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RESEARCH ARTICLE

Habitat suitability mapping for grassland species: using propagule source and grazing activity to predict colonization of restored habitat patches in a historical landscape

Rozália E. Kapás[1,2], Adam Kimberley[1,3], Sara A. O. Cousins[1]

Abstract

Introduction: The recovery of habitats following restoration requires that suitable environmental conditions, propagule sources, and adequate active management all co-occur. Identifying the extent to which these different factors co-exist can support post-restoration actions and pinpoint possible locations for colonization by plant species at a landscape scale. We studied a 400 ha landscape undergoing restoration to identify the suitable habitats for the establishment of grassland communities.
Methods: We combined environmental data for variables which are key for plant species occurrence (vegetation structure, soil moisture, slope range, cover of bedrock) with observational layers of connectivity (proximity to propagule source and livestock activity by using global positioning system collars in the landscape) to classify restored sites according to their potential to support establishment of grassland patches. Using 320 plant inventory plots (1 × 1 m) distributed over the area, we tested the relationship between suitability values from models and aspects of plant community composition.
Results: We found that plant community composition was best explained by the interactions between environmental conditions and the location of propagule source and livestock activity. Greater proximity to propagule sources and the activity of grazing animals increased the likelihood for grassland species to colonize.
Conclusions: Applying suitability maps by using spatial layers in restoration efforts can be a useful tool for locating candidate sites and planning post-restoration management actions. It would allow prioritizing certain locations where restoration could be most effective, for instance by steering the grazing regime to enhance colonization of target species.
Implications for Practice: Spatial analysis that integrates environmental conditions, distance to propagule sources, and grazing activity can effectively predict locations where grassland species are most likely to colonize successfully. Restoration actions should begin by creating and managing small, highly suitable grassland habitats that serve as core areas for colonization. Once the target species establish in these core areas, restoration actions can gradually expand to less suitable areas. Grazing livestock is essential for successful grassland restoration, and its effectiveness can be enhanced through rotational grazing, strategically moving livestock from high to low-suitability areas to maximize seed dispersal and plant establishment.

Key words: connectivity, geographical information system, GPS tracking, grassland restoration, grazing livestock, habitat suitability map

Introduction

Restoring ecosystem and habitats is high on the current international agenda, with the United Nations recently declaring the UN Decade on Ecosystem Restoration (UNEP 2010; UN 2019). In addition to conserving and restoring so-called pristine habitats, there is an increasing awareness that semi-natural habitats play an important role in maintaining biodiversity. Many such habitats have been managed for centuries or millennia through extensive farming practices such as wood cutting, burning, grazing, or mowing, for example, ancient grasslands (Anderson 2006; Bullock et al. 2011; Boch et al. 2020). These ancient semi-natural grasslands support plant species that are reliant on small-scale disturbances that remove large and woody vegetation and suppress competitive species (Dahlstrom et al. 2008; Fuller et al. 2017). Low-intensity management, such as has historically been applied

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[1]Department of Physical Geography, Stockholm University, 10691 Stockholm, Sweden
[2]Address correspondence to R. E. Kapás, email rozalia.kapas@natgeo.su.se
[3]UK Center for Ecology and Hydrology, LL57 2UW Lancaster, UK

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across many European landscapes, often results in a dynamic, heterogeneous mosaic of well-connected habitat patches where a high taxonomic and functional diversity of species are able to disperse between and recolonize suitable patches (Pykälä 2000; Poschlod & WallisDeVries 2002; Evju et al. 2015). In contrast, today's modern, intensively managed landscape is often divided into either agriculture or forestry, with only a small proportion of species-rich remnants of semi-natural or natural grassland habitat (Cousins et al. 2015; Auffret et al. 2018; Bardgett et al. 2021). Species may therefore be less able to disperse through the landscape, existing instead as isolated populations that are less resilient to environmental changes, vulnerable to competition from incoming competitive species, and at greater risk of local extinction (Plue & Cousins 2017; Hooftman et al. 2021).

Most habitat restoration schemes rely on spontaneous recovery of the plant community (Cristofoli et al. 2010; Naaf & Kolk 2015; Damschen et al. 2019). Hence, colonization success is highly dependent on the availability of suitable habitats within the restoration target area. This is primarily determined by environmental conditions such as vegetation structure, topography of the area, and available soil moisture and fertility (Török et al. 2020). Furthermore, the potential for species to disperse through space and to establish following arrival is also key to colonization of restored habitat by target plant species. The possibility for spatial dispersal is determined by species availability, ability of movement, and location of propagule sources in the surrounding landscape (Aavik et al. 2014; Prach et al. 2015; Kapás et al. 2024b), while management-induced disturbance might determine the outcome of spontaneous establishment and hence eventual colonization success (Pykälä 2005; Tälle et al. 2016). Therefore, when restoring habitats, colonization of plant species benefits from connections to species-rich sites and management activities which help the establishment and persistence of target species (Conradi & Kollmann 2016; Kapás et al. 2020; Labadessa et al. 2020). The latter can be an essential element of ensuring functional connectivity for plants, since the ability of movement for plants is dependent on vectors such as wild animals, humans, or grazing livestock both to disperse and establish within a landscape (Tischendorf & Fahrig 2000; Auffret & Plue 2014; Auffret et al. 2017).

Plant species colonization shows a delayed response to environmental change; thus, it takes time to confirm the outcome of any restoration measures which aim to improve habitat suitability, habitat availability, or connectivity (Bagaria et al. 2015; Jackson & Sax 2010; Watts et al. 2020). However, using the interactions between the geography of a landscape, the presence of existing biodiversity hotspots, which may act as a pool of colonizing species, and variation in the intensity or type of management, for instance, the presence of livestock, enables the modeling of landscape suitability that may help managers and practitioners target restoration measures where they can be most effective. Therefore, identifying locations where optimal conditions for grassland species colonization could occur would help to localize candidate sites for restoration actions, and targeted restoration measures could be planned to improve the quality and quantity of habitats in restored areas (Store & Kangas 2001; Burnside et al. 2002; Questad et al. 2014).

In this study, we investigated a 400 ha large landscape around the abandoned hamlet Stensjö, which is undergoing habitat restoration. The restoration aims to recreate the characteristic historical land use surrounding the hamlet. As restoration efforts in the area are driven by reconstructing the historical landscape with grass- and forb-dominated habitats, we focus on the potential for grassland plant communities to colonize in restored sites. Using spatial analysis combining environmental data (vegetation structure, soil moisture availability, slope gradient, and presence of rocky surfaces) with spatial connectivity-related variables, such as links to species-rich source populations and livestock activity in this landscape, we aim to determine locations where grassland species are most likely to successfully colonize following the large-scale restoration. We then test the prediction of our analyses by using vegetation surveys from established plant communities, focusing on different groups of plants such as forest specialists, grassland specialists, and grassland generalists' occurrence in the vegetation. We use grassland specialists to test the value of suitability because these species respond to the management following restoration in a shorter time frame and are indicator species for high biodiversity. These species are most likely to occur on relatively flat surfaces with an open vegetation structure on well-drained soil, and should occur more frequently with higher grazing activity and in close proximity to other species-rich sites. By understanding the interactions between local environmental conditions and restoration efforts in determining varying plant communities over a large scale, we can provide a useful tool for managers to prioritize the management practices to reach the reserve's goal.

Methods

Study Area

The Stensjö cultural reserve (400 ha) is located (57°20′45.13″N, 16°28′0.44″E) in Kalmar County in southern Sweden (Fig. 1). The hamlet has a long-history of small-scale management practices. It is managed and owned by Royal Academy of Letters, History and Antiquities and has served as a County Board Cultural reserve since 2021. Land managers and national agencies aim to recreate and preserve the cultural landscape and how it looked like approximately 120 years ago. Historical records and maps showed that the landscape was characterized by open areas with a mosaic of arable fields, meadows (wet and dry), and pastures and grazed forest in the past. Due to the multipurpose utilization of forest (e.g.; the extensive livestock grazing and as a source of timber and fuel), forests had a more open structure and likely hosted species associated to more open habitats as well as typical forest dwelling species. Land-use changes during the last 60–70 years have resulted in intensively managed conifer forest with a smaller portion of open grassland areas. During the last 10 years, there has been an increasing focus on restoring the landscape by reintroducing forest grazing, rewetting meadows and increasing animal husbandry, thus to reconstructing the traditional infield and outland system in a 180 ha area. Hence, there is a need to identify sites that are particularly suited for grassland species to colonize and could be targeted by post-restoration measures to accelerate the recovery of grassland communities.

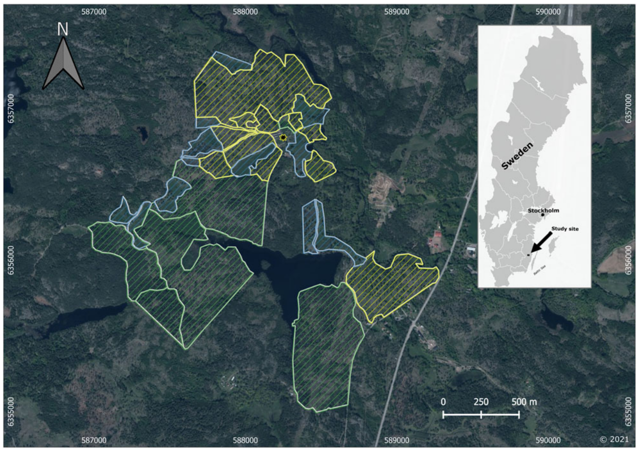

Figure 1. Aerial photograph of the study area, black-yellow star denotes the hamlet, while polygons are indicating sites that are undergoing restoration (ca. 180 ha) and subjected to grazing in the 400 ha Stensjö historical landscape. Yellow and blue dashed polygons represent areas that have been restored for more than 10 years and used as pastures or meadows. Green dashed areas have been restored in the last 5 years. Source: Lantmäteriet, SWEREF 99 TM.

Spatial Variables for Two Different Habitat Suitability Maps

We selected variables that were expected to influence the recruitment of grassland species to map the suitable habitats for target species to colonize in the area. An overview of the different variables used in the spatial analysis can be found in Table S1. In the spatial analysis, we included habitat openness to explain vegetation structure. This variable was derived by calculating the height of trees that occur in the studied areas, subtracting the Digital Elevation Model (DEM) from the Digital Surface Model. We created a binary raster layer (0.25×0.25 m) showing the presence of trees with a height greater than 5 m, and calculated the mean cover of trees taller than 5 m over each cell of a raster grid with a resolution of 2×2 m. This value describes the relative openness (i.e., % of tree cover) of each grid cell. Slope (°) was calculated and extracted from a DEM, and values for soil moisture availability from the national soil moisture map were used to describe soil conditions at sites. The study area is characterized by rocky outcrops and larger stone boulders, which may not be suitable for grassland species to colonize. Therefore, we created a binary layer with the cover of bare bedrock and boulders (%) from rock features (wider than 2 m) digitized manually based on visual interpretation from aerial photo (0.16×0.16 m) over the area.

Each grid cell in the different layers was rescaled to a 0–1 scale, based on its relative suitability for hosting grassland species in a 2×2 m resolution (Supplement S1). The rescaled values were mapped using linear interpolation and by preserving the distribution of the original values, with the exception of soil moisture. As we expect grassland communities to occur on relatively flat and open areas on well-drained soils, where livestock grazing is occurring and species are available for colonization, we scaled the habitat openness values with open and semi-open habitats as high suitability for colonization by grassland species, while closed vegetation was represented by low values. Gentle slopes were categorized as favorable conditions for colonization, while steeper slopes were classified with low values for grassland species colonization (Moeslund et al. 2013). Areas with extremely wet and dry conditions or with higher cover of rocks were categorized as limited suitability for colonization of grassland species, while grid cells with well-drained soil with few rocks were highly suitable for grassland species colonization. This was implemented by reclassifying the soil moisture using a Gaussian function and assigning the preferred value for grassland species (suitability of 1) as the midpoint (15 on the 3–65 scale), and hence suitability values decrease as the original soil moisture value moves from this midpoint towards very dry or wet. See Supplement S1 for the rescaled maps.

Spatial data on distance to species-rich propagule sources and activity of grazing animals were added to the combined environmental variables to test the effect of these variables on suitability values. Distances (Euclidean) to nearest species-rich sites were calculated using field data from available historical maps, management plans, and field observations. We delineated 16 species-rich grassland fragments, mid-field islets, and road verges in the wider landscape, which could serve as a source for colonizing species. We set a maximum distance of 250 m to calculate the potential seed dispersal from these species-rich grassland fragments. This value represents an approximate mean distance that a seed can be dispersed by assisted or unassisted vectors (Thomson et al. 2011). The grid cells close to potential source populations were classified with higher values, while grid cells far from potential colonizing species sources were classified with lower values on a scale from 0 to 1 (Supplement S1).

To evaluate how the grazing animals might affect the habitat suitability and colonization of the species in the area, we used global positioning system (GPS) positions from free-ranging cattle, stationary or rotationally grazing within the fenced grazing areas (Fig. 1). In each herd (ca. 10–15 heifers and calves), a "leader cow" has been tagged with a Pellego GPS unit (Followit AB, Sweden). GPS units collected positions from one cattle for each of four herds at 1-hour intervals in 2022, from three herds at 2-hour intervals in 2021, and from two herds at 4-hour intervals in 2020. The number of GPS fixes was counted for each grid cell (2×2 m) and then rescaled between zero and one across the 3 years of the observational period (in total 15,579 fixes). In grid cells with lower presence of animals, the probability for seeds being dispersed by animals or the likelihood for improving the site conditions through their movement-related activities was low and hence, these locations were categorized as low suitability for species establishment. Conversely, grid cells with high presence of animals represented a high suitability for grassland species to colonize. Using this data on cattle movement enabled us to assess how small-scale variation in livestock activity might influence trends in plant community composition.

We created two suitability maps from these various layers. First, we combined rescaled layers (0–1) for environmental variables (habitat openness, slope gradient, bedrock cover, and soil moisture) to map the co-occurrence of conditions with the different values for potential grassland species colonization. Here, all variables were given equal weighting. This model defines the habitat suitability for grassland species, and the values represent a relative suitability for hosting grassland species in the area, hereafter referred to as environmental suitability. In the next step, we added the rescaled proximity to propagule sources and cattle activity to create another suitability map called environmental suitability with colonization potential, to locate suitable habitats that are nearby to species-rich fragments (structural connections) and visited by livestock that enhance the dispersal and establishment of species (functional connections). We used pairwise Pearson correlation coefficients to evaluate correlations among the raster layers used to map habitat suitability. All correlation values were found to be below 0.15, indicating weak or negligible relationships between the layers. We then compared the differences between the environmental suitability model and the suitability model including distance to propagule sources and grazing activity (i.e., environmental suitability with colonization potential), which allow reflecting on the effect of available source populations and grazing animals on the degree of suitability in the study area. We rescaled the final suitability maps between 0 and 1.

All spatial layers were created in QGIS (version 3.16, QGIS Development Team 2021).

Plant Species Inventory and Grouping of Species to Test Suitability

Inventories of vascular plants were carried out four times between 2019 and 2022 in the study area. Sixty-two transects were randomly placed in different locations within the landscape, perpendicular to slopes or vegetation transition zones. Transects were 25 m long and along every 5 m, the presence of all vascular plant species (including trees, bushes, saplings, and seedlings) was recorded in a 1 × 1 m plot. The nomenclature followed Krok et al. (2013). All occurring species were categorized into three groups based on their response to mowing and grazing management (Tyler et al. 2021). A forest specialist group contained species that are negatively affected by grazing or mowing management, while grassland generalists thrive and survive in both managed and unmanaged habitats. Grassland specialists require grazing or mowing to thrive. Investigating the relationship between grassland specialist and forest specialist occurrence and different suitability maps can reveal the relationship between the habitat conditions identified by our map and plant community composition in the vegetation. See Supplement S2 for the full species list and categories for species from the inventoried plots.

Statistical Analyses

We used the plant species survey to assess the relationship between the modeled value of suitability (0–1) and the number of plant species and species groups. Total species richness summed across the 4 years of inventory data per plot and proportional species richness per different plant species groups (forest specialist, grassland generalist, and grassland specialist) were calculated. Proportional species richness per group was computed by dividing species richness of the different categories by the total species richness per plot. We fitted generalized linear mixed effect models for each response variable with appropriate distributions (four response variables in total: species richness with Poisson distribution, proportional species richness for forest specialist, grassland generalist, and grassland specialist with zero-inflated binomial distribution) using suitability values (0–1) from the environmental suitability map and environmental suitability with potential for colonization map as predictor variables separately for the two suitability maps (*glmmTMB*, McGillycuddy et al. 2025). Transects were included as a random effect to account for the design of the plant surveys. Residuals of models were checked for overdispersion (*DHARMa*, Hartig 2022), confirming normality and homogeneity of distribution.

To assess how plant community composition responds to the changes in the relative potential for grassland species to colonize, we calculated pair-wise beta-diversity between 320 surveyed plots (*vegdist*, Oksanen et al. 2019). We then calculated the difference between the two modeled suitability values, which express the changes in the conditions for being suitable and their relation to the source of propagule and grazing activity. We expect that this approach will identify the variation in community composition and how it is controlled by the environmental conditions, layers of source of propagule, and activity of grazing animals. We fitted a similar linear model with transect as a random effect for testing the relationship between the difference in conditions and beta-diversity (*nlme*, Pinheiro et al. 2020). All statistical analyses and figures were done in R version 4.1.1 (R Core Team 2021).

Results

In the environmental suitability map, which includes habitat openness, bedrock cover, slope range, and soil moisture conditions, the distribution of the suitability values was peaked in the middle of the range (between 0.50 and 0.60) for grassland species to occur (Fig. 2A). Adding spatial and functional connectivity related variables to the habitat suitability map, the shape of the histogram changed and grid cells with relatively higher values (between 0.45 and 0.75) were scattered over a larger range of the study area (Fig. 2B). This means that this landscape has a relatively large amount of habitat available for grassland colonization and these locations are spatially connected to propagule sources or visited by animals frequently, which in turn increases the suitability for grassland

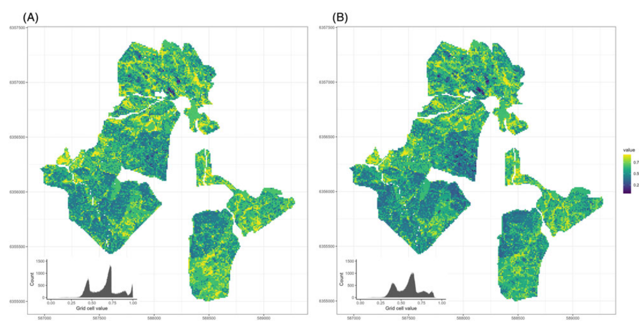

Figure 2. Habitat suitability maps over restored and grazed sites in Stensjö (southern Sweden), showing the value of suitability (low: blue—high: yellow) for colonization of grassland species under different scenarios. Map (A) shows the environmental suitability map (including habitat openness, soil moisture availability, and range of slope together with the presence of boulders). The right-hand map (B) shows the environmental suitability map with proximity to the propagule source for colonizing species and grazing livestock activity as a potential element of functional connectivity. For each map, the inset (histogram) shows the number of grid cells per suitability values.

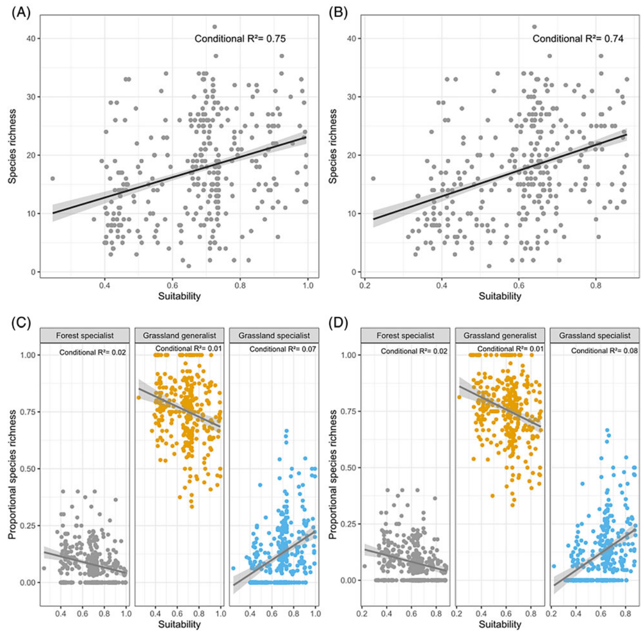

Figure 3. Relationship between the plant community data from 320 surveyed plots and mapped suitability values for (A) total species richness per environmental suitability and (B) values from environmental suitability with proximity to propagule sources and grazing livestock activity (i.e., colonization potential). Relationship between forest specialist, grassland generalist, and grassland specialist (proportional species richness) under different suitability values in environmental suitability map (C) and environmental suitability map with colonization potential (i.e., values of proximity to propagule sources and grazing livestock activity) (D). Significance values can be found in Table S2.

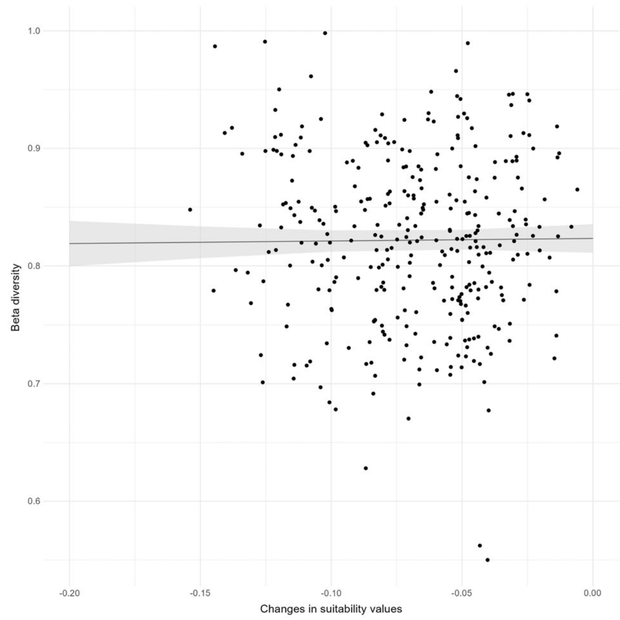

Figure 4. The modeled relationship between differences of mapped suitability values from the habitat suitability of combined environmental layers and habitat suitability model with spatial connectivity and pair-wise beta-diversity between surveyed plots (320).

species to colonize these locations. These values represent the relative suitability to other areas in the study area.

We found a total of 309 plant species in the 320 surveyed vegetation plots (Supplement S2). Using species occurrence data to evaluate the habitat suitability maps, we found that species richness correlated with the mapped values for both habitat suitability maps. Hence, higher values of relative suitability were correlated with higher species richness and spread (Table S2; Fig. 3) in both environmental suitability maps and the environmental suitability map with colonization potential. Based on the vegetation survey, we found that the proportional species richness of the three different species groups varied in relationship with the values from the suitability maps (Table S2; Fig. 3C & 3D). In general, grassland generalist plants (i.e., growing in both managed and non-managed habitats) dominated the plant communities. However, higher proportions of grassland specialist species were present when suitability values were increased, while the presence of forest specialists decreased (i.e., species that were negatively affected by grassland management) with increasing values of suitability for grassland species in both habitat suitability maps (Table S2; Fig. 3C & 3D).

There was a weak trend between the beta-diversity of surveyed plots and the differences in the suitability values between the two maps. The differences in suitability values positively affected the beta-diversity (t-value$_{[257]}$: 0.163; p-value: 0.870), resulting in higher dissimilarity among surveyed plots which was associated with a greater impact of potential from the source of propagule and grazing activity (driving higher changes in the suitability conditions) (Fig. 4).

Discussion

Our spatial analysis of co-occurring conditions for grassland species colonization showed that the majority of the landscape appears to be environmentally suitable for grassland plant species to establish according to our assumptions; hence, the relative suitability of the area for grassland restoration. Through analysis of the current vegetation pattern, we were also able to provide evidence that these habitat conditions are associated with two specific different species groups (grassland specialist vs. forest specialist) that showed different dominance related to identified conditions. This implies that large-scale interaction between vegetation structure, presence of boulders, soil moisture, gradient of slope, together with proximity to propagule sources and activities related to grazing livestock jointly affects the suitability for grassland species colonization on restored areas in the restored landscape. Thus, structural connectivity defined by the amount of suitable habitat in the surrounding landscape and functional connectivity provided by the links to sources of colonizing species via grazing livestock complement each other at a landscape scale in the colonization of species (Brudvig 2011; Auffret et al. 2017; Watson et al. 2017).

The goal with the restoration is to re-create a traditional rural landscape typical for the time period 120 years ago, when livestock husbandry and different types of grassland dominated the landscape. However, large-scale restoration from forest-dominated habitats started only a few years ago, and this was reflected in the overall species composition of the plant communities. By investigating the relationship between the mapped values of suitability and species richness of surveyed plots, it is clear that both maps with the modeled suitability values are associated with higher species richness in the vegetation. Grassland generalist species are most abundant in the established vegetation because many of the sites are still recovering from heavy disturbances where many trees, primarily coniferous trees, were removed at the initial face of the restoration. This means fewer grassland specialist species with dominance of grassland generalist and forest specialist can co-exist at the beginning of community reassembly. Forest specialist species tend to disappear more slowly from the vegetation than the grassland specialists may appear in the newly restored areas (Kotiluoto 1998; Schmid et al. 2017; Kapás et al. 2024a). This is supported by visual validations of the map of the environmental suitability with potential colonization (i.e., connectivity to species source and grazing activity) and in the field survey, where some surveyed plots with higher values are in newly restored (≤5 years) and grazed areas in the southern part of the study area. These plots have a greater proportion of forest specialist and grassland generalist and a lower portion of grassland specialist species, which reflects the slow rate of colonization by grassland specialist species. On the other hand, plots with a high portion of grassland specialist are found in restored grassland areas in the northern part of the landscape. These grassland and hay meadow areas have been restored and managed since the 1970s. Hence, these grasslands represent a good example of how the recently restored habitats with similar conditions may look like in 30 years.

The environmental suitability map alone did provide good information about the co-occurrence of optimal environmental conditions for grassland communities in the study area. However, more locations are associated with relatively higher values for being suitable for hosting grassland communities on environmental suitability with potential colonization. This is because there are more links to nearby populations and/or greater grazing pressure and dispersal potential. Therefore, this model identifies the potential locations, which will be able to recover quicker and where more grassland species can be expected in the landscape. Moreover, the changes between the suitability values show that the restoration creates homogenous habitats (i.e., disturbed soil surface), but the spatial connectivity to sources and livestock activity increases the spatial heterogeneity in the environmental conditions, which subsequently increases the potential for grassland species colonization. Differences in the suitability values between the two maps further highlight the fact that a lower beta-diversity (pairwise) (i.e., plant composition is similar) among the surveyed plots correlated with greater differences in habitat conditions. Thus, sources of colonizing species and grazing homogenize the species composition, even in areas with lower values of environmentally suitable habitats, increasing the overall suitability for grassland colonization. Overall, these results suggest that including nearby species-rich propagule sources in the landscape matrix and grazing livestock that are roaming in the landscape are key factors that determine the potential colonization niches for grassland species. This means that more grassland plants and species will be able to colonize (Öster et al. 2009; Knappová & Münzbergová 2015; Winsa et al. 2015) from nearby species pools, and grazing livestock will continue to improve the effective dispersal of plants between these locations (Fischer et al. 1996; Couvreur et al. 2004; Wagner et al. 2013), creating a positive feedback loop.

The two maps showed different amounts of suitable grassland locations. There are two factors that can explain the differences between patterns observed for changes. One is that the propagule sources for colonizing species are available in the surrounding area, and second is that the grazing animals did utilize the different habitat patches within the study area. By adding the two additional layers to the environmental suitability map, we increased the heterogeneity, which is reflected in the increased values of suitability. This, in turn, appears to affect the number of locations with higher values for colonization, and these locations were either frequently visited by livestock and/or more connected to the propagule sources; thus, they are experiencing positive effects from these two factors. It is known that livestock tend to avoid or show a preference for certain locations in a landscape (Rivero et al. 2021; Svensk et al. 2021), and many plants, especially grassland specialists, are only capable of dispersing small distances (Kiviniemi & Eriksson 1999; Thomson et al. 2011). Thus, these two factors can strongly contribute to the number of potential locations predicted by our model and have important implications for management.

Our habitat suitability maps were constructed using expert-informed scaling of environmental variables to a standardized 0–1 range, assuming a linear increase in suitability with each variable. While this approach is practical and ecologically intuitive, it simplifies potentially complex, nonlinear responses of species to environmental gradients. To improve the predictive reliability of our map, future work should aim to refine suitability indices using occurrence data and statistical modeling (i.e., data-driven suitability assessments) and not just be based on ecological knowledge and supported by the observed correlation with species richness.

Given the patterns identified by our maps, management should focus on distributing the livestock movement around areas with higher values for suitable locations and where sources of species are available for grassland colonization. This would enhance the probability for grassland species to establish first in these locations. By installing feeding or salting points near the target locations (i.e., locations with higher suitability), management can help steer livestock to these areas. The increased presence of livestock induces local disturbances and would improve soil conditions (i.e. microsites for seeds) for colonization (Gibson & Brown 1991; Kladivová & Münzbergová 2016; Kapás et al. 2024a). The activities from grazing animals are important as they open up the vegetation sward and improve the soil conditions via fertilization or soil structure modification (Bullock et al. 1994; Pakeman & Small 2005; Eichberg & Donath 2018). Furthermore, applying rotational grazing among sites that are abundant in propagule sources with sites that have a limited amount of propagule sources (or are distant from species-rich sites) would improve the functional connectivity for grassland species (Auffret et al. 2012; Wagner et al. 2013). It would enhance the effective dispersal of grassland species from propagule sources to locations with lower potential for grassland colonization (Auffret et al. 2012; Rico et al. 2012; Kapás et al. 2020). The timing of grazing would be crucial to ensure that plants have seeds and that livestock can disperse seeds into locations, and the dispersed seeds would have favorable conditions at the site to germinate and establish (Gibson & Brown 1991; Kiviniemi & Eriksson 1999).

In case of larger landscape restorations like our study area, the primary aim should be to successfully recreate a number of small-scale locations, that is, highly suitable habitats, to ensure high species diversity and high occurrence of plant specialists at a smaller scale. Hence, these locations can turn into sources of colonizing species in the larger landscape scale and afterwards, habitats with lower suitability conditions can be gradually involved in the post-restoration management plan. By applying this approach, management could fully utilize the functional connectivity offered by the grazing livestock to improve grassland habitat quality (Rico et al. 2012; Plue et al. 2019) to reach a realistic goal to help the recovery of grassland communities (Buisson et al. 2022; Nerlekar et al. 2024). While we recognize the limitations of our method, we believe it provides a useful starting point that balances simplicity and ecological insight.

In conclusion, we showed that habitat suitability maps are a useful landscape-planning tool by identifying locations that are suitable for plant colonization and to aid integrative and pro-active restoration actions (e.g. by steering the movement of animals to higher than lower suitability). It is important for the long-term persistence of biodiversity in restored landscapes that management includes the habitat complexity over large scale, but the principal aim should be to promote habitat connectivity and create more stable and sustainable grassland communities at smaller scale first (Watson et al. 2017; Aavik & Helm 2018). In addition, the quality of grassland habitats could be enhanced by linking existing and restored habitats via livestock grazing with a well-managed and planned rotationally grazing schedule.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Overview of environmental variables used in habitat suitability maps for investigating interaction between the available habitats and connectivity for potential colonization of grassland communities at a landscape scale.

Table S2. Results from models of species richness and proportional species richness for different species groups from 320 surveyed plots in Stensjö, southern Sweden.

Supplement S1. Rescaled maps.

Supplement S2. Full species list and categories for species from the inventoried plots.

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