0.036
<i>SheepConnectivity</i>	62	1	0.036	0.008	4.43	<0.001	<0.001	<0.001
<i>Elements</i> ₂₀₀₉	62	1	0.085	0.020	4.21	<0.001	<0.001	<0.001

Figure captions

Fig. 1: Conceptual model explaining patch-level species richness of habitat specialist plants. White elliptical shapes indicate hypothesized processes, grey boxes denote measurable factors and quantities. Full arrows represent hypothesized effects, whereas a dotted arrow indicates a potential indirect effect.

Fig. 2: Scatterplot of final model explaining remaining patch quality after abandonment ($Richness_{1989}$) as a linear combination of *PatchArea* and *VegetationType*. Vegetation types with dashed lines and square symbols (Types C and F) differed significantly from the reference group (Type A).

Fig. 3: Boxplot of change in patch quality between baseline and evaluation surveys ($RelativeChange$) for each of the three grazing treatments. Different letters *a*, *b* indicate significant pair-wise comparisons.

Figures

Fig. 1

Fig. 2

Fig. 3

Supporting Information

Appendix S1: Map of study area

The inset map (modified from Beinlich and Plachter 1995) shows the distribution of calcareous grasslands (grey shaded areas) in Germany and the location of the study area (red filled rectangle).

In the main map, the study area is highlighted compared to the adjacent area. The map shows the location and grazing treatment since 1989 of the 62 previously abandoned patches (square symbols) and the location of core areas within the study area (red polygons), as well as the three sheep herding systems (red, blue and green bold lines). Due to the geological and topographical situation, very few calcareous grasslands exist within several kilometers to the West, North and East of the study area, whereas to the South, there are extensive core areas in the adjacent Altmuehl valley, where the Altmuehl river cuts through the upper Jurassic limestone. The grazing system of Herd 1 continues to the West over a larger distance across the main valley, whereas Herd 3 continues to the South into and across the Altmuehl valley.

References

Beinlich, B. and Plachter, H. 1995. Ein Naturschutzkonzept für die Kalkmagerrasen der Mittleren Schwäbischen Alb (Baden-Württemberg) : Schutz, Nutzung und Entwicklung. - Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg 83, 520 pp.

629 **Appendix S2: Patch attribute data**

Grazing treatment	Patch	Clearing	Patch Area class	Patch Isolation S_i	Vegetation Type	Elements 1989	Elements 2009	Richness 1989	Richness 2009
Consistently	A5	no	4	6.36	B	1	2	27	31
	A6	no	4	6.85	B	2	2	21	37
	A7a	no	4	7.08	A	1	1	14	22
	A11	no	5	11.01	A	1	4	18	30
	A12	no	3	9.53	A	2	3	12	16
	A13	no	5	8.64	F	0	3	13	35
	A14	no	4	5.76	A	2	3	22	32
	A15	no	4	5.55	A	1	4	13	23
	A18	no	4	9.71	A	4	3	13	20
	A25	no	3	4.95	A	0	2	21	32
	A26	no	4	5.45	D	1	3	19	33
	A28a	no	4	5.69	A	2	2	14	24
	A29	no	3	5.79	D	1	3	28	35
	A31	no	5	5.30	C	1	3	20	33
	A32	no	1	5.15	D	0	1	15	22
	A33	no	5	4.24	C	0	4	19	26
	A34	no	5	3.77	C	0	4	9	31
	A38	yes	5	5.81	A	3	3	27	37
	A45	no	4	4.64	A	3	2	24	32
	A49	no	4	4.75	B	1	2	21	35
	A50	no	3	4.88	A	1	4	30	29
	A51a	no	4	5.26	A	3	4	26	30
	A52	no	4	5.81	A	1	4	21	32
	A53	no	3	6.22	D	1	3	20	24
	A55	no	5	5.87	E	0	2	25	26
	A56	no	4	7.54	A	2	1	24	29
Intermittently	A3	no	4	4.96	B	0	3	22	33
	A4	no	4	5.53	B	2	0	27	28
	A8	no	5	13.31	F	2	3	17	27
	A9	no	3	11.57	F	1	4	13	25
	A10	no	4	10.97	F	1	1	11	8
	A10a	no	4	10.71	F	1	0	12	5
	A20	yes	3	13.99	B	2	1	23	29
	A21	yes	4	11.73	A	2	5	37	38
	A22	yes	2	11.46	B	1	3	16	31

	A23	yes	3	9.27	A	0	3	21	29
	A24	yes	5	8.20	A/C	1	3	26	37
	A44	no	5	4.82	A/C	2	1	20	29
	A46	no	3	4.22	A	1	1	20	25
Ungrazed	A1	no	3	5.12	A	1	1	13	11
	A2	no	4	4.52	B	2	2	19	24
	A7	no	3	7.00	F	0	0	3	0
	A16	yes	5	5.45	A	2	3	13	16
	A17	no	3	6.89	F	1	2	11	14
	A19	no	2	14.80	B	1	0	10	6
	A27	no	3	5.70	A/C	2	1	16	20
	A28	no	4	5.50	A	1	2	25	30
	A30	no	1	6.47	A	1	0	9	6
	A35	no	3	6.56	A	1	2	14	11
	A36	no	3	4.25	D	2	4	27	26
	A37	yes	3	4.80	A	2	5	20	25
	A39	no	2	7.07	A	1	1	22	22
	A40	no	1	5.28	A	0	2	11	21
	A41	no	3	4.92	A	1	2	11	33
	A42	no	3	3.88	B	1	1	16	12
	A43	no	4	0.63	A	2	3	32	31
	A47	no	5	4.40	C	2	2	11	17
	A48	no	3	6.19	B	1	2	18	25
	A51	no	3	5.73	A	2	0	21	NA
	A54	no	2	7.77	A	0	1	18	8
	A57	no	5	7.75	A	0	0	15	8
	A58	no	5	8.23	F	1	0	18	12

Appendix S3: List of 48 habitat specialist plant species

List of 48 habitat specialist plant species. ‘Level’ indicates for each species the level of phytosociological classification at which it is considered characteristic (A = association *Gentiano-Koelerietum pyramidatae*, V = alliance *Bromion erecti*, O = order *Brometalia erecti*; C = class *Festuco-Brometea*; B = companion species). ‘Seed bank’ denotes the classification of seed bank type (1 = transient, 2 = short-term persistent, 3 = long-term persistent) and reliability (bold = ‘with high probability’, italic = ‘probably’) based on the BIOPOP trait base (Poschlod et al. 2003). An asterisk (*) indicates classification derived from seed bank longevity data in the LEDA trait base (Kleyer et al. 2008), interpreting longevity = 0 as transient, longevity = 0.5 as short-term persistence and longevity = 1 as long-term persistence. ‘Frequency’ indicates the number of patches (out of 62) where the species was recorded in the baseline survey 1989 or in the evaluation survey of 2009. Nomenclature follows (Lauber 1996).

Species	Level	Seed bank	Frequency 1989	Frequency 2009
<i>Phleum phleoides</i> (L.) H. Karst.	C	1	14	20
<i>Ajuga genevensis</i> L.	C	2	7	31
<i>Allium oleraceum</i> L.	C	1	11	10
<i>Anthyllis vulneraria</i> L. subsp. <i>vulneraria</i>	O	2	3	15
<i>Arabis hirsuta</i> (L.) Scop.	O	2	4	21
<i>Asperula cynanchica</i> L.	C	2	18	26
<i>Brachypodium pinnatum</i> (L.) P. Beauv.	C	1	60	60
<i>Bromus erectus</i> Huds. subsp. <i>erectus</i>	O	2	43	47
<i>Campanula glomerata</i> L. subsp. <i>glomerata</i>	V	2*	6	5
<i>Campanula rotundifolia</i> L.	B	2	24	46
<i>Carlina acaulis</i> L. subsp. <i>acaulis</i>	V	1	29	35
<i>Carlina vulgaris</i> L.	V	1	6	3
<i>Centaurea jacea</i> L. subsp. <i>jacea</i>	B	2	46	47
<i>Cirsium acaule</i> Scop.	A	1	13	27
<i>Dianthus carthusianorum</i> L. subsp. <i>carthusianorum</i>	O	1	25	43
<i>Erigeron acris</i> auct.	V	1	3	4
<i>Euphorbia cyparissias</i> L.	C	3	48	47
<i>Euphorbia verrucosa</i> L.	V	2	16	18
<i>Euphrasia stricta</i> J. F. Lehm.	V	2	3	3
<i>Festuca ovina</i> L.	C	1	62	58
<i>Galium verum</i> L. subsp. <i>verum</i>	C	2	58	59
<i>Gentiana ciliata</i> L.	A	1	4	9

Gentiana germanica Willd. subsp. germanica	A	1	4	1
Gentiana cruciata L.	C	3*	3	0
Helianthemum ovatum (Viv.) Dunal	O	2	44	48
Hieracium pilosella L.	B	2	15	28
Hippocrepis comosa L.	C	2	35	36
Koeleria pyramidata (Lam.) P. Beauv.	A	1	29	47
Leontodon hispidus L. subsp. hispidus	B	2	13	25
Linum catharticum L.	B	3	6	21
Lotus corniculatus L.	B	3	46	55
Medicago lupulina L.	V	3	21	36
Onobrychis viciifolia Scop.	V	1	12	23
Ononis repens L.	V	1	22	35
Ononis spinosa L. subsp. spinosa	V	1	7	8
Pimpinella saxifraga L.	C	1	44	50
Plantago media L.	B	2	45	44
Polygala comosa Schkuhr	C	1	15	23
Potentilla tabernaemontani Asch.	C	2	36	48
Prunella grandiflora (L.) Scholler	C	2	33	42
Pulsatilla vulgaris Mill.	A	2	22	24
Ranunculus bulbosus L.	V	3	11	43
Salvia pratensis L.	C	1	42	45
Sanguisorba minor Scop. subsp. minor	C	3	50	47
Scabiosa columbaria L. subsp. columbaria	O	2	32	38
Stachys recta L. subsp. recta	C	1	12	10
Thymus pulegioides L. subsp. pulegioides	B	3	47	49
Trifolium montanum L.	C	1	15	16

642

643 References:

- 644 Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M.,
645 Poschlod, P., van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M.,
646 Hermý, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P.,
647 Götzenberger, L., Hodgson, J. G., Jackel, A., Kühn, I., Kunzmann, D., Ozinga, W. A.,
648 Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H. J., Tackenberg, O., Wilmann,
649 B., Cornelissen, J. H. C., Eriksson, O., Garnier, E. and Peco, B. 2008. The LEDA Traitbase:
650 a database of life-history traits of the Northwest European flora. - J Ecol 96: 1266-1274.
- 651 Lauber, K. 1996. Flora Helvetica : Flora der Schweiz = Flore de la Suisse = Flora della Svizzera.
652 - Verlag Paul Haupt.
- 653 Poschlod, P., Kleyer, M., Jackel, A. K., Dannemann, A. and Tackenberg, O. 2003. BIOPOP - a
654 database of plant traits and Internet application for nature conservation. - Folia Geobotanica
655 38: 263-271.

656
657

658

Appendix S4: Best model explaining baseline species richness.

Bold p-values are significant at $\alpha = 0.05$. Patch A55 of vegetation type E was excluded from this analysis.

<i>Parameter</i>	<i>N</i>	<i>DF</i>	<i>Coefficient</i>	<i>SE</i>	<i>t-value</i>	<i>P-value</i>
Intercept	61	1	11.13	2.84	3.91	<0.001
<i>VegetationType</i>	61	5				<0.001^a
- Type A (reference)	30					
- Type A/C	3	1	- 1.18	3.40	- 0.35	0.730
- Type B	11	1	0.55	1.94	0.29	0.776
- Type C	4	1	-8.74	3.16	-2.77	0.008
- Type D	5	1	3.75	2.71	1.39	0.172
- Type F	8	1	-8.77	2.23	-3.94	<0.001
<i>PatchArea</i>	61	1	2.47	0.77	3.23	0.002

^a) F-test, type II SS, df = 5, F = 4.93.

Appendix S5: Differences in baseline conditions among grazing treatments

For response variables with a significant overall effect of *GrazingTreatment*, letters (*a*, *ab*, *b*) indicate significance of pair-wise comparisons (Tukey's test with family-wise significance levels of $\alpha = 0.05$). 'Types A, A/C, B, D' refers to *VegetationTypes* classified as high patch quality types, 'Types C, F' to those classified as low patch quality types based on Appendix S4.

<i>GrazingTreatment</i>	<i>All</i>	<i>Richness</i>	<i>Patch</i>	<i>Patch</i>	<i>Elements</i>	<i>Types A,</i>	<i>Types</i>
		<i>1989</i>	<i>Area</i>	<i>Isolation</i>	<i>1989</i>	<i>A/C, B, D</i>	<i>C, F</i>
	N	<i>Mean</i>	<i>Mean</i>	<i>Mean</i>	<i>Mean</i>	<i>N</i>	<i>N</i>
		<i>(SE)</i>	<i>(SE)</i>	<i>(SE)</i>	<i>(SE)</i>		
'Ungrazed'	23	16.7 (1.35)	3.2 <i>a</i> (0.24)	18.0 <i>a</i> (0.63)	1.04 (0.15)	19	4
'Consistently grazed'	26	19.8 (1.11)	4.0 <i>b</i> (0.18)	18.4 <i>a</i> (0.51)	1.19 (0.18)	21 [*]	4
'Intermittently grazed'	13	20.4 (1.97)	3.8 <i>ab</i> (0.26)	21.3 <i>b</i> (0.56)	1.23 (0.17)	9	4

^{*}) Patch A55 with vegetation type "E" was excluded.

Appendix S6: Spearman rank correlations among predictors and response variables

Correlation matrices of baseline species richness (*Richness₁₉₈₉*; Table A) and of relative change in species richness (*RelativeChange*; Table B) with their associated predictors. Asterisks indicate statistical significance (ns: not significant, *: p-value < 0.05, **: p-value < 0.01, ***: p-value < 0.001).

Table A: Baseline data	<i>Richness₁₉₈₉</i>	<i>PatchArea</i>	<i>Elements₁₉₈₉</i>	<i>VegetationType2</i>
<i>PatchArea</i>	0.188 ^{ns}			
<i>Elements₁₉₈₉</i>	0.336 ^{**}	0.144 ^{ns}		
<i>VegetationType2</i>	-0.436 ^{***}	0.344 ^{**}	-0.319 [*]	
<i>PatchIsolation</i>	-0.226 ^{ns}	-0.129 ^{ns}	0.040 ^{ns}	0.080 ^{ns}

Table B: Grazed patches	<i>RelativeChange</i>	<i>PatchArea</i>	<i>Elements₂₀₀₉</i>	<i>VegetationType2</i>	<i>PatchIsolation</i>
<i>PatchArea</i>	0.302 [*]				
<i>Elements₂₀₀₉</i>	0.570 ^{***}	0.232 ^{ns}			
<i>VegetationType2</i>	-0.016 ^{ns}	0.347 ^{**}	0.002 ^{ns}		
<i>PatchIsolation</i>	0.199 ^{ns}	-0.131 ^{ns}	0.208 ^{ns}	0.091 ^{ns}	
<i>SheepConnectivity</i>	0.577 ^{***}	0.304 [*]	0.330 ^{**}	0.032 ^{ns}	0.192 ^{ns}