

Determinants of actual functional connectivity for calcareous grassland communities linked by rotational sheep grazing

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Abstract In fragmented landscapes, plant species persistence depends on functional connectivity in terms of pollen flow to maintain genetic diversity within populations, and seed dispersal to re-colonize habitat patches following local extinction. Connectivity in plants is commonly modeled as a function of the physical distance between patches, without testing alternative dispersal vectors. In addition, pre- and post-dispersal processes such as seed production and establishment are likely to affect patch colonization rates. Here, we test alternative models of potential functional connectivity with different assumptions on source patch effects (patch area and species occupancy) and dispersal (relating to distance among patches, matrix composition, and sheep grazing routes) against empirical patch colonization rates at the community level (actual functional connectivity), accounting for post-dispersal

effects in terms of structural elements providing regeneration niches for establishment. Our analyses are based on two surveys in 1989 and in 2009 of 48 habitat specialist plants in 62 previously abandoned calcareous grassland patches in the Southern Franconian Alb in Bavaria, Germany. The best connectivity model S_i , as identified by multi-model inference, combined distance along sheep grazing routes including consistently and intermittently grazed patches with mean species occupancy in 1989 as a proxy for pre-dispersal effects. Community-level patch colonization rates depended to equal degrees on connectivity and post-dispersal process. Our study highlights that actual functional connectivity of calcareous grassland communities cannot be approximated by structural connectivity based on physical distance alone, and modeling of functional connectivity needs to consider pre- and post-dispersal processes.

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function model · Germany

Introduction

Habitat fragmentation threatens the persistence of plant populations by reducing habitat connectivity and thus affecting dispersal of pollen and seeds

between habitat fragments (Sork and Smouse 2006). While pollen flow may be sufficient to maintain genetic diversity and avoid inbreeding effects (Young and Clarke 2000; Keller and Waller 2002), habitat re-colonization after local extinction can only occur by propagule dispersal (Johst et al. 2002). Given that in most grassland plants propagules are dispersed within 1 m in the vicinity of the source (Coulson et al. 2001; Fenner and Thompson 2005), lack of connectivity by seed dispersal will limit species' ability to reach empty patches and establish new populations (Soons et al. 2004). Moreover, the colonization process may increase population genetic differentiation if propagules come from a few sources only (Whitlock and McCauley 1990; Panell and Dorken 2006), which is likely to be the case with increased fragmentation. Restoring connectivity is thus expected to avoid deleterious demographic and genetic effects mostly in small isolated populations (Frakham 2005; Aguilar et al. 2008).

Connectivity comprises two components: *structural* connectivity, which is defined by the spatial habitat configuration without reference to organism movement behavior, and *functional* connectivity, which refers to the individual behavioral response to the landscape pattern, including the scaling of inter-patch distances by maximum dispersal distance or the transversability of different land-covers in the intervening matrix, and the resulting dispersal and gene flow (Taylor et al. 1993, 2006). Assessing functional connectivity in plants remains a methodological challenge, because even for a single species it is not feasible to observe dispersal events over long distances, for more than a single source population, or over multiple seasons, and even less so for entire species assemblages (Fischer and Lindenmayer 2007).

Commonly, empirical studies of plant communities model connectivity as a function of patch area and geographic distance between patches alone and test model predictions against species occupancy data, as empirical data on colonization rates are often lacking (but see Soons et al. 2004; Herrera et al. 2011). These approaches are unlikely to capture the mechanism behind functional connectivity. As recommended by Murphy and Lovett-Doust (2004), it is necessary to incorporate a functional approach for modeling landscape connectivity including variables associated with effective dispersal through the matrix (i.e., dispersal

vectors, predation) and with local establishment (i.e., resource availability, competition), which together determine long-term species persistence. Empirical studies thus need to combine an assessment of landscape structure with biological assumptions on organism dispersal into realistic models of *potential functional connectivity*, and test these models against empirical estimates of effective dispersal (e.g., colonization rates or migration events inferred by assignment test with genetic data) that correspond to *actual functional connectivity* (Fig. 1; Calabrese and Fagan 2004; Fagan and Calabrese 2006).

Beyond dispersal per se, pre- and post-dispersal processes are likely to influence patch colonization success (Nathan and Muller-Landau 2000). For instance, population size in source patches may determine the quality and the potential number of emigrant propagules. The patch connectivity index, S_i , of the incidence function model (IFM, Hanski 1994) includes the area of source patches as a proxy for population size assuming that the carrying capacity of the focal patch is proportional to its area (Ovaskainen and Hanski 2004). While most studies include source patch variables at least in terms of patch area, focal patch properties affecting establishment have rarely been considered in landscape connectivity models (Clobert et al. 2004). For instance, availability of resources in focal patches would influence seedling establishment and thus colonization success. Hence, most measures of actual functional connectivity are likely to confound dispersal effects with post-dispersal processes when testing predictions of potential functional connectivity. To effectively inform management efforts, it is crucial to disentangle the contribution of dispersal per se from pre- and post-dispersal processes. We propose a comprehensive approach to assess and disentangle determinants of actual functional connectivity for plant species at the community level (Fig. 1). Our approach considers that actual functional connectivity (colonization rates) depends on the emigrant pool in source patches, a dispersal function reflecting the main dispersal vector, and the establishment probability of propagules in focal patches.

We apply this framework to study plant community connectivity of calcareous grasslands in Germany. Calcareous grasslands are semi-natural communities traditionally used for sheep grazing or hay production (Ellenberg 1996). They typically are nutrient poor,

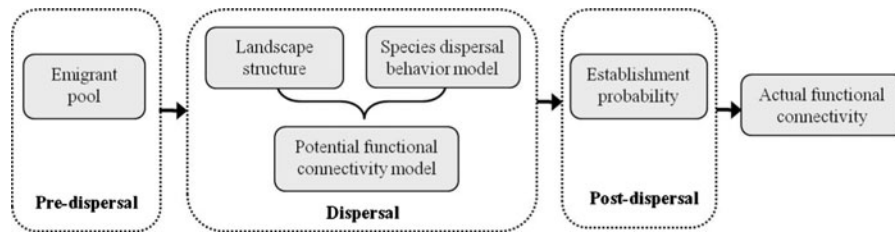


Fig. 1 Conceptual model of functional connectivity including effects relating to pre-dispersal (e.g., seed production) and post-dispersal processes (e.g., availability of regeneration

niches) that interact with potential functional connectivity to determine actual functional connectivity

unfertilized and free of herbicide or pesticide application, resulting in a high floristic and faunistic species richness of important conservation value (WallisDeVries et al. 2002). In Central Europe, since the late nineteenth century abandonment of transhumance sheep grazing followed by encroachment of natural forest succession led to a dramatic decline in calcareous grasslands with a consequent loss of biodiversity (Poschlod and WallisDeVries 2002; Bender et al. 2005). Paradoxically, preservation of natural succession is not a goal of nature conservation here because it typically leads to relatively species poor beech forests with predominantly ubiquitous species that are of no particular interest for conservation, whereas calcareous grasslands are very diverse with high numbers of habitat specialist arthropod and plant species. Within this old cultural landscape, which was deforested and subject to traditional land use since Roman times, calcareous grasslands have become important refugia for numerous endangered species and hotspots for biodiversity at the landscape scale.

In 1989 in the Franconian Alb in Bavaria, Germany, a conservation project was established aimed to restore abandoned calcareous grasslands and re-connect them with existing core areas by rotational sheep grazing. Due to extensive baseline data from 1989 for all previously abandoned patches (Boehmer et al. 1990), this project represents a unique research opportunity to study connectivity of grassland communities. Based on an evaluation survey in 2009, empirical colonization rates were observed for all 48 habitat specialist plants. Wagner et al. (submitted) showed that rotational sheep grazing significantly increased species richness of previously abandoned patches, although structural connectivity based on the physical distance between patches had no effect on species richness. Here, we use patch colonization

rates at the community level as a measure of actual functional connectivity to test multiple competing models of potential functional connectivity, including pre- and post-dispersal effects (Fig. 1). By pooling colonization events across the 48 habitat specialist species, we are able to overcome data limitations that would prevent statistical analysis at the species level.

Methods

Study site

The study area of approx. 10 km × 15 km in the Southern Franconian Alb near Weissenburg, Bavaria, Germany, comprises valleys and limestone plateaus with agricultural fields, forests, grasslands, orchards, and settlements. Between 1900 and 1960, pasture abandonment led to a dramatic regional decrease of calcareous grassland cover from 15 to 1% today (Bender et al. 2005). In the study area, calcareous grasslands declined from 970 ha in 1830 to 302 ha by the early 1990s (Dolek and Geyer 2002). In 1989, the County of Weissenburg-Gunzenhausen initiated a pilot project aimed to preserve and reconnect calcareous grasslands by implementing three independent rotational grazing systems, which connected larger, consistently grazed patches (“core areas”) with previously abandoned patches experiencing secondary succession (“abandoned patches”).

Actual functional connectivity data

All previously abandoned calcareous grasslands of at least 25 m² that had remnants of *Gentiano-Koelerietum pyramidatae* vegetation were surveyed as a basis for implementing the conservation project (Boehmer

et al. 1990). During summer and fall of 1989 and spring of 1990, complete species lists of vascular plants were recorded with Braun-Blanquet abundance information on all 62 previously abandoned calcareous grasslands in the study area (baseline survey). All 48 habitat specialist species were surveyed again during summer 2008 and spring and fall 2009 (evaluation survey) on all previously surveyed patches and in all core areas. Core areas were fully surveyed in the evaluation survey but only aggregate data are available for the baseline survey, consisting of the frequency of occurrence of each species among 11 sampled core areas. Only previously abandoned patches were included in the statistical analysis, but core areas were included in the calculation of S_i connectivity models.

Consistency between baseline and evaluation surveys was high as both were led by the same scientist. Comparisons between independent surveys by two different observers confirmed that species were reliably detected even if reproductive structures were absent, possibly with the exception of *Allium oleraceum*. As summer visits for the baseline survey were primarily done during late summer 1989, this may have affected the detectability of four plant species that flower during early summer: *Leontodon hispidus*, *Ranunculus bulbosus*, *Ajuga genevensis*, and *Linum catharticum*. To assess sensitivity to detectability, we repeated all analyses without the above-mentioned five species.

We calculated mean patch colonization rates C_i , at the community level including all 48 habitat specialist plants for each previously abandoned patch i as $CR_i = C_i / (48 - \text{Richness}_{1989_i})$, where C_i is the number of species present in the evaluation survey, but absent in the baseline survey divided by the species absent in patch i in the baseline survey. We thus scaled the observed number of colonization events in each patch by the maximum possible net number of colonizations among the 48 specialist species.

The interpretation of CR_i as community-level patch colonization rate relies on the assumption that species were reliably detected in both surveys and that colonization did not occur from the seed bank. The majority of habitat specialist species in this system is known to have a transient or short-term persistent seed bank. However, long-term persistent seed bank has been reported for eight species: *Ranunculus bulbosus*, *Medicago lupulina*, *Lotus*

corniculatus, *Sanguisorba minor*, *Thymus pulegioides*, *Gentiana cruciata*, *Euphorbia cyparissias*, and *Linum catharticum* (Poschlod et al. 2003). To assess sensitivity to seed bank persistence, we repeated all analyses without these eight species.

Management records

The grazing regime 1989–2009 of each of the 62 previously abandoned patches was classified based on archived management records and current maps of grazing routes combined with shepherd interviews. Thus, 26 of the previously abandoned patches were consistently grazed since the beginning of the conservation project, which means that 400–800 ewes were herded through each patch 3–5 times per year; 13 patches were intermittently grazed, i.e., not grazed all years from 1990 to 2009, or only later in the season, or they were only grazed initially for a few years after the start of the project. The remaining 23 patches were not included in the three grazing systems and thus remained ungrazed from 1989 to 2009.

Models of potential functional connectivity

We parameterized a patch connectivity index, S_i , to test competing dispersal models and source patch effects. The S_i index quantifies distances (d_{ij}) between focal patch i and each source patch j using a negative exponential dispersal kernel with a constant scaling parameter α (Hanski 1994; Ovaskainen and Hanski 2004).

$$S_i = \sum_{i \neq j} \exp(-\alpha d_{ij}) A_j \cdot p_j$$

Parameter A_j refers to the area (ha) of source patch j , and in a single species model, parameter p_j indicates source patch occupancy (present = 1, absent = 0). For our community-level model, we averaged baseline species occupancy p_{jk} over all 48 species k , resulting in $p_j = \sum_k p_{jk} / 48$, so that $0 \leq p_j \leq 1$. All core areas received the value of $p_j = 0.75$ derived from the aggregate baseline data. Substituting patch-level occupancy data from the evaluation survey did not improve model fit.

We modeled the effect of potential dispersal vectors with five alternative dispersal models

Table 1 Description of the distance models included for the estimation of each incidence function model (IFM) of the patch connectivity S_i

Distance measure (d_{ij})	Description	Units
(a) Geographic distance	Straight line distance from the center of the focal patch i to the center of each other source patch j	km
(b) Matrix resistance	Straight line distance cutting through forest from the center of the focal patch i to the center of each other source patch j	km
(c) Consistently grazed	Number of patch-to-patch steps from focal “consistently” grazed patch i to each other “consistently” grazed patch j within each grazing system A value of 100 was assigned to ungrazed patches, to “intermittently” grazed patches, and to grazed patches from different grazing systems	Integer
(d) Consistently or intermittently grazed	Number of patch-to-patch steps from “consistently” or “intermittently” grazed focal patch i to each other “consistently” or “intermittently” grazed patch j within the same grazing system A value of 100 was assigned to ungrazed patches and to grazed patches from different grazing systems	Integer
(e) Grazed within the same system	Same value of 1 assigned to all grazed patches within the same grazing system, whereas a value of 100 was assigned to ungrazed patches or grazed patches from different grazing systems	1 or 100

(Table 1) by modifying the distance parameter d_{ij} in the S_i index. The simplest model, *geographic distance* (Table 1a), is a null model that assumes seeds are dispersed by wind as a simple diffusion process without an effect of the landscape matrix. The second model, *matrix resistance* (Table 1b), assumes that seeds are dispersed by simple diffusion, but seeds are intercepted by forest in the intervening matrix. The remaining three models assume sheep to be the main dispersal vector: the *consistently grazed* model (Table 1c) assumes that grazing needs to be consistent, i.e., every year and throughout the season, to effectively transport seeds between patches along the grazing route; the model implies that distance in terms of the number of patches traversed between two patches i and j matters (i.e., distance effect). The *consistently or intermittently grazed* model (Table 1d) is similar to the previous model, but some degree of grazing is assumed sufficient to effectively transport seeds. The *grazed within the same system* model (Table 1e) is a null model for dispersal by sheep as it includes no distance effect, i.e., it assumes that seeds transported by sheep are equally likely to reach all grazed patches within the same grazing system.

Dispersal capacity accounted for by parameter α is unknown for our set of 48 specialist species. In a sensitivity analysis varying α from 0.1 to 50 with increments of 0.1, we found that $\alpha = 0.2$ resulted in

the best or second best fit between patch colonization rates, CR_i , and each of the five dispersal models (i.e., highest positive Pearson correlation), hence we used this value for the final models.

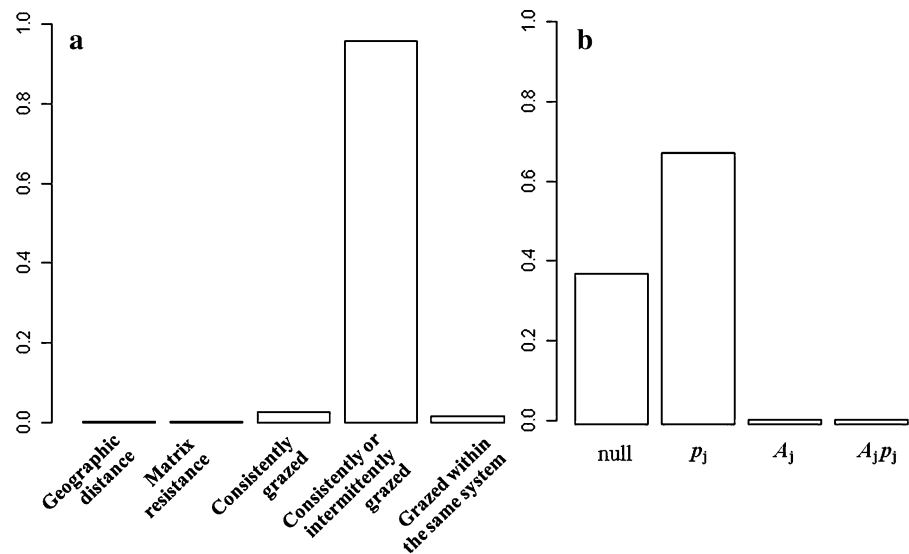
Pre-dispersal effects

For each distance measure, d_{ij} , we calculated four alternative S_i connectivity indices with different assumptions on source patch effects. Model 1 does not include source patch effects A_j or p_j , and thus assumes that all patches are equal sources of propagules, so that patch connectivity S_i depends only on distance d_{ij} between patches. Model 2 includes patch area (A_j), assuming that seed production is proportional to habitat area. Model 3 includes only mean patch species occupancy p_j . Model 4 includes both source patch parameters, assuming that the emigrant propagule pool depends on habitat area (A_j) and species occupancy (p_j).

Post-dispersal effects

We recorded in each previously abandoned grassland how many types of dynamic structural elements were present that are likely to create regeneration niches for the establishment of habitat specialist species (post-dispersal effect): rock debris, erosion, ant hills, and small mammal burrows.

Fig. 2 Relative importance of parameters in the S_i connectivity model. Each bar shows for one version of the distance parameter d_{ij} (a) or pre-dispersal effects (b; *null* = no pre-dispersal effect, p_j = mean patch occupancy in baseline survey, A_j = patch area, and $Ap_j = A_j \cdot p_j$) the sum of Akaike model weights w_m of all candidate models m of connectivity S_i containing that parameter



Data analysis

We used multi-model inference with the function *dredge* in the R library *MuMIn* to rank each of the 20 S_i connectivity models for explaining patch colonization rates, CR_i . For each parameter in the S_i connectivity index, we summed Akaike model weights w_m over all S_i models that contained the parameter of interest to assess its relative importance. For the best performing S_i connectivity index, we performed significance tests and residual analysis and assessed model fit with adjusted R^2 . Subsequently, for the full regression model including the best S_i connectivity index and the number of structural elements in 2009, we applied variation partitioning (Legendre and Legendre 1998) to assess the unique and shared contributions of each factor.

Results

Based on multi-model inference, *consistently or intermittently grazed* was by far the best dispersal model explaining patch colonization rates (CR_i ; relative importance = 0.96, Fig. 2a). For the pre-dispersal effects, the best model was Model 3 with mean species occupancy in 1989 (p_j ; relative importance = 0.63, Fig. 2b), followed by Model 1 (*null*; relative importance = 0.35, Fig. 2b) that only

incorporated distance effects. Interestingly, when source patch area (A_j) was included (Models 2 and 4) the model performed worse than without pre-dispersal effects (Fig. 2b). Thus, the best S_i connectivity index included d_{ij} as *consistently or intermittently grazed* and mean species occupancy p_j as pre-dispersal effect. This model (AIC = -62.6, $w = 0.46$) had well behaved residuals and explained 24% (R_{adj}^2 , $df = 1$ and 59, $F = 19.5$, P value < 0.001) of the variation in community-level patch colonization rates CR_i . Neither the *geographic distance* model (P value = 0.28) nor the *matrix resistance* model (P value = 0.15), both including mean species occupancy p_j , were statistically significant for explaining patch colonization rates CR_i .

Post-dispersal effects in terms of the number of structural elements present alone explained 26% of the variation in CR_i (R_{adj}^2 , $df = 1$ and 59, $F = 22.3$, P value < 0.0001; Fig. 3). Combining S_i and the number of structural elements in the full regression model significantly increased the variance explained to 37% (R_{adj}^2 , $df = 2$ and 58, $F = 18.3$, P value < 0.0001). This model had well-behaved residuals without influential outliers. Variation partitioning showed that the unique contribution of the number of structural elements was 13% of the total variation and the unique contribution of the S_i connectivity index was 11%, with a shared variance of 13%. Repeating the analysis without five species with

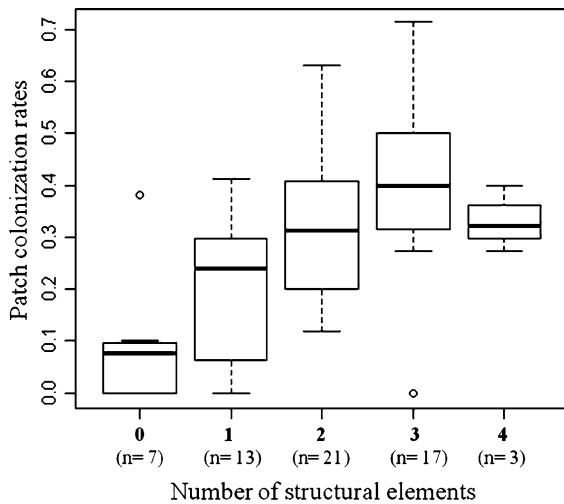


Fig. 3 Side-by-side boxplots of community-level patch colonization rates CR_i for different numbers of structural elements providing regeneration niches (rock debris, small mammal burrows, erosion, ant hills) present in focal habitat patches in 2009

potential issues of detectability between surveys and eight species likely presenting a long-term persistent seed bank did not change the nature or statistical significance of the results (Table 2).

The *consistently and intermittently grazed* model potentially confounds the effects of connectivity by

grazing per se and a distance effect. Omitting the ungrazed patches from the final model estimation reduced the variance explained overall and both by the connectivity model S_i and the structural elements, but all effects remained statistically significant (Table 2). In contrast, further omitting the distance effect by substituting the *grazed within the same system* distance model resulted in an overall non-significant regression model. Similarly, omitting the pre-dispersal effect p_j resulted in non-significant contributions of both the connectivity model S_i and the structural elements (Table 2).

Discussion

Our results clearly demonstrate the importance of connectivity in terms of sheep as dispersal vector for patch colonization at the community level for grassland plant species. Wagner et al. (submitted) found no significant effect of connectivity as calculated from the physical distance between patches, which corresponds to our *geographic distance* model without pre-dispersal effects. We tested alternative dispersal models and found strong evidence that dispersal does depend on distance but in terms of the number of patches that sheep need to traverse

Table 2 Variation partitioning and sensitivity analysis of final model

Data	d_{ij}	p_j	R^2_{adj}	Structural elements	Shared	S_i only
All	Consistently or intermittently grazed	Yes	0.37***	0.13***	0.13	0.11***
Without 5 species with detectability issues	Consistently or intermittently grazed	Yes	0.31***	0.12**	0.11	0.07**
Without 8 species with long-term persistent seed bank	Consistently or intermittently grazed	Yes	0.36***	0.16***	0.13	0.07**
Only grazed patches	Consistently or intermittently grazed	Yes	0.15*	0.07*	0.01	0.07*
Only grazed patches	Grazed within the same system	Yes	0.08 (n.s.)	0.08	0	0
Only grazed patches	Consistently or intermittently grazed	No	0.12*	0.07	0.02	0.03

Each line shows the total variance explained (R^2_{adj}), the unique variance explained by post-dispersal effects (*structural elements*) and by the connectivity model (S_i only) as well as their shared variance explained (*shared*). Models differ by the species or patches included (*data*) and by the inclusion of pre-dispersal effect p_j in the connectivity model S_i . Asterisks indicate statistical significance of the regression model (R^2_{adj}) and of partial regression coefficients (based on Type II sums of squares) for post-dispersal effects (Structural elements) and connectivity (S_i only) (*** P value < 0.001; ** P value < 0.01; * P value < 0.05, n.s.: P value \geq 0.1)

between two sites along grazing routes. This effect remained significant when omitting the variation due to grazed versus ungrazed patches. Although we cannot rule out that a species may have been overlooked in a survey or colonized a patch from the seed bank, our results appear to be robust as omitting species with potential issues of detectability or ability to form a long-term persistent seed bank did not change the nature or statistical significance of the results.

Available evidence from empirical studies in calcareous grasslands based on patch occupancy data showed no consistent trends regarding the effects of habitat loss and isolation. For instance, some studies found that species richness is mostly explained by geographic proximity between patches (e.g., Geertsema 2005; Adriaens et al. 2006; Joshi et al. 2006; Bruckmann et al. 2010), whereas other studies found that patch area is the main predictor of patch species richness (e.g., Krauss et al. 2004; Bisteau and Mahy 2005). The lack of robust and consistent trends may be due to an oversimplified assessment of habitat connectivity and the use of indirect measures of actual functional connectivity, such as patch occupancy patterns instead of colonization rates. For these studies, functional connectivity was assumed to depend exclusively on the source patch area and the physical distances between patches, which ignored the biological processes behind actual functional connectivity (Taylor et al. 1993, 2006).

Probability of patch re-colonization after extinction will decrease as habitat isolation increases (Geertsema 2005; Joshi et al. 2006). However, for plants, dispersal vectors that are likely to transport propagules over longer distances enable plants to partly overcome such limitation (Bruun and Fritzboeger 2002; Nathan et al. 2008). For habitat specialists of calcareous grassland pastures (*Gentiano-Koelerietum pyramidatae* vegetation), sheep are assumed to act as the main dispersal vector (Fischer et al. 1996). Empirical evidence, however, is limited to small field experiments measuring seed adhesive potential and seed distance traveled on few tamed sheep or with experimental coats (Moussie et al. 2005; Manzano and Malo 2006), by germination experiments of dung samples (Kuiters and Huiskes 2010), or indirectly inferred by contrasting species occupancy data between grazed patches with varying grazing history (Reitalu et al. 2010). Our results thus confirm with

empirical data at the landscape scale the role of sheep as dispersal vector for the maintenance of calcareous grassland biodiversity.

From the strong support for connectivity in terms of *consistent or intermittent grazing*, we conclude that some amount of rotational sheep grazing may be sufficient for many species. However, further research is needed to assess whether early flowering species were equally likely to be dispersed to patches that are grazed only later in the season after crop harvesting in surrounding fields. The clear support for a distance effect in terms of number of patches traversed by sheep between two patches suggests that most seeds dispersed by sheep do not stay on the sheep for a long time. This is consistent with previous experimental results, where most seeds fell off the wool within the first days, although both morphologically adapted and non-adapted species were found to persist in the wool for over a month (Fischer et al. 1996).

Repeating our analysis for ungrazed patches only showed no significant effect of connectivity, neither for simple diffusion models (*geographic distance* model, P value = 0.8) nor for the models that assume seeds to be intercepted by intervening forest (*matrix resistance*, P value = 0.9). Since some ungrazed patches experienced colonization events, these events may depend on turbulent wind conditions, where the distance and direction of dispersal may be unpredictable (Soons et al. 2004; Bolli 2009), or other dispersal vectors such as machinery, wild or domestic animals, or humans. Further research using molecular methods may be able to identify likely sources of known colonizations and thus provide further insight into connectivity.

Source patch area is widely used as a proxy of population size and thus of seed production (Moilanen and Hanski 2006). However, including patch area decreased rather than increased explanatory power of the S_i connectivity index, suggesting that habitat area may not be a good proxy for population size for most calcareous grassland plants. Here we did not include population size data as this would require modeling at the species level with binary response data, for which a considerably larger data set would be needed.

In contrast to habitat area, mean species occurrence in 1989 (p_i) significantly improved the model fit of the S_i connectivity index. It is reasonable to expect that if source patches provide a more diverse

propagule pool, community-level patch colonization rates of nearby connected patches will be higher. This positive association supports existing empirical evidence showing that after local species extinction, restoration success of calcareous grasslands depends on diversity of the species pool in nearby patches (Kahmen et al. 2002).

Once a viable seed arrives in a patch of suitable habitat, seedling establishment will be influenced by species interactions (e.g., predation, competition, population density; Orrock et al. 2006) and local environmental conditions (regeneration niches, disturbance; Boehmer 1994; Rusch and Fernandez-Palacios 1995; Willems and Bik 1998). Accounting for post-dispersal processes in terms of the number of dynamic structural elements providing regeneration niches improved model fit R_{adj}^2 markedly from 0.24 to 0.37. While connectivity and post-dispersal effects were correlated, their unique contributions were of the same magnitude (0.11 and 0.13, respectively). Given the highly stochastic nature of the dispersal process and the additional variation that is likely introduced by further post-dispersal factors affecting establishment, growth and mortality (Clobert et al. 2004), the R_{adj}^2 of 0.37 can be considered rather high for a community-level analysis. Further analysis is needed to assess to what degree these results depend on species traits.

Conclusions

Our results show that patch colonization rates at the community level for habitat specialist plant species of calcareous grasslands depend on: (1) the availability of propagules in source patches, (2) the presence of sheep as dispersal vector, at least intermittently, and distance related to the time consumed by sheep herds between source and focal patches, and (3) the number of structural elements providing a variety of regeneration niches for propagule establishment. Modeling connectivity for plant communities based on the physical distance between patches alone (structural connectivity) without considering dispersal vectors and how they respond to landscape structure (potential functional connectivity) may lead to erroneous conclusions about the determinants and importance of functional connectivity in plants. It is equally important to recognize that measures of actual

functional connectivity like colonization rates are the result of dispersal and post-dispersal processes. Thus post-dispersal effects may introduce noise when the focus of interest is on dispersal per se. Based on our comprehensive approach (Fig. 1), it was possible to assess the unique contribution of each process to actual functional connectivity, which is an important concern for species conservation.

This study fills an important research gap regarding the determinants of actual functional connectivity in plant communities (Erik and Priya 2003; Fischer and Lindenmayer 2007) by testing competing connectivity models of seed dispersal with empirical colonization data at the community level. This direct approach is a considerable improvement over indirect methods based on patch occupancy data (Fagan and Calabrese 2006). Comprehensive landscape connectivity assessments that use direct estimates of actual functional connectivity, such as colonization rates and consider pre- and post-dispersal effects are much needed to effectively inform conservation efforts aimed to mitigate, revert or prevent biodiversity loss in fragmented landscapes.

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