Dispersal of open habitat and woodland plant species using semi-open landscapes as stepping stones

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Eliane Angharad Travers

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Erstbetreuer: Prof. Dr. Werner Härdtle, Leuphana Universität Lüneburg
Zweitbetreuer: Prof. Dr. Diethart Matthies, Philipps-Universität Marburg
Erstgutachter: PD Dr. Andreas Fichtner, Leuphana Universität Lüneburg
Zweitgutachter: Prof. Dr. Diethart Matthies, Philipps-Universität Marburg
Drittgutachter: Prof. Dr. Joachim Schrautzer, Christian-Albrechts-Universität zu Kiel

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What you do makes a difference, and you have to decide
what kind of difference you want to make.

- Jane Goodall

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Summary

Biodiversity loss has advanced at an alarming rate in recent years. Man-made habitat fragmentation is one of the major reasons for plant diversity loss. The increase of changing land use and infrastructure expansion impedes the genetic exchange between populations and drives the loss of genetic diversity resulting in population losses and species extinction. On top, habitat fragmentation potentiates the effects of climate change, by hindering much needed species migration and adaptation to shifts in phenology or species range. To counteract the adverse effects of habitat fragmentation, linear dispersal corridors were introduced to connect same-type habitats with each other and enhance species dispersal between these habitats. In an exhaustive literature review, this thesis has dealt with the benefits and shortcomings of linear dispersal corridors for plant dispersal and has shown that the results for successful plant dispersal are mixed and that linear dispersal corridors are not always a perfect solution. This thesis then focusses on the possibility of linear dispersal corridors (e.g. woodlands) forming a barrier for other habitat types (e.g. open habitats) and with that, becoming an obstruction for plant dispersal (e.g. open habitat species).

Looking for alternative solutions for plant dispersal, this thesis concentrates on European pasture landscapes, which have been managed by livestock grazing over centuries and today, are made up by a mosaic of open habitat patches, single trees and tree groups and feature a high phytodiversity. The high structural diversity of these semi-open pasture landscapes offers a variety of environmental conditions and therefore, these semi-open pasture landscapes are able accommodate species with various habitat requirements. Taking the structural diversity of these so-called "semi-open habitats" into account, they may be able to simultaneously connect patches of both open habitats and woodlands and serve as a "semi-open corridor" promoting species dispersal of both habitat types. However, due to plants' sessile character and thus limited dispersal power, plants' diaspores may not be able to disperse through the full extent of a corridor during a single dispersal event. The seeds may have to recruit seedlings and reproduce after establishment, so that a new seed can disperse further. In this case, semi-open corridors act as stepping stones and therefore, the complete plant life cycle must be taken into consideration when researching plant dispersal into semi-open habitats. Thus, an observational study surveying the occurrence of open habitat and woodland plant species in semi-open habitats and an experimental setup with open habitat and woodland plant species sown into semi-open habitats investigating their recruitment ability in two different geographical settings in Germany form the basis of this thesis.

By comparing the vegetation of surrounding open habitats and woodlands with semi-open habitats in the observational study, I was able to show that 73% of open habitat species and 39% of woodland species were also recorded in semi-open habitats. Plant communities of semi-open habitats were more similar to open habitats than to plant communities of woodlands. About two-thirds of woodland species were not present in semi-open habitats, mainly driven by stenoecious behaviour and dispersal-limitations such as high seed mass, short-distance dispersal mechanisms or having a transient seed bank and a high flowering age. Species' site requirements such as light and soil moisture also restricted woodland species in their migration. However, semi-open habitats still offered shelter to about one third of the woodland species. Therefore, this thesis confirms that woodland and open habitat plant species can occupy semi-open habitats. In addition, semi-open habitats featured a high phytodiversity and may be potential species pools for the colonisation of adjacent habitats.

The recruitment success of the open habitat and woodland species sown into plots in semi-open habitats during the experimental setup was driven by a species identity effect and to a lesser extent by a species type effect. Recruitment strongly depended on functional species traits and environmental setting (e.g. canopy closure) and differed between geographical settings. Species' seed mass regulated recruitment in the first years. Later the species requirement for light and the effects of the site's canopy closure also became relevant. This thesis was investigating different disturbance treatments to deduce management recommendations. As a result, I found that recruitment was promoted when the topsoil was removed beforehand.

Open habitat and woodland species were both present in semi-open habitats, woodland species clearly limited by their stenoecious traits. Both were also able to germinate and recruit in semi-open habitats, showing different success rates depending on the local setting and their individual species traits. Therefore, this thesis provides evidence that semi-open corridors allow to mitigate the effects of habitat fragmentation for open habitat and woodland plant species by offering stepping stone habitats for their dispersal, to a certain extent. The results of both studies also emphasize the need for highly structurally diverse semi-open habitats, which offer a variety of site conditions that can shelter species with different habitat requirements. The gained knowledge helps to improve our understanding of what drives the dispersal of open habitat and woodland species and how we can manage semi-open corridors accordingly.

Zusammenfassung

Der Verlust der biologischen Vielfalt ist in den letzten Jahren in alarmierendem Tempo fortgeschritten. Die vom Menschen verursachte Fragmentierung von Lebensräumen ist einer der Hauptgründe für den Verlust der Pflanzenvielfalt. Die zunehmende Veränderung der Landnutzung und der Ausbau der Infrastruktur verhindern den genetischen Austausch zwischen den Populationen und treiben den Verlust der genetischen Vielfalt voran, was zu Populationsverlusten und zum Aussterben von Arten führt. Darüber hinaus verstärkt die Lebensraumfragmentierung die Auswirkungen des Klimawandels, indem sie die dringend benötigte Ausbreitung von Arten und die Anpassung an Veränderungen in der Phänologie oder im Artenspektrum verhindert. Um den negativen Auswirkungen der Lebensraumfragmentierung entgegenzuwirken, wurden lineare Ausbreitungskorridore eingeführt, die gleichartige Lebensräume miteinander verbinden und die Ausbreitung von Arten zwischen diesen fördern. Die vorliegende Dissertation hat sich in einer umfassenden Literaturrecherche mit den Vorteilen und Nachteilen linearer Ausbreitungskorridore für die Ausbreitung von Pflanzen befasst und zeigt auf, dass die Ergebnisse für eine erfolgreiche Ausbreitung von Pflanzen unterschiedlich ausfallen und dass lineare Ausbreitungskorridore nicht immer eine perfekte Lösung darstellen. Diese Dissertation konzentriert sich anschließend auf die Möglichkeit, dass lineare Ausbreitungskorridore (z. B. Wald) eine Barriere für andere Lebensräume (z. B. Offenland) bilden und damit ein Hindernis für die Ausbreitung von Pflanzen (z. B. Offenlandarten) darstellen.

Auf der Suche nach alternativen Lösungen für die Ausbreitung von Pflanzen konzentriert sich diese Dissertation auf europäische Weidelandschaften, die seit Jahrhunderten durch die Beweidung mit Vieh bewirtschaftet werden und heute aus einem Mosaik von Offenland, Einzelbäumen und Baumgruppen bestehen und eine hohe Phytodiversität aufweisen. Die hohe Strukturvielfalt dieser halboffenen Weidelandschaften bietet eine Vielzahl von Standortbedingungen, so dass diese halboffenen Weidelandschaften Arten mit unterschiedlichen Lebensraumansprüchen beherbergen können. In Anbetracht der strukturellen Vielfalt dieser so genannten "halboffenen Lebensräume" könnten sie in der Lage sein, gleichzeitig Offenländer und Wälder miteinander zu verbinden und als "halboffener Korridor" zu dienen, der die Ausbreitung von Arten beider Lebensräume fördert. Aufgrund des sesshaften Charakters von Pflanzen und der damit verbundenen begrenzten Ausbreitungsfähigkeit sind die Diasporen der Pflanzen jedoch möglicherweise nicht in der Lage, sich während eines einzigen Ausbreitungsvorgangs über die gesamte Ausdehnung eines Korridors zu verbreiten. Die Samen müssen möglicherweise Sämlinge rekrutieren und sich nach der Etablierung vermehren, damit sich ein neuer Samen weiterverbreiten kann. In diesem Fall dienen halboffene Korridore als Trittsteine, so dass bei der Erforschung der Ausbreitung von Pflanzen in halboffene Lebensräume der gesamte Lebenszyklus der Pflanzen berücksichtigt werden muss. Daher bilden eine Beobachtungsstudie, in der das Vorkommen von Offenland- und Waldpflanzenarten in halboffenen Lebensräumen untersucht wurde, sowie ein Versuchsaufbau mit Offenland- und

Waldpflanzenarten, die in halboffene Lebensräume zur Untersuchung ihrer Rekrutierungsfähigkeit ausgesät wurden, in zwei verschiedenen geografischen Lagen in Deutschland die Grundlage für diese Dissertation.

Durch den Vergleich der Vegetation der umliegenden Offenländer und Wälder mit den halboffenen Lebensräumen in der Beobachtungsstudie konnte ich aufzeigen, dass 73 % der Offenlandarten und 39 % der Waldarten auch in den halboffenen Lebensräumen zu finden sind. Die Pflanzengemeinschaften der halboffenen Lebensräume waren denen der Offenländer ähnlicher als den Pflanzengemeinschaften der Wälder. Etwa zwei Drittel der Waldarten kamen in halboffenen Lebensräumen nicht vor, was vor allem auf stenöke Eigenschaften und Ausbreitungseinschränkungen zurückzuführen ist, wie z. B. eine hohe Samenmasse, Ausbreitungsmechanismen über kurze Entfernungen oder eine flüchtige Samenbank und ein hohes Blühalter. Auch die Standortanforderungen der Arten wie Licht und Bodenfeuchtigkeit schränkten die Waldarten in ihrer Ausbreitung ein. Halboffene Lebensräume boten dennoch etwa einem Drittel der Waldarten Schutz. Diese Dissertation bestätigt also, dass Wald- und Offenlandpflanzenarten halboffene Lebensräume besiedeln können. Darüber hinaus wiesen halboffene Lebensräume eine hohe Phytodiversität auf und können potenzielle Artenpools für die Besiedlung benachbarter Lebensräume sein.

Der Rekrutierungserfolg der Offenland- und Waldarten, die während des Versuchsaufbaus in Plots in halboffenen Lebensräumen ausgesät wurden, wurde durch einen Artenidentitätseffekt („species identity") und in geringerem Maße durch einen Artengruppeneffekt („species type") bestimmt. Die Rekrutierung hing stark von den funktionalen Merkmalen der Arten und den Standortbedingungen ab (z. B. Kronenschluss) und unterschied sich je nach geografischer Lage. In den ersten Jahren wurde die Rekrutierung durch die Samenmasse der Arten bestimmt. Später wurden auch die Lichtbedürfnisse der Arten und die Auswirkungen des Kronenschlusses des Standorts relevant. In dieser Dissertation wurden verschiedene Bodenstörungen untersucht, um daraus Empfehlungen für die Bewirtschaftung abzuleiten. Dabei stellte ich fest, dass die Rekrutierung gefördert wurde, wenn der Oberboden vorher entfernt wurde.

Sowohl Offenland- als auch Waldarten waren in halboffenen Lebensräumen zu finden, wobei die Waldarten durch ihre stenöken Eigenschaften eindeutig eingeschränkt waren. Beide waren auch in der Lage, in halboffenen Lebensräumen zu keimen und zu rekrutieren, wobei die Erfolgsquoten je nach den örtlichen Gegebenheiten und den Merkmalen der einzelnen Arten unterschiedlich waren. Daher liefert diese Dissertation den Beweis, dass halboffene Korridore die Auswirkungen der Lebensraumfragmentierung für Offenland- und Waldpflanzenarten abschwächen können, indem sie ihnen bis zu einem gewissen Grad Trittsteinhabitate für ihre Ausbreitung bieten. Die Ergebnisse beider Studien unterstreichen auch die Notwendigkeit strukturell sehr vielfältiger halboffener Lebensräume, die eine Vielzahl von Standortbedingungen bieten, die Arten mit unterschiedlichen Lebensraumansprüchen beherbergen können. Die gewonnenen Erkenntnisse tragen dazu bei, besser zu verstehen, was die Ausbreitung von Offenland- und Waldarten fördert und wie wir halboffene Korridore entsprechend bewirtschaften können.

1. General Introduction

1.1 Habitat fragmentation and its consequences

Land use changes and infrastructure expansion have resulted in increased landscape fragmentation, deterioration of habitat quality and habitat loss (Haddad *et al.* 2015; Hadley & Betts 2016; Evans *et al.* 2017). The remaining patches of many habitats are often separated from each other in an unsuitable landscape matrix. Consequently, plant dispersal between habitat patches is limited and habitat re-colonisation has become increasingly difficult. Especially in small and fragmented populations of plants, changes in population dynamics, such as reduced pollination and the lack of genetic exchange result in diminished genetic diversity, facilitate population losses and an increased risk of species extinction (Young *et al.* 1996; Fahrig 2003; Matthies *et al.* 2004, Xiao *et al.* 2016). Dispersal-limited plant species in particular are affected by habitat fragmentation (Plue & Cousins 2018).

On top of that, interactions between global change drivers and habitat fragmentation may exacerbate the negative effects on biodiversity. For example, climate change causes shifts in the range of species or their phenology. Habitat fragmentation in turn inhibits species migration and adaptation and therefore, may potentiate the effects of climate change (Leimu *et al.* 2010). The lack of genetic exchange due to limited species migration and habitat re-colonisation accelerates species extinction in the face of climate change (Christmas *et al.* 2016; Auffret *et al.* 2017). Therefore, there is urgency to mitigate the negative effects of habitat fragmentation (Opdam 2004; Heller & Zavaleta 2009; Leimu *et al.* 2010; Beier 2012; Barber *et al.* 2015), and large-scale networks are needed to preserve biodiversity in the long term.

1.2 Linear dispersal corridors and stepping stones: Benefit and shortcomings

"Dispersal corridors" and "stepping stones" have been proposed to mitigate the negative effects of progressing habitat fragmentation and have been established across the landscape to connect isolated patches of the same habitat type (Keitt *et al.* 1997; Rosenberg *et al.* 1997; Damschen *et al.* 2014; Saura *et al.* 2014; Herrman *et al.* 2016; Kormann *et al.* 2016). Dispersal corridors are often defined as linear structures (Forman & Godron 1986; Csuti 1991; Wilkerson 2013) which are similar to the habitat patches which are to be connected and differ from the surrounding matrix (Barrett & Bohlen 1991; Vos *et al.* 2002). Various forms of dispersal corridors have been established for different habitat types. For example, hedgerows have been used to connect woodland patches, roads and paths connect pastures and grasslands and rivers serve as link for many different types of habitats (Kirchner *et al.* 2003; Damschen *et al.* 2006; Roy & de Blois 2006). These dispersal corridors are considered to serve as habitat linkages and by connecting isolated habitat patches with each other, movement and dispersal between these habitat patches is enhanced (Rosenberg *et al.* 1997; Tewksbury *et al.* 2002). By facilitating the re-colonisation of habitat patches where species have become extinct and by increasing gene flow between isolated populations, dispersal corridors have the potential to alleviate the effects of habitat fragmentation (Mech & Hallett 2001; Tewksbury *et al.* 2002). However, there are also concerns that corridors may facilitate the spread of invasive species and diseases, increase edge effects, and act as additional barriers between habitat patches (Simberloff & Cox 1997; Dobson *et al.* 1999; Eggers *et al.* 2010; Krewenka *et al.* 2011; Dennis *et al.* 2013; Haddad *et al.* 2014).

While the implications of linear dispersal corridors for animal dispersal have been comprehensively researched, little is known about their value for plant dispersal (Tewksbury *et al.* 2002; Calçada *et al.* 2013; Damschen *et al.* 2014). Due to their sessile character and thus limited dispersal power, the effectivity of corridors is more difficult to evaluate for plants than for animals (Csuti 1991; Vos *et al.* 2002*).* First, diaspores may not be able to disperse through the full extent of a corridor during a single dispersal event. Secondly, the seeds may have to recruit seedlings in a corridor and reproduce to develop a new seed which disperses further (Figure 1). Thus, it may take several generations for new diaspores to colonise target habitat patches (Damschen *et al.* 2008; Figure 1). In this case, corridors act as stepping stones (Pearson & Dawson 2005; Suárez-Esteban *et al.* 2016). For successful recruitment upon arrival, seeds require appropriate environmental conditions (Eriksson 2000; Nathan 2006). Thirdly, plant diaspores strongly depend on vectors and external agents to be dispersed (Bonn & Poschlod 1998; Jongman *et al.* 2004; Carlo *et al.* 2013; Liira & Paal 2013) which in turn may also be affected by habitat fragmentation (Leimu *et al.* 2010). Therefore, success of species dispersal through corridors depends strongly on the availability of suitable dispersal agents and/or on appropriate environmental conditions to accommodate for the different plant life stages (Calçada *et al.* 2013; Lõhmus *et al.* 2014). Hence, creating a suitable corridor for plant dispersal is challenging. So far, the difficulty of monitoring the stochastic diaspore dispersal and seedling establishment at target habitat patches has restricted the research on plant dispersal through corridors (Murphy & Lovett-Doust 2004).

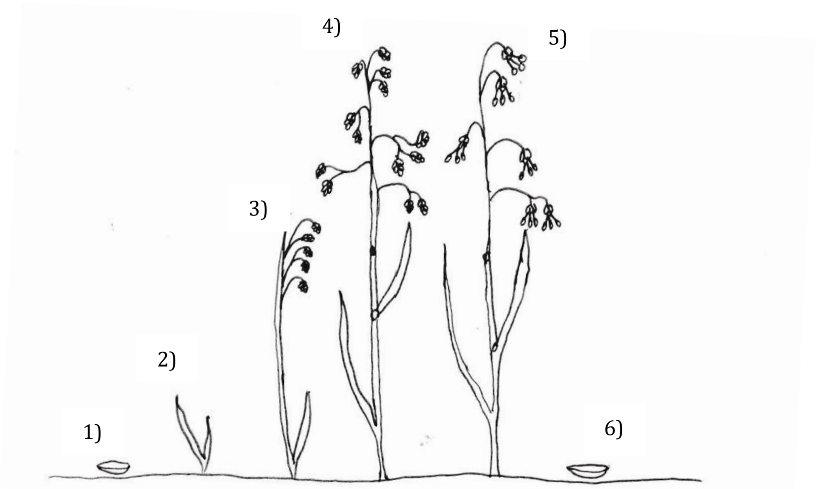

Figure 1: Simplified schematic overview of a plant life cycle using the example of Briza media illustrating the different stages which must be considered during plant dispersal: 1) seed germination, 2) emergence, 3) establishment, 4) persistence, 5) reproduction and again 6) seed germination.

To date research of various linear corridor types has shown successful plant dispersal through these corridors (Tewksbury *et al.* 2002; Townsend & Levey 2005; Calçada *et al.* 2013; Suárez-Esteban *et al.* 2013). However, other linear corridor types failed to connect isolated habitat patches (McCollin *et al.* 2000). Using the example of hedgerows, they failed to serve as dispersal corridor for stenoecious woodland species. Woodland species often only occurred in low abundances in hedgerows, and stenoecious species such as ancient woodland indicators were not recorded (McCollin *et al.* 2000; Roy & de Blois 2006; Bailey 2007; Wehling & Diekmann 2009). Many woodland species were only found in hedgerows close to the woodlands, and their density decreased further away from woodland donor populations. This is a result of environmental differences between hedgerows and woodlands (Corbit *et al.* 1999; Sarlöv Herlin & Fry 2000; Wehling & Diekmann 2009). While hedgerows are often more nutrient-rich, drier and have higher light availability, woodland interiors contain less nutrients, feature a humid microclimate and a closed canopy (Roy & de Blois 2006; Wehling & Diekmann 2008). Moreover, the presence of woodland species in hedgerows depended on their dispersal characteristics. Animal-dispersed plants dispersed were recorded farther from woodlands, however wind-dispersed species were found more closely to the woodland edges (Corbit *et al.* 1999; Sarlöv Herlin & Fry 2000; Wehling & Diekmann 2009). Species using vegetative dispersal showed very limited dispersal into hedgerows (McCollin *et al.* 2000). Most herbaceous woodland species are dispersal-limited short-distance dispersers and less likely to benefit from dispersal corridors (Calçada *et al.* 2013). Several generations would have to recruit and reproduce in the hedgerow corridor for the next generation to travel onwards (Brunet & von Oheimb 1998; Calçada *et al.* 2013). These species are more likely to use corridors as stepping stones and if corridors are not able to cater for the different life stages, they cannot accommodate these species (Orrock & Damschen 2005). The success rate of linear dispersal corridors is highly interconnected to species' environmental requirements and corridor specificity.

The efficacy of linear dispersal corridors also highly depends on corridor shape and the surrounding matrix. The matrix, the environment surrounding the corridor, is often thought to be uniform, however, it may be diverse and strongly interact with the corridor (Baum *et al.* 2004; Bender & Fahrig 2005; Wilkerson 2013). Nevertheless, the effect of the matrix on linear dispersal corridors is often not noted. Also, the linear shape of dispersal corridors results in increased edge effects. External influences such as agricultural fertilisers, pesticides and mulching may impact corridor edges (Simberloff *et al.* 1992; Van Dorp 1996; Haddad *et al.* 2011) and depending on the width of the corridor, may also affect corridor interiors. The efficacy is also related to the structural difference between corridor and matrix (Anderson & Jenkins 2006; Hilty *et al.* 2006). Corridors have shown a spill over effect into the surrounding habitats where species richness in the matrix increased up to 10 to 18% than before the corridor existed (Brudvig *et al.* 2003). A highly hostile or structurally different matrix, on the other hand, can impair the success of the dispersal corridor (Kupfer *et al.* 2006; Van Geert *et al.* 2010). When plant species depend on dispersal vectors, they may have a lower chance to disperse if the vectors are affected by the matrix (Prevedello & Vieira 2010; Van Geert *et al.* 2010; Van Geert *et al.* 2014).

A largely underestimated limitation in corridor research is the creation of new dispersal barriers when linear corridors are intersecting another habitat. Most corridors were designed to connect patches of one type of habitat with each other. However, corridors can also act as barriers for species dispersal if they intersect other habitat types (Dobson *et al.* 1999; Van Dijk *et al.* 2014). For example, hedgerows frequently connect isolated woodland patches, but hedgerows often run through meadows and pastures separating grassland patches from each other. Also, grassland habitats along power lines may act as corridor for pioneer or grassland species (Lampinen *et al.* 2015). However, power lines often intersect woodlands creating barriers for woodland species (Luken *et al.* 1991; Eyitayo 2014). Especially in large landscape mosaics with different habitat types, dispersal corridors can create new barriers which increase the effects of habitat fragmentation (Forman & Alexander 1998; Hess & Fischer 2001; Kuefler *et al.* 2010). European pasture landscapes such as the Luneburg Heath and the Swabian Jura form such landscape mosaics consisting of open habitats such as heathland and grasslands as well as woodlands. Open habitat corridors crossing woodland to link open habitats with each other impede the dispersal of woodland species and *vice versa* (Eggers *et al.* 2010) and can have harmful effects on species dispersal in intersected habitats (Assmann & Janssen 1999; Dobson *et al.* 1999; Campagne *et al.* 2009; Van Dijk *et al.* 2014). Especially dispersal-limited plant species or species reliant on habitat-specific vectors are limited in their movement across corridors of other habitat types (Campagne et al 2009). These barriers also hinder the establishment of stenoecious plants in stepping stones due to the lack of suitable environmental conditions, thus, these plant species fail to colonise new habitat patches. Consequently, linear dispersal corridors seem to be a useful tool to link habitats surrounded by a hostile matrix such as infrastructure or arable land, but they do not qualify for connecting large landscape mosaics.

1.3 Overcoming the weaknesses of linear dispersal corridors with semi-open corridors

Grazing and alternate husbandry have produced vast pasture landscapes stretching across Europe over the last centuries which feature a very high species diversity (Poschlod *et al.* 1998; Finck *et al.* 2002; Jedicke 2015). These pasture landscapes are characterised by a mosaic of open habitat patches and single trees, tree groups and shrubs (Bergmeier *et al.* 2010; Figure 2). The combination of grazing management and successional developments in these landscapes have led to a structural heterogeneity of open as well as densely vegetated patches with differing canopy closures (Popp & Scheibe 2013), including soft transitions between open landscapes and smaller forest patches (Poschlod *et al.* 1998; von Oheimb *et al.* 2006; Jedicke 2015). The comprehensive structural diversity in turn resulted in a variety of environmental conditions (i.e. light availability, soil moisture and nutrient levels). Therefore, these landscapes are able to accommodate species with various habitat requirements (Bergmeier *et al.* 2010) and are often referred to as “semi-open habitats” (Eggers *et al.*

2010). In Europe, semi-open habitats are characterised by an extraordinary species richness and host a large proportion of the European biodiversity, including many endangered animal and plant species (Poschlod *et al.* 1998; Luick 2009; Jedicke 2015). However, abandonment, afforestation and the increase of intense farming practices have resulted in deterioration and loss of these landscapes (Bergmeier *et al.* 2010). The remains of these landscapes are protected in many parts of Europe nowadays, and management schemes are devised to conserve their structural and biological diversity (von Oheimb *et al.* 2006).

Figure 2: Different types of semi-open pastures in the Lueneburg Heath (a) with Calluna vulgaris, Vaccinium myrtillus and different oak trees (Quercus robur, Q. petraea) and in the Swabian Jura (b) with Bromus erectus, Juniperus communis, Prunus spinosa and scattered oak and beech trees (Quercus robur, Fagus sylvatica).

The mosaic structure and the patchy distribution of open and densely vegetated areas in semi-open pasture landscapes contrast with the linear structure of conventional corridors (Figure 3). Due to the structural diversity, semi-open habitats are able to shelter both species of woodlands and open habitats simultaneously (Eggers *et al.* 2010). As a consequence, semi-open habitats may possibly act as corridors (“semi-open corridors”) for both woodland and open habitat species. Instead of forming an uninterrupted crossing to one habitat type, semi-open corridors offer a sequence of stepping stones for many species and provide ecotones between different habitat types (Poschlod *et al.* 1998; von Oheimb *et al.* 2006; Jedicke 2015). Therewith, they also reduce the sharp contrast between corridors and the surrounding matrix and counteract edge effects (i.e. by forming softer edges; Haddad *et al.* 2014). From a species conservation perspective, the establishment of semi-open corridors could thus be a promising approach to mitigate the effects of habitat fragmentation and avoid the barrier-effects which are caused by conventional corridors that intersect other habitat types. The positive effects of semi-open corridors have been demonstrated on the dispersal of both woodland and open habitat ground beetles (Eggers *et al.* 2010). However, little is known about the suitability of semi-open corridors for plant dispersal, and whether semi-open habitats can facilitate the dispersal of both woodland and open habitat species. As mentioned above, plant species strongly depend on vectors for dispersal or have to be provided with stepping stones as a way of step-by-step dispersal. In order to serve as stepping stone and to support the dispersal process of plants, semi-open corridors must accommodate for the different plant life stages by offering appropriate environmental conditions for reproduction, but also serve as corridors for dispersal vectors.

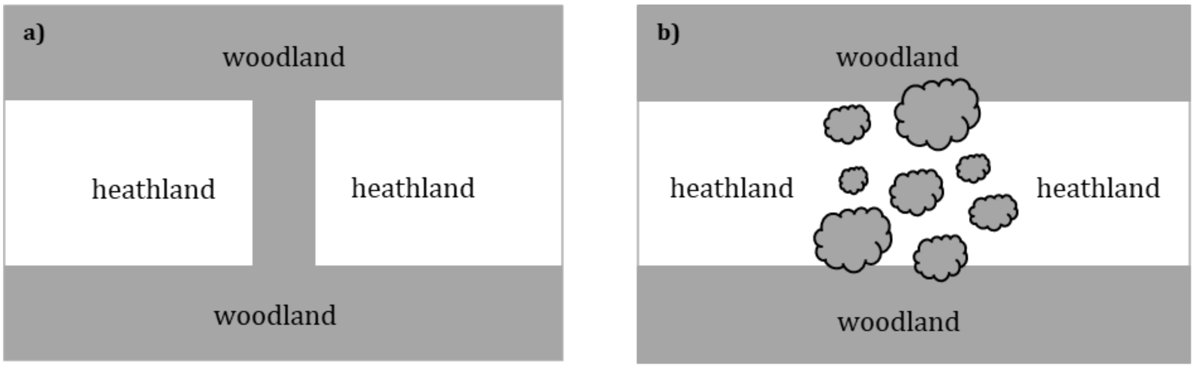

Figure 3: Schematic illustration of (a) a linear woodland corridor dissecting a heathland creating a barrier for heathland species, and (b) a semi-open corridor featuring a mosaic of trees, shrubs and open patches offering stepping stone habitats for species of both woodlands and heathlands.

1.4 Aims and research questions

In the face of ongoing biodiversity losses in cultural landscapes there is an urgent need to create measures that are appropriate to mitigate the adverse effects of habitat fragmentation. As linear corridors have not always been able to counteract the consequences of habitat fragmentation, semi-open corridors are introduced as a new concept to limit habitat fragmentation effects on a landscape-level that cannot be offset by linear corridors. To date there is no information available how semi-open habitats can act simultaneously as corridors for woodland and open habitat plant species.

This thesis analysed the potential of semi-open corridors as a tool to mitigate the impairments of habitat fragmentation in cultural landscapes on woodland and open habitat plants species. It was conducted within the framework of the research and development project "*Ecological role of semi-open corridors*" ("*Ökologische Funktion von halboffenen Verbundkorridoren")* funded by the Federal Agency for Nature Conservation (*Bundesamt für Naturschutz*). The project quantified to what extent semi-open habitats – comprised of wooded and open habitat patches – may serve different plants species as dispersal corridors. As traditional linear dispersal corridors mostly connect similar habitat types and would form a barrier between different habitat types, semi-open habitats such as wood edges, woodland pastures or semi-open pastures could be a possible solution to interconnect different habitat types and thus overcome habitat fragmentation and its damages. The scope of the research project included research on the role of semi-open corridors for dispersal of invertebrate and vascular plant species of woodlands and open habitats. To allow a broad applicability of the implementation of semi-open corridors, the study took different geographical locations and with that, different geological and edaphic conditions, into account and carried out research in different habitat types across Germany.

The research addressed the following questions:

1) What research has been done on linear and semi-open plant dispersal corridors to date and what are their benefits and shortcomings?
2) Do woodland and open habitat species occur in semi-open habitats and which species traits and environmental factors drive or limit their occurrence in semi-open habitats?
3) Are woodland and open habitat species able to germinate and establish themselves in semi-open habitats and which factors influence this process?

1.5 Thesis outline

The following chapters comprise three single publications which are part of the present thesis as well as the general synthesis.

Chapter 2 represents a literature review which analysed the development and previous applications of linear dispersal corridors to mitigate habitat fragmentation. To this end it contrasts the benefits and shortcomings of linear dispersal corridors and depicts the advantages of semi-open corridors compared to linear dispersal corridors in European landscapes. Based on this review two scientific research articles are presented covering the second and third research questions.

Chapter 3: This observational study describes the application of a natural plant inventory of semi-open landscapes and their surrounding habitats in two studied geographical regions to investigate whether woodland and open habitat species occur in semi-open habitats. The analyses of environmental factors and life-history traits of the recorded plant species explains what drives their presence.

Chapter 4: To identify the effects that regulate the recruitment of seedlings, i.e. the process from seed germination, emergence, establishment of an autotrophic seedling and persistence (Figure 1; Fenner & Thompson 2005; Larson *et al.* 2015;), of woodland and open habitat plant species in semi-open habitats, a seed addition experiment was performed by sowing woodland and open habitat species into semi-open habitats and analysing the influence of environmental factors and intrinsic species characteristics on recruitment.

Chapter 5 gives a general synthesis on the findings of the thesis and summarises the consequences for the use of semi-open corridors for plant dispersal, their management, and their application in a wider nature conservation perspective.

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2. Corridors as a tool for linking habitats – shortcomings and perspectives for plant conservation

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Abstract

Habitat fragmentation and isolation are considered important causes of biodiversity loss in cultural landscapes. To counter the negative effects of fragmentation such as reduced connectivity and increased risks of population extinction due to stochastic processes and genetic erosion, it has been proposed to establish linear ecological corridors to facilitate dispersal between isolated habitat patches. We summarise the current knowledge on the potential benefits and limitations of corridors for reducing the negative effects of habitat fragmentation on plant populations. We address the opportunities and problems that are associated with linear corridors and advocate the use of semi-open corridors as an alternative that might overcome some shortcomings of conventional corridors for plants. Observational and experimental studies have found that various types of linear corridors can increase plant dispersal. Other linear structures such as paths, roads and railways and streams may also function to a certain extent as corridors, although mostly for widespread species. Because plants are highly dependent on external agents such as animals or wind to reach new habitats, the effectivity of corridors is strongly influenced by their structural features and suitability for animal dispersers. However, many plant species can only use corridors for long-distance dispersal if they can also use them as stepping stone habitats where they can establish, grow, reproduce and then disperse further. This dispersal critically depends on suitable light conditions and disturbance regimes, and on a sufficient width of a corridor to reduce edge effects. Thus, hedgerows appear to be suitable corridors for some forest species but are too narrow for forest specialists from the interior of woodlands. Corridors do not only have positive effects but may also facilitate the spread of invasive species. Moreover, a potentially underestimated negative effect of linear corridors is that they may actually create new dispersal barriers when they intersect other habitats. For example, linear woodland corridors that intersect grasslands may successfully connect patches of woodland but simultaneously form strong barriers for grassland species and increase the fragmentation of their populations. As an alternative to linear corridors, we recommend “semi-open corridors” that simultaneously connect patches of both open habitats and woodlands and promote the dispersal of species of both types of habitat. This idea is based on the various types of semi-open landscapes in

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[1] Referencing style in Chapter 2 follows the guidelines of the journal of publication.

Europe that have been formed by grazing with livestock, resulting in a mosaic of open habitats, groups of trees or shrubs and small woodland patches and are characterised by a high diversity of environmental conditions on a small scale. Wide corridors of such semi-open habitats may avoid the strong edge and barrier effects associated with linear corridors and provide suitable stepping stone habitats for species with different habitat requirements.

2.1 Introduction

Changes in land use and the expansion of infrastructure have resulted in the loss of many habitats, deterioration in the quality of the remaining habitats and increased fragmentation of the landscape (Haddad *et al.*, 2015; Hadley & Betts, 2016; Evans *et al.*, 2017). The remaining patches of many types of habitats are often small and isolated from each other in an unsuitable landscape matrix. As a result, both the movement of animals and the dispersal of plants have become more restricted and the connectivity between habitat patches has been reduced (Uroy *et al.*, 2019). Small and fragmented populations of plants face an increased risk of extinction due to environmental stochasticity and reduced pollination (Fahrig, 2003; Matthies *et al.*, 2004). Fragmented populations are also more prone to genetic drift and inbreeding which results in the loss of genetic variability, reduced fitness and less resilience in the face of environmental change (Fischer and Matthies, 1998a,b; Kéry *et al.*, 2000; Xiao *et al.*, 2016).

To counteract the adverse effects of habitat fragmentation and isolation it has been proposed to create ecological corridors and stepping stone habitats (Diamond, 1975; Wilson & Willis, 1975; Keitt *et al.*, 1997; Saura *et al.*, 2014; Herrman *et al.*, 2016; Kormann *et al.*, 2016). Climate change has increased the urgency for such measures to mitigate the negative effects of fragmentation (Opdam & Wascher, 2004; Heller & Zavaleta, 2009; Beier, 2012; Barber *et al.*, 2015).

Ecological corridors have been defined as linear habitat patches which connect isolated habitats with each other and thus allow movement and dispersal between habitats (Rosenberg *et al.*, 1997; Tewksbury *et al.*, 2002). They can benefit populations by increasing the gene flow between isolated populations and facilitate the re-colonisation of habitat patches where species have become locally extinct. However, concerns have been raised that corridors may also have negative effects such as facilitating the spread of diseases and of invasive species, producing edge effects and even creating barriers between habitats (Simberloff & Cox, 1987; Dobson *et al.*, 1999; Eggers *et al.*, 2010; Krewenka *et al.*, 2011; Dennis *et al.*, 2013; Haddad *et al.*, 2014).

While the benefits and possible negative effects of corridors for animal dispersal have been intensively studied, far less is known about plant dispersal through corridors (Tewksbury *et al.*, 2002; Calçada *et al.*, 2013; Damschen *et al.*, 2014; Uroy *et al.*, 2019). As plants are sessile, the effectivity of corridors for them is more difficult to assess than for animals (Csuti, 1991; Vos *et al.*, 2002*)*. Plants strongly depend on animal vectors and external agents for dispersal of their diaspores

(Bonn & Poschlod, 1998; Jongman *et al.*, 2004) and need favourable environmental conditions for the successful establishment of seedlings (Eriksson, 2000). Diaspores may not be able to travel the full length of a large corridor, but a plant may be able to establish itself in such a corridor and reach new habitat patches several generations later (Damschen *et al.*, 2008). To facilitate this, corridors must be suitable for the different life stages of a plant (Calçada *et al.*, 2013; Lõhmus *et al.*, 2014). The complexity of tracking the stochastic dispersal of diaspores over potentially large distances and the establishment of plants at new habitat patches has limited the extent of research on plant dispersal through corridors (Murphy & Lovett-Doust, 2004).

We summarise the current knowledge on the potential benefits and limitations of linear corridors intending to reduce the negative effects of fragmentation on plant populations. We carried out an exhaustive search for literature on the use of corridors by plants in the Web of Science and Google Scholar. We also studied the grey literature published by nature conservation organisations and authorities. To limit the scope of this paper, we do not cover dispersal of pollen. We address the opportunities and problems that are associated with linear corridors for plants and advocate the use of an alternative type of corridor (semi-open corridors) that might overcome several shortcomings of conventional corridors.

2.2 What are corridors?

There is no generally agreed definition of what a corridor is in the literature. They have been defined by shape, size or function (Merriam, 1984; Rosenberg *et al.*, 1997) and termed "wildlife movement corridors", "dispersal corridors", "landscape linkages" or "ecological corridors" (Bond, 2003). Most authors agree, however, that the habitat of a corridor has to be similar to the habitat of the patches which it is supposed to connect and that its structure differs from that of the surrounding matrix (Barrett & Bohlen, 1991; Vos *et al.*, 2002). Corridors are supposed to mitigate the problems caused by habitat fragmentation by increasing the gene flow between populations and counteracting genetic erosion, and facilitate the re-establishment of locally extinct populations and the colonisation of new habitat patches (Tewksbury *et al.*, 2002; Christie & Knowles, 2015).

Often, corridors are thought of as linear structures (Wilkerson, 2013), but corridors may also be continuous, narrow patches of vegetation (e.g. Merriam, 1984), narrow strips of land (Forman & Godron, 1986), or continuous remnants of habitat between otherwise isolated patches (Beier & Noss, 1998; Gregory & Beier, 2014). Consequently, there is no agreement about the width corridors should have. Some authors think of corridors as narrow strips (Merriam, 1984, Hobbs, 1992; Collinge, 1996), while others demand that corridors should be very wide (at least 50 m) and provide mesic conditions to cater for a wide range of species, and yet others, that their width should be matched to the requirements of the species expected to use the corridor (Riffell & Gutzwiller, 1996; Van Dorp *et al.*, 1997; Vos *et al.*, 2002). The width of corridors may also depend on whether corridors are considered to be areas that allow species to move but that do not function as a habitat themselves (Rosenberg *et al.*, 1997), or whether they should also serve as habitats (Dobson *et al.*, 1999). Despite the varying definitions of the term corridor, there is agreement that dispersal corridors must provide some kind of linkage between several habitat patches by facilitating the movement of species.

2.3 Corridors for plants

Creating a corridor suitable for plant movement is challenging. Plants are highly dependent on external agents to spread to new habitat patches (Noss ,1987; Liira & Paal, 2013; Carlo *et al.*, 2013), and a lack of dispersal vectors can limit diaspore dispersal, particularly if the vectors are themselves also affected by habitat fragmentation (Murphy & Lovett-Doust, 2004; Evans *et al.*, 2012). The predominant dispersal agents may differ between habitat types and strongly affect the efficiency of dispersal. For example, woodland understorey plants are mostly dispersed by ants and slugs or their own vegetative propagation (Robinson *et al.*, 1992; Matlack, 1994; Brunet & von Oheimb, 1998; Türke *et al.*, 2010; Frei *et al.*, 2012). Consequently, they are likely to be more dispersal-limited than species of open habitats which are primarily dispersed by wind or large vertebrates (Willson, 1993; Damschen *et al.*, 2014).

While the diaspores of many plants show adaptations to specific dispersal modes, the relationship between a morphologically defined dispersal syndrome and long-distance dispersal is often poor and dispersal may be achieved mainly by vectors to which plants show no obvious adaptations (Higgins *et al.*, 2003; Bonn, 2004; Calçada *et al.*, 2013). For example, seeds of many woodland understorey plants in temperate regions possess an elaiosome which makes them attractive to ants and these plants are therefore considered to be dispersed by ants (myrmecochorous plants, Handel *et al.*, 1981). Dispersal by ants does indeed take place but is restricted to a few metres per year (Higashi *et al.*, 1989; Kalisz *et al.*,1999; Heinken, 2004) and can only be relevant for short-range spread within habitats. So-called myrmecochorous plants thus rely on other vectors for long-distance dispersal to reach new habitats, such as transport by larger animals. Central and northern European "myrmecochorous" woodland plants could not have reached their current habitats after the ice age from their southern European refuges by relying on ants for their dispersal.

Corridors may allow diaspores to reach a suitable target habitat patch in a single dispersal event, but often the distance that has to be travelled along a corridor will be too long in relation to the dispersal capacity of a species. In such cases the diaspores may travel further by secondary dispersal events through the corridor and reach their target. Corridors can also function as stepping stones for plants if seeds can germinate and the resulting plants grow and reproduce in the corridors (Suárez-Esteban *et al.*, 2016; Pearson & Dawson, 2005). When plants have to establish themselves and reproduce in the corridor, it may take several generations and thus potentially many years to complete colonisation of a new habitat. Thus, the extent to which corridors may serve as stepping stones or as habitat links for plants strongly depends on factors such as the prevailing light conditions, the width of the corridor, its structural suitability and the disturbance regime (e.g. by grazing; Noss, 1987; Liira & Paal, 2013). The shape of the corridor and the type of matrix also influence the chances of seedling establishment. Due to the shape of corridors, edge effects are more pronounced in corridors than in the matrix habitat and environmental conditions in the interior of narrow corridors can be inappropriate for (stenoecious) plant species (Wilkerson, 2013). The effects of the matrix on the corridor are often disregarded, but corridor edges can be affected by external impacts such as agricultural fertilisers, herbicides and mulching (Simberloff *et al.*, 1992; Van Dorp, 1996; Haddad *et al.*, 2011). The structural difference between corridor and matrix increases with the intensity of these impacts (Anderson & Jenkins, 2006; Hilty *et al.*, 2006).

While the environment surrounding the corridor is often assumed to be uniform, it may be heterogeneous and its interactions with the corridor should not be disregarded (Baum *et al.*, 2004; Bender & Fahrig, 2005; Wilkerson, 2013). For example, plants growing in corridors in longleaf pine savanna have shown a spillover effect into the surrounding matrix of mature pine forests, which in some cases led to a plant species richness in the matrix that was 10% to 18% higher than before the corridor existed (Brudvig *et al.*, 2009). In contrast, a highly hostile matrix or a strong structural contrast between corridor and matrix (such as between forest fragments and intensive agricultural landscapes) can negatively influence the success of the dispersal corridor (Kupfer *et al.*, 2006; Van Geert *et al.*, 2010). It has also been suggested that plant species which depend on dispersal vectors may have a lower chance to disperse if the matrix affects those vectors (Prevedello & Vieira, 2010; Van Geert *et al.*, 2010; Van Geert *et al.*, 2014).

2.4 Effectiveness of plant movement through various types of corridors

The effectiveness of corridors for the dispersal of a plant species depends on the dispersal ability of the species and the interactions between the corridor and dispersal agents. These processes have been extensively studied in experimental corridors established at the Savannah River National Environmental Research Park in South Carolina, USA (Tewksbury *et al.*, 2002; Haddad *et al.*, 2003; Levey *et al.*, 2005; Townsend & Levey, 2005; Damschen *et al.*, 2006; Haddad *et al.*, 2011; Haddad *et al.*, 2014; Damschen *et al.*, 2014). In a matrix of dense pine plantations, patches of open successional pine woodland with a rich understorey were connected by corridors of the same habitat, while unconnected patches of open habitat served as controls (Damschen *et al.*, 2006). The dispersal of seeds was mainly due to birds (Tewksbury *et al.*, 2002; Levey *et al.*, 2005; Townsend and Levey, 2005) and in the connected patches the number of bird-dispersed seeds and plant diversity were higher than in unconnected patches (Haddad *et al.*, 2003; Damschen *et al.*, 2006). Thus, corridors can promote plant dispersal and genetic exchange if they are suitable for the required animal vectors

(Tewksbury *et al.*, 2002; Townsend & Levey, 2005). Some animal species travelled along the edges and moved through the matrix instead of using the corridor (Levey *et al.*, 2005). Nevertheless, species richness increased at a faster rate in connected than in unconnected patches. This suggests that corridors may not only provide a direct dispersal link but may direct the movement of species not using corridors (Haddad *et al.*, 2003; Levey *et al.*, 2005).

Other studies at the same site investigated the role of wind as a dispersal agent. For wind-dispersed species, dispersal into the target patches was 15% higher for connected than for unconnected habitat patches (Damschen *et al.*, 2014). In contrast to the dispersal of animal-dispersed species, the dispersal of wind-dispersed species depended on the orientation of the corridors, which were most effective when they were aligned to the prevailing wind direction (Damschen *et al.*, 2014).

Linear landscape elements such as trails, fire breaks, roads and road verges can also serve as corridors, even though this is not their primary function (Tikka *et al.*, 2001; Van Geert *et al.*, 2010; Meunier & Lavoie, 2012; Suárez-Esteban *et al.*, 2013a,b). Trails and fire breaks can promote the dispersal of seeds dispersed by small vertebrates and birds along these linear structures (Suárez-Esteban *et al.*, 2013a,b). Electric powerline corridors can provide habitats for grassland species, especially when they are on dry soils and characterised by a history as open areas (Lampinen *et al.*, 2015). Railway lines can also connect habitats with each other and increase species similarity between isolated sites (Tikka *et al.*, 2001; Auffret & Cousins, 2013). Moreover, railway verges have been found to provide habitats for semi-natural grassland plants and functional connectivity for some plant species, while not facilitating the spread of highly mobile invasive species (Vandevelde & Penone, 2017).

The role of roads as dispersal corridors has been intensively studied. Along roads diaspores are mainly dispersed by wind or vehicles (Tikka *et al.*, 2001; Bonn, 2004; Zwaenepoel *et al.*, 2006; Kowarik & Von der Lippe, 2011; Von der Lippe & Kowarik, 2012; Auffret & Cousins, 2013). Secondary wind dispersal in road corridors was able to move diaspores over 100 m (Kowarik & Von der Lippe, 2011). Even the uplift created by cars carried typically wind-dispersed seeds along for up to 8 m and seeds without adaptations to wind dispersal for 1 m (Von der Lippe *et al.*, 2013). However, the dispersal power of wind depends on the type of road: smooth surfaced roads enhanced wind dispersal, whereas cobbled roads slowed down or stopped dispersal (Kowarik & Von der Lippe, 2011).

Motor vehicles managed to disperse more than 50% of the species that were also dispersed by livestock, and within ten minutes of attachment to a vehicle, seeds may travel over several kilometres (Auffret & Cousins, 2013). If seeds adhere to vehicles for longer times, they may be dispersed over long distances. Seeds attached to vehicles have been found to travel more than 200 km. However, seed retention and thus dispersal depends on weather conditions and on seed mass. During wet weather seeds do not disperse as far as during dry weather (Taylor *et al.*, 2012). Small seeds have the greatest potential to be dispersed by vehicles (Zwaenepoel *et al.*, 2006; Von der Lippe

& Kowarik, 2012), but the probability that large seeds were also dispersed increased when they were present in large numbers (Von der Lippe & Kowarik, 2012; Auffret & Cousins, 2013). However, human-mediated dispersal along linear structures such as roads or railway lines is only effective when there are target habitats in their vicinity.

Aquatic corridors such as rivers, streams and ditches can also support plant dispersal (Naiman *et al.*, 1993; Johannson *et al.*, 1996; Van Dijk *et al.*, 2014; De Jager *et al.*, 2018) and various types of aquatic corridors have been shown to connect and maintain or increase species richness of isolated habitats (Johannson *et al.*, 1996; Kirchner *et al.*, 2003; Calçada *et al.*, 2013; De Jager *et al.*, 2018). However, the effects of river corridors are not all positive, as they may also facilitate the spread of invasive species (Čuda *et al.*, 2017). Dispersal by water is mostly in the direction of the water flow (but see Kirchner *et al.*, 2003) and most important for plants that are predominantly hydrochorous (Johansson *et al.*, 1996; Bonn & Poschlod, 1998). Nonetheless, water can also serve as a secondary dispersal mode for other species, e.g. woodland plants (Calçada *et al.*, 2013). In northern France, streams formed a corridor between a source woodland and isolated woodland patches and assisted in maintaining similar species communities in these woodlands (Calçada *et al.*, 2013). Even smaller linear structures such as ditch banks showed an increase in species richness in the connected patches (Van Dijk *et al.*, 2014). Both hydrochorous species as well as species with other dispersal adaptations played a part in the increased species richness. Depending on the type of water body, dispersal may be slow or fast, as large rivers can carry diaspores faster to a target habitat than streams or ditches (Säumel & Kowarik, 2010; Calçada *et al.*, 2013; Van Dijk *et al.*, 2014). The effectivity of streams and rivers as dispersal corridors also depends on their vegetation and on the size of transported seeds. In a study of dispersal in lowland streams, large seeds were generally dispersed over longer distances than smaller seeds, because small seeds became more quickly entrapped in vegetation (De Jager *et al.*, 2018).

Hedgerows are typical linear elements in many landscapes and have frequently been suggested as corridors for woodland species (McCollin *et al.*, 2000; Deckers *et al.*, 2004; Roy & De Blois, 2006). Many studies have indeed shown that woodland plants can be found in hedgerows, but the degree to which hedgerows function as efficient corridors is controversial as several studies did not find forest specialists in hedgerows (Fritz & Merriam 1993; French & Cummins 2001; Wehling & Diekmann 2008) or did not find increased connectivity for woodland species (Pérez-Hernández *et al.*, 2015).

Several factors influence the suitability of hedgerows as habitats and thus their potential as corridors for forest herbs, such as their proximity to forests, their structure, their width, and their history and age (Corbit *et al.*, 1999; Closset-Kopp *et al.*, 2016). Many woodland species found in hedgerows were only recorded in hedgerows close to woodlands, and the density of species declined with increasing distance to woodland. As a consequence, many species typical for the interior of woodlands (i.e. indicators for ancient woodlands) were missing in hedgerows (McCollin *et al.*, 2000;

Roy & de Blois, 2006; Bailey, 2007; Wehling & Diekmann, 2009). The higher frequency of woodland species in hedgerows close to woodlands is attributed to the favourable environmental conditions nearby and reduced distances for the diaspores to travel (Corbit *et al.*, 1999; Sarlöv Herlin & Fry, 2000; Wehling & Diekmann, 2009). Plants dispersed by animals, e.g. by birds and mice, were found further away from woodlands in the hedgerows, whereas wind-dispersed species were concentrated close to the woodland edges (Corbit *et al.*, 1999; Sarlöv Herlin & Fry, 2000; Wehling & Diekmann, 2009).

Hedgerows are structurally different from woodlands, as they are often more nutrient-rich, have a drier microclimate, and have higher levels of light than woodland interiors (Roy & de Blois, 2006; Wehling & Diekmann, 2008). However, their suitability for forest herbs is strongly influenced by their width, the amount of shade they provide and their orientation (Forman & Baudry, 1984; Wehling & Diekmann, 2008). Since the ecological conditions in hedgerows are more similar to those of forest edges than to those of the interior of woodlands, they are often inappropriate as corridors for species of the interior of woodlands (McCollin *et al.*, 2000). In wider hedgerows, however, site conditions are more similar to those of forests, and these therefore contain more woodland herbs (Burel & Baudry, 1990). Wider hedgerows are also less affected by the negative influences from surrounding intensively managed farmland such as pesticides and by fertilisers which stimulate the growth of competitive ruderal species (Closset-Kopp *et al.*, 2016).

The occurrence of species in hedgerows is strongly affected by historical factors such as the age of a hedgerow and its origin. Dispersal along a hedgerow corridor is likely to be very slow, because several generations have to establish themselves in the corridor and to reproduce to allow the next generation to disperse further along the corridor (Brunet & von Oheimb, 1998; Calçada *et al.*, 2013). The diversity of plant species in hedgerows may therefore increase with its age. In very old hedgerows some species are likely to occur not because they colonised the hedgerow, but as remnants of the former forest flora that survived when the forest was converted into a hedgerow (Peterken & Game, 1981; Corbit *et al.*, 1999; Deckers *et al.*, 2004).

To sum up, hedgerows appear to be suitable corridors for some types of forest species, in particular if they are wide and exist for a long time. Poorly dispersed forest specialists require long-term stable habitats such as old hedgerows and wooded corridors to establish and spread (Corbit *et al.*, 1999; Paal *et al.*, 2017). Species which are limited to dispersal by vegetative propagation have little chance to spread into hedgerows at all (McCollin *et al.*, 2000), and many species typical for ancient woodlands are thus less likely to benefit from such corridors (Calçada *et al.*, 2013). However, hedgerows also provide habitats for other species, as they do typically not only contain species of forests and forest-edges, but also species of open fields (Forman & Baudry, 1984; McCollin *et al.*, 2000; Deckers *et al.*, 2004).

Although corridors are normally thought of as structural components of a landscape, animals that disperse plants have sometimes been called "mobile" corridors (Tewksbury *et al.*, 2002; Bugla

& Poschlod, 2005; Levey *et al.*, 2005; Manzano & Malo, 2006). The distance and directionality of dispersal by animals depend on the species and size of the animals (Higgins *et al.*, 2003). Large animals can carry seeds for several kilometres, whereas invertebrate species only manage to disperse seeds over a few meters (Poschlod *et al.*, 1998; von Oheimb & Brunet, 1998; Heinken, 2004). Sheep, for example, can carry significant amounts of diaspores (both internally or externally) for several kilometres (Fischer *et al.*, 1996; Manzano & Malo, 2006). Fischer *et al.* (1996) showed that diaspores can be carried for around one hundred days in the fleece of a sheep, but persistence of attachment depends on the characteristics of the seed (Manzano & Malo, 2006). Diaspores with special morphological adaptations to adhesion persisted in higher numbers in the fleece of sheep than those without such adaptations (Manzano & Malo, 2006). Transportation by herded animals may lead to long-distance dispersal, because the possible crossing of non-target habitats facilitates the arrival in distant habitat patches (Poschlod *et al.*, 1998). Long-distance dispersal of diaspores by animals can therefore be an alternative to the establishment of corridors. Dispersal by animals is, however, only successful if the diaspores are transported to a suitable target habitat where they can establish themselves upon arrival. Birds are considered to be particularly good dispersers in fragmented landscapes as they can provide long-distance dispersal and relocate seeds to patches with ideal habitat characteristics (Hewitt & Kellman, 2002; Carlo *et al.*, 2013; Carlo & Tewksbury, 2014).

2.5 Limitations and possible negative effects of corridors

Corridors have been proposed as an approach to counter the effects of increasing habitat fragmentation and they have been created in many ways. Their effectiveness for facilitating plant dispersal, however, is still a matter of debate (Tewksbury *et al.*, 2002; Damschen *et al.*, 2006; Gilbert-Norton *et al.*, 2010). A meta-analysis of corridor studies by Gilbert-Norton *et al.* (2010) concluded that plants are more likely to benefit from corridors than animals. However, this meta-analysis included only studies from the corridor experiment at the Savannah River Site, USA, set in pine plantations and the results cannot necessarily be applied to other habitat types. The different opinions on what counts as a corridor impede the comparison of studies and a generalisation of results (Wilkerson, 2013). Although studies on corridors have found an increase in species exchange between connected habitats in comparison to unconnected habitats, the success depended on the corridor type and on the type of species under consideration (Damschen *et al.*, 2006; Kowarik & Von der Lippe, 2011; Pérez-Hernández *et al.*, 2015; Vandevelde & Penone, 2017). The use of hedgerows as corridors for the dispersal of woodland species often showed limited success, implying restricted use of them as corridors (McCollin *et al.*, 2000; Wehling & Diekmann, 2009). While corridors of different structure and connecting different kinds of habitats have been studied and their suitability for plants relying on different modes of dispersal, such as on animal vectors or wind, have been investigated (Townsend & Levey, 2005; Damschen *et al.*, 2014), comparatively little is known about the suitability of corridors as stepping stone habitats that allow plant establishment, growth, reproduction and further dispersal (Hewitt & Kellman, 2002; Evans *et al.*, 2012; Calçada *et al.*, 2013).

Apart from failing to provide connectivity, corridors may actually have negative effects on the species composition and diversity of plant communities. For example, corridors such as streams, trails and roads may increase the spread of predators and pathogens (Sullivan *et al.*, 2011), create negative edge effects (Haddad *et al.*, 2014), enhance seed predation (Orrock & Damschen, 2005) and facilitate the spread of exotic species (Benninger-Truax *et al.*, 1992; Tikka *et al.*, 2001; Hansen & Clevenger, 2005; von der Lippe & Kowarik, 2007; Säumel & Kowarik, 2010; Wells *et al.*, 2012; Resasco *et al.*, 2014). Opinions do, however, differ on whether invasive species benefit much from corridors. It has been suggested that corridors are mostly utilised by generalist species that are characterised by their high dispersal ability (Liira & Paal, 2013; Lõhmus *et al.*, 2014), which is true for many invasive species. However, invasive species may not need corridors for their dispersal, because they are often opportunistic, tend to be good dispersers, and do not depend on specific habitat types (Damschen *et al.*, 2006; Barnaud *et al.*, 2013; Wilkerson, 2013; Haddad *et al.*, 2014).

A recent review of the potential negative effects of corridors concluded that overall, there was little support for concerns that the construction of habitat corridors may have negative consequences (Haddad *et al.*, 2014). The authors found that corridors had both positive and negative effects on antagonists of target species, and similarly, that increased edge effects due to corridors had both positive and negative effects on target species, but that there was little evidence that corridors caused the invasion of unwanted species (Haddad *et al.*, 2014).

A potential negative effect of corridors that may have been underestimated is the creation of new dispersal barriers when linear corridors are intersecting another habitat. Linear corridors can only connect habitat patches of one habitat type and there is a risk that they create new barriers for species of other habitat types. Especially in a landscape consisting of a mosaic of different habitat types, barriers caused by corridors can even increase landscape fragmentation (Forman & Alexander, 1998; Hess & Fischer, 2001; Kuefler *et al.*, 2010). Examples for such landscape mosaics are European pasture landscapes such as the Lueneburg Heath or the Swabian Alb which consist of open habitats such as heathland and grasslands as well as woodlands. The creation of open habitat corridors running through woodland to connect open habitats with each other may cause a barrier for woodland species, while creating a woodland corridor through open habitats may cause a barrier for the plants of open habitats (Eggers *et al.*, 2010). The creation of new barriers can have a detrimental effect on species dispersal in the intersected habitats (Assmann & Janssen, 1999; Dobson *et al.*, 1999; Campagne *et al.*, 2009; van Dijk *et al.*, 2014). In particular, plant species which are strongly dispersal-limited or dependent on habitat-specific dispersal vectors have no chance to cross corridors made up of other habitat types or landscape structures (Campagne *et al.*, 2009) and are affected by these new barriers. Therefore, linear corridors appear to be a useful tool to connect habitats separated by an antagonistic, hostile matrix such as settlements or intensively used agricultural fields, but they may not be suitable to link habitats in large landscape mosaics, because they may result in additional habitat fragmentation. An example are landscapes that are part of the European NATURA 2000 network.

2.6 An alternative to traditional corridors: semi-open corridors

Semi-open corridors have been proposed as an alternative to traditional corridors that may avoid many of the potential problems of traditional corridors (Eggers *et al.*, 2010). The idea of semi-open corridors is based on the various types of semi-open landscapes in Europe that have been formed by grazing of sheep, horses and cattle (Poschlod *et al.*, 1998; Manzano & Malo, 2006; Jedicke, 2015). These landscapes consist of a mosaic of open habitats formed by heathlands, calcareous or acidic grasslands and groups of trees or shrubs of different extensions, occurring at variable distances from each other. The high structural diversity resulting from alternating open and shaded habitat patches of differing densities results in frequent gradients of environmental conditions such as light availability, soil moisture and micro-climate (Kleyer *et al.*, 2002; Schmidt *et al.*, 2017). The semi-open landscapes show a high structural diversity and are very species-rich (Poschlod *et al.*, 2005; Luick, 2009; Jedicke, 2015), as they provide suitable habitats for species with different habitat requirements.

Semi-open corridors aim to simultaneously connect patches of both open habitats and woodlands and promote the dispersal of species from both types of habitat (Travers *et al.* 2021). Areas within semi-open corridors with closed canopies such as groups of trees or small remnant patches of woodland resemble woodland interiors more than hedgerows and can provide woodland species with the conditions they need, while species from open habitats can occupy the open patches. Semi-open corridors can have a large extension which decreases edge effects and lowers the influence of the matrix habitats. As the contrast between semi-open corridors and the surrounding matrix is much lower than for traditional linear corridors, semi-open corridors present less of a barrier (Murphy & Lovett-Doust, 2004; Eggers *et al.*, 2010; Haddad *et al.*, 2014). Instead of providing a continuous link between patches of one type of habitat, semi-open corridors offer a high density of stepping stone habitats for species with different habitat requirements and also provide soft transitions (ecotones) between different types of habitat (Poschlod *et al.*, 1998; von Oheimb *et al.*, 2006; Jedicke, 2015).

The potential of semi-open corridors to simultaneously connect different types of habitats has been shown for flightless carabid beetles in a study in the Lueneburg Heath in northern Germany (Eggers *et al.*, 2010). Stenoecious species of both woodlands and heathlands were found to use semi-open corridors as habitats and to immigrate into them from open and woodland areas, indicating that semi-open corridors can serve as stepping stones for species of different habitat types and thus connect them without creating new barriers (Eggers *et al.*, 2010)

The development of semi-open corridors would require the least management efforts in regions that, due to their history of land use, already contain many of the structures that are typical for semi-open corridors, for example structurally diverse woodland edges, woodland pastures, open scrubland or semi-open pastures. Establishment of semi-open corridors might require only small changes to current management (e.g. to allow succession in grazed open habitats) and would not only connect previously isolated habitats but could also increase the structural and species diversity of the landscape.

Where no supporting elements yet exist, semi-open corridors could also be newly developed by creating gaps in pieces of woodland or by allowing controlled succession in open habitats. The creation of semi-open corridors could be particularly appropriate in landscapes with a high proportion of protected, but isolated habitats such as calcareous grasslands, heaths and patches of woodland. Connecting remnant patches of these habitats by conventional linear corridors would require strong transformation of large areas of land and the extensive corridors of one type of habitat could form barriers for species of other habitat types. Semi-open corridors would avoid these problems and create networks of different habitats.

To successfully fulfil their function, semi-open corridors must be managed appropriately on a long-term basis. Grazing has been very important for the development of many semi-open landscapes in the past and is probably important in creating and maintaining semi-open corridors (Finck *et al.*, 2002). Controlled grazing can provide a cost-effective way of preventing the establishment of dense woodland. Moreover, grazing animals such as sheep, cattle and horses have been found to transport seeds over long-distances (Pakeman, 2001; Couvreur *et al.*, 2004; Manzano & Malo, 2006) and may thus increase the functionality of semi-open corridors to connect habitat patches. Grazing animals also disturb the soil and create gaps which may facilitate the establishment of species and enhance the suitability of semi-open corridors as stepping stone habitats (von Oheimb *et al.*, 2006; Jedicke, 2015).

In conclusion, using semi-open corridors as an approach to simultaneously connect open habitats and woodland on a large scale might help to overcome the limitations of linear corridors in large landscape mosaics. However, more research is needed to understand how effective semi-open corridors as connective links for plants of different habitats are. Specific questions that need to be answered include: Which types of landscape qualify for semi-open corridors? Which factors facilitate or limit the dispersal of plant species in semi-open corridors? How well do semi-open corridors function as stepping stone habitats? How can we effectively manage semi-open corridors to support plant dispersal? The ability of woodland and open habitat plant species to cope with environmental conditions in corridors should be studied using experimental approaches. Moreover, monitoring programmes are needed to explore the effect of different management regimes and to understand the effects of different stages of succession on the dispersal of species in corridors. These monitoring programmes may provide answers to the question of how to manage semi-open landscapes more effectively as plant dispersal corridors.

In the face of increasing land-use changes and urban expansion, new integral concepts and approaches must be developed to create habitat networks which serve different types of species to effectively counteract the problem of large-scale habitat fragmentation. Establishing semi-open corridors could be a first step towards developing sustainable connecting links and stepping stone habitats for species of both woodlands and open habitat.

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3. The potential of semi-open habitats to function as dispersal corridors for species of both woodlands and open habitats

Published article:

Travers, E., Pitz, W. T., Fichtner, A., Matthies, D., & Härdtle, W. (2021). The role of semi-open habitats as dispersal corridors for plant species of woodlands and open habitats. Applied Vegetation Science, 24, e12526. https://doi.org/10.1111/avsc.12526[2]

Abstract

Questions: European pasture landscapes have been shaped by grazing and alternate husbandry. They are structurally characterised by mosaics of open habitat patches, individual trees and groups of trees or shrubs. We investigated whether these semi-open habitats may act as stepping stones and thus as dispersal corridors for both plants from woodlands and open habitats to mitigate habitat fragmentation effects. We (i) contrasted the plant communities in semi-open habitats with those of woodlands and open habitats, and (ii) explored which life-history traits or environmental requirements are associated with the presence or absence of species in semi-open habitats.

Location: Swabian Jura, S-Germany; Lueneburg Heath, N-Germany

Methods: We selected four study sites in two contrasting landscapes and conducted vegetation surveys and analysed canopy closure and soil chemical properties in four different habitat types: woodlands, semi-open habitats with high and low canopy closure and open habitats. We tested whether habitat type affected species composition, identified habitat-specific indicator species and compared Ellenberg indicator values for light and moisture and species' dispersal and establishment traits across these habitat types.

Results: Plant communities of woodlands were significantly different from those of all other habitat types, whereas open habitats showed some similarities to semi-open habitats. On average, 73% of open habitat and 39% of woodland species were present in semi-open habitats. Habitat requirements as well as dispersal and establishment traits of woodland species were often more specialised and differed from species of the other habitat types, making them less capable for dispersal into semi-open habitats.

Conclusions: Semi-open corridors have the potential to connect patches of open habitats and to a lesser extent also of woodlands without creating new barriers for either habitat type. Thus, semi-open corridors may counteract habitat fragmentation effects and are a promising tool for biodiversity conservation, particularly in fragmented pasture landscapes.

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[2] Referencing style in Chapter 3 follows the guidelines of the journal of publication.

3.1 Introduction

Changes in land use have resulted in the increasing fragmentation of many habitats (Haddad *et al.*, 2015; Evans *et al.*, 2017). As a consequence, plants of these habitats increasingly occur in isolated and small populations (Matthies *et al.*, 2004). Fragmented populations have a higher risk of extinction because of greater sensitivity to demographic, environmental and genetic stochasticity (Honnay and Jacquemyn, 2007). Reduced population size and increased isolation of fragmented populations result in increased inbreeding, reduced gene flow and a loss of genetic variability through genetic drift (Fischer and Matthies, 1998a; Honnay *et al.*, 2005; Schlaepfer *et al.* 2018). This in turn can reduce the fitness of plants in these populations (Fischer and Matthies, 1998b; Willi *et al.*, 2006) and their potential to adapt to changing environmental conditions (Kéry *et al.*, 2004; Walisch *et al.*, 2012), further increasing the risk of extinction. The re-colonisation of habitat fragments from which a plant species has become extinct is often difficult because of their isolation (Xiao *et al.*, 2016; Schlaepfer *et al.* 2018). To counteract the negative effects of fragmentation it has been suggested to create linear dispersal corridors to connect isolated patches of habitats (Rosenberg *et al.*, 1997; Damschen *et al.*, 2014), and various forms of corridors to increase dispersal and serve as habitat links have been studied (Kirchner *et al.*, 2003; Damschen *et al.*, 2006; Roy and de Blois, 2006).

Linear corridors are usually designed to connect patches of similar vegetation with each other (Rosenberg *et al.*, 1997). For example, hedgerows have been used to connect isolated woodland patches (Wehling and Diekmann, 2009). However, if corridors intersect other habitat types they can also act as barriers for the dispersal of species of those habitats (Dobson *et al.*, 1999; Eggers *et al.*, 2010; van Dijk *et al.*, 2014). Poorly dispersed species in particular may be affected by this barrier-effect, and the positive effects of a corridor on species of one type of habitat might be outweighed by barrier-effects on species of another habitat.

In many parts of Europe, traditional land-use management such as extensive grazing and alternate husbandry have created pasture landscapes (Finck *et al.*, 2002; Jedicke, 2015). In recent decades, these landscapes have been transformed by the onset of succession due to changes in habitat management (Poschlod *et al.*, 2005). Many of these former pastures are now characterised by a mosaic of open habitat patches and individual trees, groups of trees or shrubs with different degrees of canopy closure (Bergmeier *et al.*, 2010; Popp and Scheibe, 2013). The high structural diversity results in heterogeneous environmental conditions which can accommodate species with strongly varying habitat requirements (Bergmeier *et al.*, 2010). These so-called semi-open landscapes are among the most species-rich habitats in Europe and host a large proportion of the biodiversity in Europe, including many endangered plant and animal species (Jedicke, 2015). Today, in many parts of Europe, remnants of these landscapes are protected, and management schemes have been designed to preserve their structural and biological diversity (von Oheimb *et al.*, 2006).

Due to their mosaic character, semi-open habitats may support animal species of both woodlands (e.g. high forests) and open habitats (e.g. grasslands, heathlands; Eggers *et al.*, 2010) by acting as corridors for them and thus providing a link between (separated) habitat patches. Thus, the promotion of semi-open corridors could be a promising approach to mitigate the effects of habitat fragmentation and avoid the barrier-effects that are caused by traditional linear corridors when they intersect other habitat types. However, it remains unclear to what extent semi-open corridors might also facilitate the dispersal of plants. The dispersal ability of many plant species is poor, and these species need stepping stone habitats that allow them to colonise suitable new habitat patches over several generations (Brederveld *et al.*, 2011; Saura *et al.*, 2014).

We investigated whether semi-open habitats are suitable to act as stepping stones and thus as dispersal corridors for plants of both woodland and open habitats. We contrasted the species composition of four habitat types: woodlands, semi-open habitats with high and low canopy closure and open habitats. We compared life-history traits and realised ecological niches of species growing in those habitat types to identify factors that favour the suitability of semi-open habitats for certain species. Specifically, we asked (i) whether plant communities of semi-open habitats contain species of both woodlands and open habitats, and (ii) which species traits or environmental requirements explain best the differences between species occurring and not occurring in semi-open habitats?

3.2 Materials and methods

3.2.1 Study area

The study was carried out in two contrasting landscapes that differ in soil conditions and prevailing plant communities: the Swabian Jura in S-Germany and the Lueneburg Heath in N-Germany (Table 1). Both regions have a long history of livestock grazing, which is still continuing today (Beinlich and Plachter, 1995; Cordes *et al.*, 1997). However, changes in habitat management have facilitated the onset of succession which produced extensive areas of semi-open habitats (following the definition of Finck *et al.*, 2002). Those are characterised in the Swabian Jura by calcareous grasslands with shrubs and trees of *Juniperus communis*, *Prunus spinosa* and *Quercus robur*, and in the Lueneburg Heath by heathlands with *Juniperus communis*, *Betula pendula*, *Quercus* spp. and *Pinus sylvestris*. The shrubs and trees occur at different densities and ages across the semi-open habitats (Eggers *et al.* 2010).

Table 1: Characterisation of the two study regions

Region	Co-ordinates	Altitude range (m a.s.l)	Mean yearly temperature (°C)	Mean yearly precipitation (mm)	Prevailing soil type	Prevailing plant communities
Swabian Jura	48° N/ 9° E	c. 600 - 1000	c. 8	850	Leptosols, Cambisols	*Gentiano-Koelerietum* grasslands, *Galio odorati-Fagetum* woodlands
Lueneburg Heath	53° N/ 9° E	c. 90 - 170	c. 10	700	Podsols	*Genisto-Callunetum* heathlands, *Betulo-Quercetum* woodlands

3.2.2 Study and sampling design

In summer 2013, four study sites of 25 ha each were randomly selected in each region. At each study site we randomly selected five plots of 5 m x 4 m of each of four types of habitats (i.e. 80 plots overall in each region): Woodlands (W), semi-open habitats where canopy closure was high (SOH; Swabian Jura: 66-98%; Lueneburg Heath: 69-96%), semi-open habitats where canopy closure was low (SOL; Swabian Jura: 20-56%; Lueneburg Heath: 36-77%), and open habitats (O). In both regions, woodland with dense canopies (following the definition of Peterken (1993)) and open habitats were located adjacent to the semi-open habitats and transitioned into those. In each plot we determined all vascular plants and epigaeic bryophytes and estimated their cover and that of shrubs (1 – 5 m), trees of the lower canopy (5 – 10 m), and of the upper canopy (> 10 m; if these layers were developed; Dierschke, 1994). Nomenclature is based on Jäger (2011) for vascular plants and Frahm and Frey (2004) for bryophytes.

3.2.3 Environmental variables of the study sites

A hemispherical photograph was taken 1 m above ground in the centre of each plot with a fish-eye lens (Nikon, Fisheye Converter FC-E8 0.21x, Japan) to characterise the light conditions (Beckschäfer *et al.*, 2013). Canopy closure was quantified for each plot using Gap Light Analyzer 2.0 (Cary Institute of Ecosystem Studies, 1999).

To study soil conditions, we randomly took five samples of the upper mineral horizon in each plot, pooled them and determined the pH (H_2O) value, the base saturation and the C/N ratio using standard procedures (see Steubing and Fangmeier, 1992). Soil nitrogen and carbon content were determined with a CN-analyser (Elementaranalysator Vario El Cube, Hanau, Germany).

Both in the Swabian Jura and the Lueneburg Heath canopy closure of the semi-open habitats was intermediate between that of the woodlands and open plots (Table 2; Appendix S1). C/N-ratios in the different habitat types per region were similar, but open and semi-open habitats with low canopy closure tended to have higher base saturation and pH-values. Site conditions between regions were not compared because of entirely different bedrocks, soil types and habitat structures.

Table 2: Canopy closure and soil chemistry in the four studied habitat types in the Swabian Jura and the Lueneburg Heath: W, woodland; SOH, semi-open habitat with high canopy closure; SOL, semi-open habitat with low canopy closure; O, open habitat. Habitat comparisons were conducted using analysis of variance with study site as a block factor, followed by Tukey's multiple comparison procedure (N = 20 per habitat type). Different letters indicate significant differences ($p_{adj.} < 0.05$) between habitat types within a region.

	Swabian Jura				Lueneburg Heath			
	W	SOH	SOL	O	W	SOH	SOL	O
Canopy closure (%)	93^{a}	86^{b}	36^{c}	24^{d}	86^{a}	81^{a}	61^{b}	27^{c}
C/N	13.9^{a}	12.9^{a}	12.8^{a}	11.8^{a}	25.3^{a}	23.8^{a}	23.5^{a}	25.4^{a}
Base saturation (%)	84.8^{a}	89.9^{ab}	97.0^{b}	98.8^{b}	13.9^{a}	21.3^{a}	34.4^{b}	66.4^{c}
pH $_{(H2O)}$	6.5^{a}	6.4^{a}	7.4^{b}	7.6^{b}	4.0^{a}	4.2^{ab}	4.4^{b}	4.7^{c}

3.2.4 Analyses of the species composition of habitat types and plant traits

All statistical analyses were conducted in R version 3.5.2 (R Core Team, 2018). We applied generalized linear models for multivariate data (GLM_{mv}, using the *manyglm* function of the mvabund R package (Wang *et al.*, 2012)) to evaluate differences in plant species composition between habitat types. To account for differences between local site conditions, we used study site as block factor. This model-based approach allows to test for location effects by accounting for the mean-variance relationship of untransformed multivariate data (Warton *et al.*, 2012). Models were fitted with a negative binomial distribution and significance of predictors was assessed by likelihood ratio tests with 1000 iterations. For pairwise comparisons we applied a Bonferroni correction. Variation in species composition with habitat type was visualised using non-metric multidimensional scaling (NMDS, using the *metaMDS* function of the vegan R package (Oksanen *et al.*, 2015)) with two (Swabian Jura data) and three dimensions (Lueneburg Heath data), respectively. Increasing the number of dimensions for the ordination of the Lueneburg Heath data resulted in a substantial reduction of the ordination stress (2-dimensions: 0.18; 3-dimensions: 0.11). The NMDS was performed on a matrix of Bray-Curtis dissimilarities based on square-root transformed abundance data (i.e. species cover). Moreover, we included those environmental variables in the ordination plot that showed significant correlations with NMDS-axes (using the *envfit* function of the vegan R package).

We applied an Indicator Species Analysis (ISA; Dufrêne and Legendre, 1997) using the package indicspecies (De Cáceres and Legendre, 2009) to test for significant associations of species with specific habitat types. Indicator species for individual habitat types and combinations of habitat types were identified in the community matrix using indicator value indices. These indicator values range from zero (no indication) to one (perfect indication). To test the significance of the indicator value of each species for a certain habitat type or combination of habitats, 999 permutations were run.

In addition, we identified species that were not classified as indicator species (due to low within-habitat type constancy values of ≤ 15%), but exclusively occurred in one habitat type or a combination of two or three different habitat types. These species are henceforth referred to as 'rare species'. Moreover, we identified species that were found in all four habitat types. These species showed low between-habitat type differences in constancy values (≤ 15%).

To investigate whether dispersal or establishment processes were limiting the presence of species of woodland and open habitats in semi-open habitats, we analysed life-history traits (as community weighted means) of all herbaceous species and their realised ecological niches in each plot (Garnier *et al.*, 2004). To this end, we evaluated the life-history traits seed mass, dispersal mechanism, seed bank longevity, age at first flowering (as listed by Kleyer *et al.*, 2008) and propagation mode (Fitter and Peat, 1994) for the species for which data were available. If there were several different records for seed mass, we used the mean value. We differentiated between the following modes of dispersal: self-dispersal, dispersal by wind, short-distance dispersal by animals (by invertebrates), and long-distance dispersal by animals (by vertebrates).

For some traits, such as dispersal mode, the database distinguishes several trait classes (cf. Table 3), and a species could be assigned by different authors to a different class. To account for inconsistent literature records for a trait of a species, we calculated 'weighted trait values' (i.e. number of literature records per trait class divided by the total number of records for a trait of a given species) and then used these values to calculate community weighted means for a trait class (obtained by weighting the species' trait values with the species' relative cover in a plot of a respective habitat type; Garnier *et al.*, 2004). We calculated community weighted means for habitat comparisons including all herbaceous species present in a plot for two reasons. Trait combinations in plant communities have been shown to be predominantly filtered by local-scale factors such as disturbance (incl. management), fine-scale soil conditions, microclimate, or biotic interactions (Bruelheide *et al.*, 2018). Community weighted traits means thus can be considered as appropriate indicators for (local-scale) environmental conditions that determine the plant species composition of a focal habitat. Moreover, we wanted to include both specialists and generalists present in a habitat type, because both groups contribute to the species combination and richness typical of a habitat type (particularly in the Lueneburg Heath). In addition to trait analyses, we calculated Ellenberg light and moisture indicator values (EIV) weighted by species' cover (Ellenberg *et al.*, 1992; Jäger, 2011) to assess between-type differences in realised ecological niches (Table 3). Differences in trait means and weighted EIV between habitat types ($N = 20$) were assessed by analysis of variance followed by Tukey's multiple comparison procedure after accounting for variation between study sites (block factor; type-I sum of squares). Models were fitted for each region separately. This variance modelling framework was preferred, because it allows analysing mean-variance relationships based on untransformed data (Zuur *et al.*, 2009; using the packages nlme (Pinheiro *et al.*, 2018) and multcomp

(Hothorn *et al.*, 2008)). For all models, residual plots indicated no violation of model assumptions according to Zuur *et al.* (2009).

Table 3: Ellenberg indicator values and life-history traits of species used in the comparison of the four habitat types. Proportion of species (%) for which each trait type was available is given for the Swabian Jura (SWA) and the Lueneburg Heath (LH).

Ellenberg indicator values			Dispersal traits			Establishment traits		
	SWA	LH		SWA	LH		SWA	LH
EIV	*100*	*100*	*Seed dispersal type*	*82*	*69*	*Seedbank type*	*79*	*69*
Light			Self-dispersal			Transient seedbank, < 1 year		
Moisture			Wind-dispersal			Short-term seedbank, 1-5 years		
			Short-distance animal-dispersal (by invertebrates)			Long-term seedbank, > 5 years		
			Long-distance animal-dispersal (by vertebrates)					
			Propagation type	*56*	*71*	*Age of flowering*	*64*	*50*
			Propagation by seeds only			< 1 year until flowering		
			Vegetative propagation only			1-5 years until flowering		
			Propagation by seeds & vegetatively			> 5 years until flowering		
			Seed mass	*100*	*100*			

3.3 Results

3.3.1 Species composition among the plant communities of the four habitat types

For both regions, we found significant effects of habitat type (Swabian Jura: L: 3909, $p < 0.001$; Lueneburg Heath: L: 612, $p < 0.001$) and study site (Swabian Jura: L: 1728, $p < 0.001$; Lueneburg Heath: L: 582.6, $p < 0.001$) on species composition. Overall, the effects of habitat type were stronger than those of study site (especially in the Swabian Jura), as indicated by the magnitude of the L-ratio.

The NMDS ordination showed clusters of the plots corresponding to the four habitat types in the Swabian Jura and the Lueneburg Heath (Figure 4a and 4b). NMDS axes reflected a gradient of light (Swabian Jura: $r^2 = 0.72$, $p < 0.0001$; Lueneburg Heath: $r^2 = 0.74$; $p < 0.0001$) and nutrient availability (Swabian Jura: pH: $r^2 = 0.44$, $p < 0.0001$; base saturation: $r^2 = 0.08$, $p = 0.03$; Lueneburg Heath: pH: $r^2 = 0.45$, $p < 0.0001$; base saturation: $r^2 = 0.62$, $p < 0.0001$; Figure 4). In the NMDS ordination of the vegetation in the Swabian Jura, the W-plots formed a distinct cluster and were significantly different from all other habitat types (all comparisons $p_{\text{adj.}} < 0.05$; Appendix S2), while plots of the other habitat types were grouped closer together (Figure 4a). SOH-plots showed the largest within-habitat type variation, and species composition differed significantly from that of other habitat types (all comparisons $p_{\text{adj.}} < 0.01$; Appendix S2), despite some overlap with SOL-plots (Figure 4a). O- and SOL-plots showed the largest similarity in species composition with lowest within-habitat type variation (Figure 4a and Appendix S3). In the Lueneburg Heath, plant species composition of the four habitat types was more similar than in the Swabian Jura (Figure 4b), but all habitat types differed significantly from each other in their species composition (all comparisons $p_{adj.} < 0.01$: Appendix S2). W-plots showed similarities to SOH and SOL in the NMDS. Community composition of O-plots showed only some overlap with SOL. Within-habitat type variation was high in all habitat types, except for open habitats (Figure 4b).

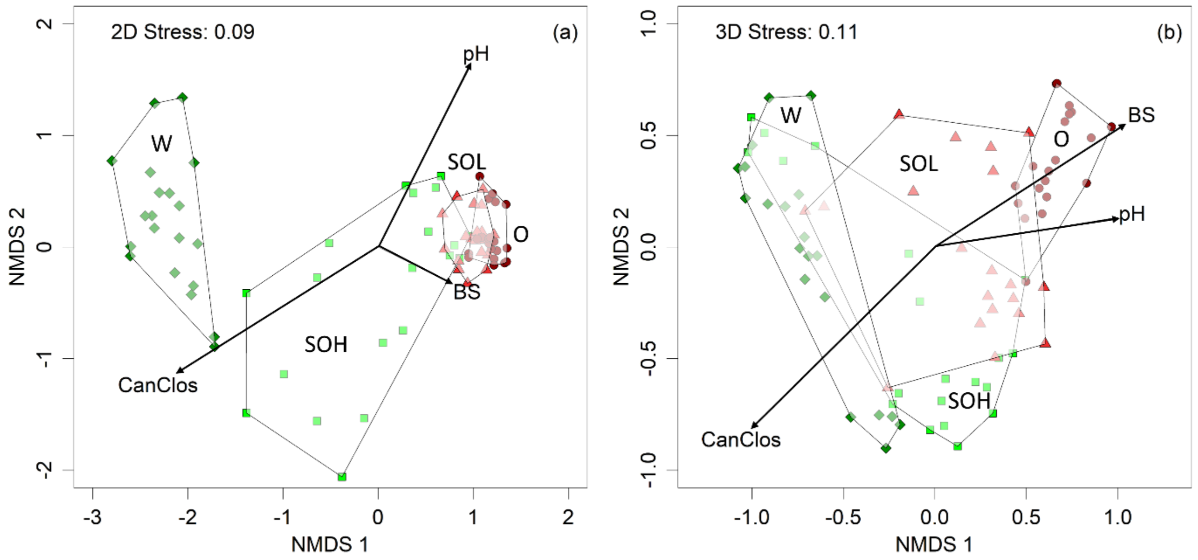

Figure 4: Nonmetric multidimensional scaling of the plant communities of the four habitat types in (a) the Swabian Jura and (b) the Lueneburg Heath; woodland (W); semi-open habitat with high canopy closure (SOH) and low canopy closure (SOL); open habitat (O). Significant environmental factors are fitted as vectors: pH, base saturation (BS) and canopy closure (CanClos).

3.3.2 Indicator species and species richness of the habitat types

We recorded a total of 244 plant species (221 vascular plants, 23 bryophytes) in the Swabian Jura and 53 plant species (43 vascular plants, 10 mosses) in the Lueneburg Heath. About one third (Swabian Jura: 39%; Lueneburg Heath: 30%) of the plant species proved to be indicator species, i.e. showed a significant affinity either to a habitat type or a combination of habitat types (Table 4a, all species with $p \leq 0.05$ are listed in Appendices S4 and S5).

Most species (about two-thirds) proved to be 'rare species', and some species occurred across all habitat types (Table 4b; for constancy tables see Appendices S6 and S7 and for complete species lists of habitat types see Appendices S8 and S9).

In the Swabian Jura, 93 species were found in W-plots, of which 23 proved to be indicator species for the W-habitat type. In addition, a further 34 rare species appeared only in W-plots. Thus, 57 species (61%) were restricted to woodlands, but W-plots also shared a total of 27 (indicator and rare) species (29%) with semi-open corridors. In the Lueneburg Heath, the number of indicator and rare species restricted to W was much lower (three and six out of 27 species, respectively (i.e. 33% in total). In addition, W-plots had a total of 13 species (48%) in common with semi-open corridors.

In the Swabian Jura, 110 species were found in O-plots, but only 11 (indicator and rare) species were restricted to this habitat type (10%). A total of 89 species (81%) in O-plots also occurred in semi-open corridors (including the species which occurred across all habitat types). In the Lueneburg Heath, overall species richness of O-plots was lower than in the Swabian Jura (36 species), and only four (indicator and rare) species were restricted to this habitat type (11%). O-plots, in turn, had a total of 23 species (64%) in common with semi-open corridors (including the species which occurred across all habitat types).

Table 4: Total species richness and number of (a) indicator species and of (b) 'rare species' for the four individual habitat types and for combinations of these habitats in the Swabian Jura and the Lueneburg Heath. W, woodland; SOH, semi-open habitat with high canopy closure; SOL, semi-open habitat with low canopy closure; O, open habitat (for the sake of clarity, the table only considers habitat combinations that are characterised by more than one species). In addition, the number of species is given that appeared in all habitat types.

(a)	Swabian Jura				Lueneburg Heath			
Habitat	W	SOH	SOL	O	W	SOH	SOL	O
Total species richness	93	162	120	110	27	33	34	36
	23				3			
		12						
			2				3	
				1				1
	3	▨			2	▨	▨	
		5	▨					
		17	▨	▨				
			31	▨			4	▨

(b)	Swabian Jura				Lueneburg Heath			
Habitat	W	SOH	SOL	O	W	SOH	SOL	O
Total species richness	93	162	120	110	27	33	34	36
	34				6			
		34				3		
			6				3	
				10				3
	7	▨	▨	▨	8	▨	▨	▨
	13	▨			1	▨		
	4	▨	▨		2	▨	▨	
		8	▨					
		27	▨	▨		9	▨	▨
			7	▨			2	▨

In the Swabian Jura, SOH- and SOL-plots were characterised by the highest species richness (162 and 120, respectively) of all habitat types. A total of 46 (indicator and rare) species were restricted to SOH-, and eight to SOL-plots. In contrast, overall species richness of SOH- and SOL-plots in the Lueneburg Heath was lower than in O-plots. Three indicator species were typical of SOL-plots, and three rare species each were found in SOL- and SOH-plots.

3.3.3 Community weighted trait means and mean Ellenberg indicator values of habitat types

In the Swabian Jura seeds of species growing in SOL- and O-plots were much smaller than those of species in SOH- and W-plots. At least two-thirds of the species found in the SOH-, SOL- and O-plots were dispersed by vertebrates over long-distances (Table 5; Appendix S1), while self-dispersal, dispersal by wind and short-distance dispersal by invertebrates was much less common among the species. In contrast, W-plots had a significantly lower proportion of species with long-distance dispersal by animals but also a significantly higher proportion of species that were self-dispersed and dispersed by invertebrates over short distances. In SOH- SOL- and O-plots a higher proportion of species exclusively propagated by seeds, whereas species in W-plots were more likely to propagate vegetatively (Table 5).

In the Lueneburg Heath we found patterns of seed mass similar to the Swabian Jura (Table 5; Appendix S1). However, the proportion of long-distance animal-dispersed species was very high across all habitat types, including W-plots (Table 5). While species of SOH-, SOL- and O-plots were more likely to also disperse via wind-dispersal, W-plots contained more species which were short-distance animal-dispersed. Self-dispersal played a minor role for species of all habitat types in the Lueneburg Heath. Species with vegetative propagation tended to be more frequent in W- and SOH-plots, whereas the proportion of species which are able to propagate by both seeds and vegetatively was higher across SOH-, SOL- and O-plots (Table 5).

Table 5: Community weighted means of dispersal and establishment traits and mean Ellenberg indicator values (EIV) for the different habitat types in the Swabian Jura and the Lueneburg Heath (W, woodland; SOH, semi-open habitat with high canopy closure; SOL, semi-open habitat with low canopy closure; O, open habitat; N = 20 per habitat type). Different letters indicate significant differences ($p_{adj.} < 0.05$) between habitat types within a region.

	Swabian Jura				Lueneburg Heath			
Trait	W	SOH	SOL	O	W	SOH	SOL	O
Seed mass (mg)	9.3^{a}	4.2^{b}	2.4^{c}	2.2^{c}	20.2^{a}	10.9^{ab}	6.1^{bc}	0.3^{c}
Seed dispersal type								
% self-dispersed	24^{a}	9^{bc}	8^{b}	11^{c}	0.2^{a}	2^{ab}	1^{b}	1^{ab}
% wind-dispersed	11^{a}	16^{a}	15^{a}	15^{a}	3^{a}	9^{b}	9^{b}	14^{c}
% dispersed by invertebrates	18^{a}	5^{bc}	4^{b}	6^{c}	6^{a}	5^{ab}	3^{b}	1^{c}
% dispersed by vertebrates	48^{a}	70^{bc}	73^{b}	68^{c}	90^{a}	84^{ab}	85^{ab}	85^{b}
Propagation type								
% propagated by seeds	22^{a}	58^{b}	77^{c}	78^{c}	9^{a}	8^{a}	3^{a}	2^{a}
% propagated vegetatively	49^{a}	9^{b}	1^{b}	2^{b}	55^{a}	32^{ab}	16^{bc}	1^{c}
% propagated by both types	29^{ab}	33^{b}	22^{ab}	20^{a}	36^{a}	60^{ab}	81^{bc}	97^{c}
Seed bank type								
% with transient seedbank	87^{a}	84^{a}	84^{a}	83^{a}	77^{a}	57^{b}	49^{b}	28^{c}
% with short-term seedbank	5^{a}	12^{b}	11^{b}	12^{b}	15^{a}	28^{b}	29^{b}	38^{c}
% with long-term seedbank	8^{a}	4^{a}	5^{a}	5^{a}	8^{a}	15^{b}	22^{b}	34^{c}

	Swabian Jura				Lueneburg Heath			
Age of flowering								
% flowering within a year	6^{a}	26^{b}	35^{b}	32^{b}	43^{a}	23^{b}	25^{b}	7^{c}
% flowering after 1-5 years	88^{a}	73^{b}	65^{b}	68^{b}	55^{a}	62^{ab}	75^{b}	90^{c}
% flowering after > 5 years	6^{a}	1^{a}	0.3^{a}	0.1^{a}	2^{a}	15^{b}	0.3^{a}	3^{ab}
Ellenberg Indicator Values (EIV)								
Mean EIV for light	3.3^{a}	6.5^{b}	7.3^{c}	7.4^{c}	5.6^{a}	5.6^{ab}	6.4^{b}	7.5^{b}
Mean EIV for moisture	5.1^{a}	4.4^{b}	3.9^{c}	3.7^{c}	4.9^{ac}	4.5^{b}	4.7^{ab}	5.0^{c}

In the Swabian Jura, the proportion of species with a transient seed bank was very high and that of species with a persistent seed bank was low across habitat types (Table 5; Appendix S1). SOH- SOL- and O-plots, however, contained a higher proportion of species with short-term seedbanks than W-plots. In the Lueneburg Heath, W-plots contained the highest proportion of species with a transient seed bank, whereas the proportion of species with short- and long-term seed banks was higher in SOH-, SOL- and O-plots.

In both regions, the species from different habitats varied in the length of their vegetative phase. While in the Swabian Jura the proportion of species with a short vegetative phase increased with the openness of the habitats (i.e. from W to O; Table 5; Appendix S1) and that of species flowering only after a prolonged time of growth decreased, in the Lueneburg Heath the proportion of species with a short vegetative phase (< one year) was highest in W-plots and that of species with a longer vegetative phase was higher in SOH, SOL- and O-plots (Table 5).

In both regions, the mean Ellenberg indicator values for light increased with the openness of the habitats (i.e. from W to O; Table 5; Appendix S1). Conversely, in the Swabian Jura the mean indicator value for moisture decreased with habitat openness, but we found no clear pattern for the indicator values for soil moisture in the Lueneburg Heath. While in the Swabian Jura, only the SOL-plots were very similar to the O-plots in their light and moisture conditions as indicated by the mean indicator values, in the Lueneburg Heath, SOH-plots also showed similarities to the light conditions of SOL- and O-plots.

3.4 Discussion

3.4.1 Plant communities and species composition in semi-open habitats

Our results demonstrate that the composition of the plant community of semi-open habitats show a great overlap with that of open habitats and to a lesser extent with that of woodlands. Furthermore, several species showed a clear preference for semi-open habitats, particularly in the Swabian Jura. This explains the extraordinary phytodiversity of semi-open habitats found in this region.

Overall, the plant species composition of semi-open habitats was more similar to that of open habitats than to that of woodlands. This was reflected by both the results of the analysis of species composition and the analyses of indicator/rare species, according to which only a small proportion of plant species (Swabian Jura: 10%; Lueneburg Heath: 11%) was restricted to O-plots. In contrast, many species occurred in both SO- and O-plots, indicating that species of open habitats successfully disperse into semi-open habitats and cope well with the environmental conditions there. This corroborates that semi-open habitats can provide appropriate stepping stones for many open habitat species, and that this function was realised both in the limestone landscape of the Swabian Jura and in the Lueneburg Heath region with its acidic soils.

In contrast to the situation in open habitats, a higher proportion of species in the W-plots (61% in the Swabian Jura and 33% in the Lueneburg Heath) was restricted to that type of habitat. This suggests that woodland species are either more stenoecious or have a lower dispersal ability than species of open habitats (Dzwonko, 2001; Härdtle *et al.*, 2003; Schmidt *et al.*, 2011). In fact, many of the species only found in W-plots could be characterised as ‘ancient woodland species’ (e.g. *Helleborus viridis* and *Cephalanthera damasonium* in the Swabian Jura), whose populations are mostly restricted to sites with a continuous forest cover for more than 200 years (Hermy *et al.*, 1999). However, c. 29% (Swabian Jura) and 48% (Lueneburg Heath) of all species in the W-plots were also found in the SO-plots, suggesting that semi-open habitats can serve as stepping stones for at least some woodland species. Remarkably, at least some SOH-plots in the Swabian Jura contained the ancient woodland species *Helleborus viridis* and *Cephalanthera damasonium* and species that are less habitat-specific and hence appeared in woodlands and open habitats (e.g. *Viola hirta* and *Potentilla erecta*; Schmidt *et al.*, 2011). The presence of both stenoecious and euryoecious species in SO-plots suggests that a range of species with different environmental requirements can inhabit semi-open habitats, likely attributable to spatially heterogeneous conditions with regard to light, temperature, air humidity or soil moisture (Dierschke, 1974). This interpretation is supported by a study of Eggers *et al.* (2010) of the composition of the carabid beetle community of semi-open corridors in the Lueneburg Heath, in which both stenoecious woodland and open landscape species were found in the same pitfall traps established in SO-plots.

A number of indicator and rare species were specific to semi-open habitats in both regions (particularly in the Swabian Jura). Many of these species are typical of fringe and ruderal communities (e.g. of the Trifolio-Geranietea or Geo-Alliarion; Leuschner and Ellenberg, 2018), which occur neither in forests with closed canopies nor in completely open habitats.

3.4.2 Occurrence of species in semi-open habitats in relation to their traits and environmental requirements

An understanding of the mechanisms that drive the occurrence of species in semi-open habitats is important for an assessment of the potential of that habitat type to connect other habitats. The successful establishment of a population at a site depends on several processes: seed dispersal, plant establishment upon arrival and reproduction (Hampe, 2011). Seed dispersal is only successful if the dispersed seed is able to establish and produce a new generation. For semi-open habitats to function as a stepping stone habitat, these processes must be repeated in them by several generations until a target habitat is reached. A species' potential to establish itself in semi-open habitats may therefore be limited by the ability to produce descendants either by seed or vegetatively, by dispersal, or by low establishment.

Our trait analyses suggest that the low occurrence of woodland species in semi-open habitats could be related to both limited dispersal and establishment. Although a high proportion of woodland species may be dispersed by vertebrates and thus potentially over long-distances, the species are also dispersed by invertebrates such as ants (Brunet & von Oheimb, 1999), and are self-dispersed or spread by vegetative propagation. However, these modes of dispersal are very inefficient (in terms of long-distance dispersal; Brunet and von Oheimb, 1999; von Oheimb *et al.*, 2009). As a consequence, ancient woodland species in particular are dispersal limited. For example, the ant-dispersed *Anemone nemorosa* shows migration rates of 0.2 m year^{-1} (Wulf, 1997; Brunet and von Oheimb, 1999) and *Melampyrum pratense* of 0.91 m year^{-1} (Heinken, 2004).

In contrast, more than three-quarters of the species of semi-open and open habitats were adapted to long-distance animal-dispersal. Historically, these man-made landscapes have been shaped by transhumance (Poschlod and Bonn, 1998), and even today livestock grazing is an important conservation measure to preserve these landscapes (e.g. to prevent shrub encroachment and to support seed dispersal). Seed dispersal by large animals such as cattle and sheep through adhesion (and endozoochory) may even result in long-distance transports, for instance over several hundred kilometres (Manzano and Malo, 2006; Couvreur *et al.*, 2004). On top of that, semi-open and open habitats contained also a higher proportion of wind-dispersed species than woodlands. Adaptations to wind-dispersal and low seed mass may facilitate long-distance dispersal of species of semi-open and open habitats (Damschen *et al.*, 2014). As a result, the general ability to disperse is higher for O- than for W-species, which also facilitates their dispersal into semi-open habitats.

A significant proportion of species of semi-open and open habitats of both the Swabian Jura and the Lueneburg Heath were more likely to have either a short- or long-term seed bank than woodland species. While the seeds of many O-species can persist up to five years in the soil, the longevity of the seeds of many W-species is less than one year (Hopfensperger, 2007; Bossuyt and Honnay, 2008). Persistent seed banks provide species with the capability to survive unfavourable environmental conditions and allow them to germinate once environmental conditions have improved (Bazzaz, 1979; Bossuyt and Honnay, 2008). For example, species which preferably grow in the darker conditions of SOH may germinate once semi-open habitats have developed a denser shrub or tree layer. W-species with transient seed banks have to germinate within a year in semi-open habitats; otherwise, their seeds become non-viable and dispersal fails. Flowering age also showed habitat-specific differences. Most W-species of the Swabian Jura, for example, need several years to reach flowering and produce seeds, which in turn might delay establishment in SO-plots. In contrast, about one-third of SO- and O-species are able to flower within the first year after germination, which in turn might facilitate early propagation.

Analyses of the realised ecological niches suggest that abiotic site conditions can act as a filter for the establishment of species in semi-open habitats. The requirements of species in woodlands in terms of light and soil moisture differed clearly from that of species of semi-open and open habitats, supporting the conclusion that environmental conditions limit the suitability of semi-open habitats for woodland species. Species of SOL-habitats in the Swabian Jura showed the same light and soil moisture requirements as open habitat species and the establishment of species from open habitats was less likely to be inhibited in SOL-habitats due to site conditions.

In the Lueneburg Heath, patterns were less clear, which also corresponds to the patterns of life-history traits recorded. Although species in woodlands had significantly lower light requirements, the differences to species of semi-open and open habitats were small. Therefore, W-, SOH-, SOL- and O-species in the Lueneburg Heath had similar light demands.

The differences in traits and site requirements of the species of the Swabian Jura and the Lueneburg Heath may be explained by differences in site management history, vegetation structure, phenology or soil conditions (e.g. calcareous vs. acidic sites, *Fagion* vs. *Quercion* forest communities, and *Mesobromion* vs. *Genistion* communities in the Swabian Jura and the Lueneburg Heath, respectively; cf. Leuschner and Ellenberg, 2018). Between-region differences in traits (e.g. seed propagation, seedbank type, and flowering age) – particularly with regard to open habitats (i.e. *Bromion* vs. *Genistion* communities) – are strongly shaped by differences in land use management and history. In the Swabian Jura, *Bromion* communities are shaped by a long history of grazing (Leuschner and Ellenberg, 2018). As a consequence, plant species have been favoured that are adapted to and depend on (epi-)zoochory, i.e. dispersal of seeds by grazing animals such as sheep (Bonn and Poschlod, 1998; Bonn, 2004). In contrast, open landscapes in the Lueneburg Heath (i.e. *Genistion* communities) have been subject to a long-lasting mixture of different management regimes (i.e. mowing, prescribed burning, sod-cutting, grazing; Härdtle *et al.*, 2006), which in turn favours plants that are propagated by both seeds and vegetatively, and whose re-establishment (after a total removal of the aboveground biomass due to sod-cutting or prescribed burning) benefits from the formation of long-term seedbanks. In addition, open landscapes in the Lueneburg Heath often are characterised by the dominance of dwarf shrubs (e.g. *Calluna vulgaris*) that are well adapted to these management measures. This in turn explains the low proportion of species with low flowering age (i.e. within the first year).

3.4.3 Conclusions

Our findings suggest that semi-open habitats have the potential to mitigate the effects of habitat fragmentation by serving as stepping stones and thus as dispersal corridors – at least in the two cultural landscapes investigated. We found that on average 73% of open habitat species (81% in the

Swabian Jura and 64% in the Lueneburg Heath) and 39% of woodland species (29% in the Swabian Jura and 48% in the Lueneburg Heath) were also present in semi-open habitats (i.e. SOL and/or SOH). This indicates that semi-open habitats can potentially act as stepping stones for species of open habitats and, to a lesser degree, of woodlands on their way to reach another target habitat and thus contribute to preserve the phytodiversity of woodland and open habitats in fragmented landscapes (Benayas *et al.*, 2008). Furthermore, semi-open corridors were very heterogeneous between study sites and characterised by a high phytodiversity, in part attributable to species that were only found in these habitats. Semi-open habitats are both hotspots of phytodiversity and potential species pools for the colonisation of adjacent habitats. However, there are limits to the suitability of semi-open habitats as corridors and they do not function for all species. About two-thirds of woodland species were not recorded in semi-open habitats, likely attributable to the stenoecious behaviour and dispersal-limitation of woodland species. This suggests that semi-open corridors do not work for the majority of woodland species. Moreover, it remains unclear to what extent this concept may work for regions with different environmental settings (e.g. other types of bedrock, soil or climatic conditions) and species assemblages.

In summary, our results show the potential of semi-open habitats for species conservation by providing suitable interim habitats for species in particular for those of open habitats and to a lesser extent for those of woodlands. Restoration strategies should therefore consider the development of semi-open corridors to alleviate barrier-effects and to mitigate the effects of habitat fragmentation.

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3.6 Supporting Information

3.6.1 Appendix S1: Results of the ANOVA tests for the comparison of the light and soil characteristics and species traits.

Table 1: Light and soil characteristics between habitat type and study site

	Swabian Jura		Lueneburg Heath	
	F-value	P-value	F-value	P-value
Canopy Openness				
Study site	0.79	0.5	12.53	< 0.001
Habitat type	440.33	< 0.001	191	< 0.001
C/N				
Study site	6.83	< 0.001	3.01	< 0.05
Habitat type	2.94	< 0.05	1.67	0.18
Base saturation				
Study site	7.02	< 0.001	5.91	< 0.001
Habitat type	8.08	< 0.001	40.31	< 0.001
pH (H2O)				
Study site	7.37	< 0.001	2.08	0.11
Habitat type	20.62	< 0.001	17.15	< 0.001

Table 2: Species traits and environmental requirements between habitat type and study site

	Swabian Jura		Lueneburg Heath	
	F-value	P-value	F-value	P-value
Seed mass				
Study site	6.65	< 0.001	6.55	< 0.001
Habitat type	12.39	< 0.001	22.02	< 0.001
Self dispersal				
Study site	0.84	0.48	2.05	0.11
Habitat type	11.75	< 0.001	6	< 0.05
Wind-dispersal				
Study site	3.52	< 0.05	2.7	0.05
Habitat type	1.73	0.17	40.71	< 0.001
Short-distance dispersal				

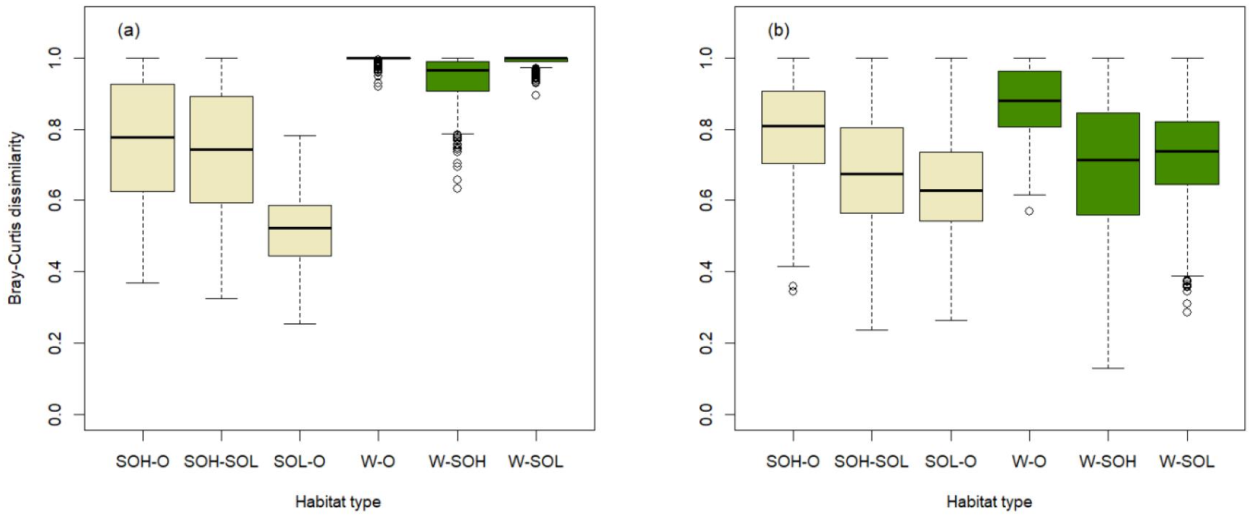
	Swabian Jura		Lueneburg Heath	
	F-value	P-value	F-value	P-value
Study site	0.81	0.49	3.86	< 0.05
Habitat type	20.78	< 0.001	49.32	< 0.001
Long-distance dispersal				
Study site	1.38	0.26	0.52	0.67
Habitat type	16.56	< 0.001	4.72	< 0.05
Seed propagation				
Study site	9.59	< 0.001	6.31	< 0.001
Habitat type	30.85	< 0.001	2.11	0.11
Vegetative propagation				
Study site	4.72	< 0.05	55.83	< 0.001
Habitat type	20.45	< 0.001	21.1	< 0.001
Seed and vegetative propagation				
Study site	13.2	< 0.001	64.54	< 0.001
Habitat type	3.61	< 0.05	61.02	< 0.001
Transient seedbank				
Study site	4.45	< 0.05	11.57	< 0.001
Habitat type	2.17	0.1	161.63	< 0.001
Short-term seedbank				
Study site	10.82	< 0.001	11	< 0.001
Habitat type	18.99	< 0.001	105.61	< 0.001
Long-term seedbank				
Study site	4.19	< 0.05	10.09	< 0.001
Habitat type	2.02	0.12	134.45	< 0.001
Flowering within a year				
Study site	2.84	< 0.05	7.42	< 0.001
Habitat type	55.29	< 0.001	48.83	< 0.001
Flowering after 1-5 years				
Study site	7.19	< 0.001	1.24	0.3
Habitat type	17.44	< 0.001	35.97	< 0.001
Flowering after 5 years				
Study site	1.92	0.13	0.45	0.72
Habitat type	3.07	< 0.05	5.56	< 0.05
Ellenberg Indicator Value for light				
Study site	4.91	<0.05	10.94	< 0.001
Habitat type	197.5	< 0.001	196.73	< 0.001
Ellenberg Indicator Value for moisture				
Study site	8.12	< 0.001	27.21	< 0.001
Habitat type	115.71	< 0.001	23.83	< 0.001

3.6.2 Appendix S2: Results of generalized linear models for the effects of habitat type on plant species composition fitted for each region separately.

P-values were adjusted using the Bonferroni method to account for multiple comparisons among habitat types (woodland (W); semi-open habitat with high canopy closure (SOH) and low canopy closure (SOL); open habitat (O)).

	Swabian Jura	Lueneburg Heath
W-SOH	< 0.01	< 0.01
W-SOL	< 0.01	< 0.01
W-O	< 0.05	< 0.01
SOH-SOL	< 0.01	< 0.01
SOH-O	< 0.01	< 0.01
SOL-O	< 0.01	< 0.01

3.6.3 Appendix S3: Bray-Curtis dissimilarities of the square-root transformed abundance data of the different habitat types of the (a) Swabian Jura and the (b) Lueneburg Heath.



3.6.4 Appendix S4: Significant and non-significant indicator species of single habitat types in the Lueneburg Heath and the Swabian Jura.

(woodland (W); semi-open habitat with high canopy closure (SOH) and low canopy closure (SOL); open habitat (O)). ***P < 0.001, **P < 0.01, *P < 0.05. Nomenclature follows Jäger (2011) for vascular plants and Frahm & Frey (2004) for bryophytes

Species	W	SOH	SOL	O
	Lueneburg Heath			
Hypnum cupressiforme	0.50**	.	.	.
Polytrichum formosum	0.49***	.	.	.
Scleropodium purum	0.46**	.	.	.
Frangula alnus	0.39	.	.	.
Quercus robur	0.38	.	.	.
Dryopteris carthusiana	0.34	.	.	.
Corynephorus canescens	0.22	.	.	.
Fagus sylvatica	0.22	.	.	.
Prunus serotina	0.22	.	.	.
Trientalis europaea	0.22	.	.	.
Dicranum scoparium	0.22	.	.	.
Epilobium angustifolium	.	0.22	.	.
Poa pratensis	.	0.22	.	.

Species	W	SOH	SOL	O
Taraxacum officinale agg.	.	0.22	.	.
Rumex acetosella	.	.	0.56**	.
Scorzoneroides autumnalis	.	.	0.52**	.
Festuca rubra	.	.	0.50**	.
Cytisus scoparius	.	.	0.22	.
Juncus effusus	.	.	0.22	.
Prunus spinosa	.	.	0.22	.
Tanacetum vulgare	.	.	.	0.45*
Luzula campestris agg.	.	.	.	0.36
Polytrichum piliferum	.	.	.	0.3
Leucanthemum vulgare	.	.	.	0.22
Juncus squarrosus	.	.	.	0.22
Pohlia nutans	.	.	.	0.22
Swabian Jura				
Asarum europaeum	0.92***	.	.	.
Galium odoratum	0.92***	.	.	.
Mercurialis perennis	0.83***	.	.	.
Fraxinus excelsior	0.81***	.	.	.
Acer pseudoplatanus	0.81***	.	.	.
Fagus sylvatica	0.77***	.	.	.
Acer campestre	0.76***	.	.	.
Galeobdolon luteum	0.74***	.	.	.
Anemone nemorosa	0.71***	.	.	.
Ulmus glabra	0.71***	.	.	.
Oxalis acetosella	0.67***	.	.	.
Viola reichenbachiana	0.67***	.	.	.
Hordelymus europaeus	0.64***	.	.	.
Poa chaixii	0.62***	.	.	.
Adoxa moschatellina	0.55***	.	.	.
Aegopodium podagraria	0.50**	.	.	.
Lamium maculatum	0.50**	.	.	.
Paris quadrifolia	0.50***	.	.	.
Hedera helix	0.48*	.	.	.
Ajuga reptans	0.45*	.	.	.
Lathyrus vernus	0.45**	.	.	.
Polygonatum multiflorum	0.45*	.	.	.
Euonymus europaeus	0.44*	.	.	.
Phyteuma spicatum	0.39	.	.	.
Aconitum lycoctonum	0.39	.	.	.
Carex digitata	0.32	.	.	.
Carex sylvatica	0.32	.	.	.
Dryopteris filix-mas	0.32	.	.	.
Geranium robertianum	0.32	.	.	.
Impatiens noli-tangere	0.32	.	.	.
Lilium martagon	0.32	.	.	.
Neottia nidus-avis	0.32	.	.	.
Polygonatum verticillatum	0.32	.	.	.
Ribes rubrum	0.32	.	.	.
Viola mirabilis	0.32	.	.	.
Actaea spicata	0.22	.	.	.
Alliaria petiolata	0.22	.	.	.
Athyrium filix-femina	0.22	.	.	.
Bromus benekenii	0.22	.	.	.
Carex montana	0.22	.	.	.

Species	W	SOH	SOL	O
Clematis vitalba	0.22	.	.	.
Heracleum sphondylium	0.22	.	.	.
Impatiens parviflora	0.22	.	.	.
Melampyrum pratense	0.22	.	.	.
Pulmonaria obscura	0.22	.	.	.
Pulmonaria officinalis	0.22	.	.	.
Rhamnus cathartica	0.22	.	.	.
Sanicula europaea	0.22	.	.	.
Scrophularia nodosa	0.22	.	.	.
Stachys sylvatica	0.22	.	.	.
Tilia cordata	0.22	.	.	.
Viburnum opulus	0.22	.	.	.
Fissidens taxifolius	0.22	.	.	.
Plagiochila porelloides	0.22	.	.	.
Polytrichum formosum	0.22	.	.	.
Porella platyphylla	0.22	.	.	.
Rhizomnium punctatum	0.22	.	.	.
Thamnobryum alopecurum	0.22	.	.	.
Dactylis glomerata	.	0.68***	.	.
Viola hirta	.	0.67***	.	.
Fragaria vesca	.	0.63**	.	.
Rhytidiadelphus triquetrus	.	0.59***	.	.
Helleborus viridis	.	0.55**	.	.
Brachypodium sylvaticum	.	0.55***	.	.
Crataegus rhipidophylla	.	0.50**	.	.
Veronica chamaedrys	.	0.48***	.	.
Glechoma hederacea	.	0.45*	.	.
Potentilla erecta	.	0.45*	.	.
Cephalanthera damasonium	.	0.42*	.	.
Holcus lanatus	.	0.4	.	.
Astragalus glycyphyllos	.	0.39*	.	.
Galium aparine	.	0.39	.	.
Ranunculus lanuginosus	.	0.39	.	.
Rhytidiadelphus squarrosus	.	0.39	.	.
Scleropodium purum	.	0.37	.	.
Sorbus intermedia	.	0.36	.	.
Festuca pratensis	.	0.36	.	.
Anthericum ramosum	.	0.35	.	.
Anthriscus sylvestris	.	0.32	.	.
Arrhenatherum elatius	.	0.32	.	.
Artemisia vulgaris	.	0.32	.	.
Clinopodium vulgare	.	0.32	.	.
Convolvulus arvensis	.	0.32	.	.
Hypochaeris radicata	.	0.32	.	.
Sorbus aucuparia	.	0.32	.	.
Brachythecium velutinum	.	0.32	.	.
Picea abies	.	0.29	.	.
Poa nemoralis	.	0.29	.	.
Aesculus hippocastanum	.	0.22	.	.
Alchemilla vulgaris	.	0.22	.	.
Bellis perennis	.	0.22	.	.
Berberis vulgaris	.	0.22	.	.
Bromus sterilis	.	0.22	.	.
Calamagrostis epigejos	.	0.22	.	.

Species	W	SOH	SOL	O
Carex muricata	.	0.22	.	.
Carpinus betulus	.	0.22	.	.
Cerastium holosteoides	.	0.22	.	.
Galeopsis speciosa	.	0.22	.	.
Galeopsis tetrahit agg.	.	0.22	.	.
Lolium perenne	.	0.22	.	.
Molinia arundinacea	.	0.22	.	.
Poa pratensis	.	0.22	.	.
Prunus avium	.	0.22	.	.
Ribes uva-crispa	.	0.22	.	.
Sedum reflexum	.	0.22	.	.
Stellaria graminea	.	0.22	.	.
Viburnum lantana	.	0.22	.	.
Brachythecium glareosum	.	0.22	.	.
Eurhynchium hians	.	0.22	.	.
Fissidens dubius	.	0.22	.	.
Homalothecium lutescens	.	0.22	.	.
Trifolium campestre	.	.	0.61***	.
Ligustrum vulgare	.	.	0.47*	.
Campanula rotundifolia	.	.	0.34	.
Genista pilosa	.	.	0.28	.
Calamagrostis varia	.	.	0.22	.
Equisetum arvense	.	.	0.22	.
Fragaria viridis	.	.	0.22	.
Gymnadenia conopsea	.	.	0.22	.
Phleum pratense	.	.	0.22	.
Potentilla heptaphylla	.	.	0.22	.
Carex caryophyllea	.	.	.	0.49**
Calliergonella cuspidata	.	.	.	0.42
Pinus sylvestris	.	.	.	0.38
Anthoxanthum odoratum	.	.	.	0.32
Inula hirta	.	.	.	0.32
Vicia hirsuta	.	.	.	0.32
Polygala vulgaris	.	.	.	0.28
Ajuga genevensis	.	.	.	0.22
Centaurea scabiosa	.	.	.	0.22
Cichorium intybus	.	.	.	0.22
Cirsium eriophorum	.	.	.	0.22
Euphorbia verrucosa	.	.	.	0.22
Ononis arvensis	.	.	.	0.22
Ononis repens	.	.	.	0.22

3.6.5 Appendix S5: Significant and non-significant indicator species of habitat type combinations in the Lueneburg Heath and the Swabian Jura.

(woodland (W); semi-open habitat with high canopy closure (SOH) and low canopy closure (SOL); open habitat (O)). ***P < 0.001, **P < 0.01, *P < 0.05. Nomenclature follows Jäger (2011) for vascular plants and Frahm & Frey (2004) for bryophytes

Species	W+SOH	W+SOH +SOL	W+SOH +O	W+SOL	W+SOL +O	SOH+ SOL	O+SOH	O+SOH +SOL	O+SOL
Lueneburg Heath									
Sorbus aucuparia	.	0.78***	.	.	.	.	.	.	.
Vaccinium myrtillus	.	0.73***	.	.	.	.	.	.	.

Species	W+SOH	W+SOH +SOL	W+SOH +O	W+SOL	W+SOL +O	SOH+ SOL	O+SOH	O+SOH +SOL	O+SOL
Luzula multiflora	.	0.42	.	.	.	.	.	.	.
Rubus idaeus	.	0.41	.	.	.	.	.	.	.
Hypnum jutlandicum	.	.	0.56	.	.	.	.	.	.
Molinia caerulea	.	.	0.45	.	.	.	.	.	.
Pleurozium schreberi	.	.	.	.	0.76*	.	.	.	.
Betula pendula	.	.	.	.	0.5	.	.	.	.
Galium saxatile	.	.	.	.	0.29	.	.	.	.
Agrostis capillaris	.	.	.	.	.	0.59*	.	.	.
Plantago lanceolata	.	.	.	.	.	.	0.3	.	.
Carex pilulifera	.	.	.	.	.	.	.	0.53*	.
Pilosella officinarum	.	.	.	.	.	.	.	0.52	.
Hypericum perforatum	.	.	.	.	.	.	.	0.45	.
Rhytidiadelphus	.	.	.	.	.	.	.	0.37	.
Achillea millefolium	.	.	.	.	.	.	.	0.32	.
Polytrichum juniperinum	.	.	.	.	.	.	.	0.32	.
Veronica officinalis	.	.	.	.	.	.	.	0.26	.
Calluna vulgaris	.	.	.	.	.	.	.	.	0.95***
Pinus sylvestris	.	.	.	.	.	.	.	.	0.81***
Festuca ovina agg.	.	.	.	.	.	.	.	.	0.53*
Betula pubescens	.	.	.	.	.	.	.	.	0.52**
Hieracium lachenalii	.	.	.	.	.	.	.	.	0.44
Holcus mollis	.	.	.	.	.	.	.	.	0.38
Gnaphalium sylvaticum	.	.	.	.	.	.	.	.	0.22
Swabian Jura									
Geum urbanum	0.58**	.	.	.	.	.	.	.	.
Lonicera xylosteum	0.54**	.	.	.	.	.	.	.	.
Vicia sepium	0.47*	.	.	.	.	.	.	.	.
Crataegus monogyna	0.46	.	.	.	.	.	.	.	.
Sambucus nigra	0.42	.	.	.	.	.	.	.	.
Helleborus foetidus	0.39	.	.	.	.	.	.	.	.
Primula elatior	0.35	.	.	.	.	.	.	.	.
Acer platanoides	0.32	.	.	.	.	.	.	.	.
Melica nutans	0.32	.	.	.	.	.	.	.	.
Mycelis muralis	0.32	.	.	.	.	.	.	.	.
Urtica dioica	0.32	.	.	.	.	.	.	.	.
Daphne mezereum	0.27	.	.	.	.	.	.	.	.
Brachythecium rutabulum	0.22	.	.	.	.	.	.	.	.
Homalothecium sericeum	0.22	.	.	.	.	.	.	.	.
Plagiomnium rostratum	0.22	.	.	.	.	.	.	.	.
Plagiomnium undulatum	.	0.32	.	.	.	.	.	.	.
Euphorbia amygdaloides	.	.	.	0.35	.	.	.	.	.
Valeriana officinalis agg.	.	.	.	0.27	.	.	.	.	.
Ctenidium molluscum	.	.	.	.	0.29	.	.	.	.
Taraxacum officinale agg.	.	.	.	.	.	0.76***	.	.	.
Cornus sanguinea	.	.	.	.	.	0.56*	.	.	.
Galium album	.	.	.	.	.	0.54**	.	.	.
Poa angustifolia	.	.	.	.	.	0.52**	.	.	.
Knautia arvensis	.	.	.	.	.	0.43	.	.	.
Acinos arvensis	.	.	.	.	.	0.42*	.	.	.
Thlaspi perfoliatum	.	.	.	.	.	0.41	.	.	.
Tragopogon pratensis	.	.	.	.	.	0.39	.	.	.
Prunella vulgaris	.	.	.	.	.	0.39	.	.	.
Lotus maritimus	.	.	.	.	.	0.38	.	.	.

Species	W+SOH	W+SOH +SOL	W+SOH +O	W+SOL	W+SOL +O	SOH+ SOL	O+SOH	O+SOH +SOL	O+SOL
Trisetum flavescens	.	.	.	.	.	0.34	.	.	.
Picris hieracioides	.	.	.	.	.	0.27	.	.	.
Helictotrichon pubescens	.	.	.	.	.	0.22	.	.	.
Stachys recta	.	.	.	.	.	.	0.51*	.	.
Festuca rubra	.	.	.	.	.	.	0.4	.	.
Primula veris	.	.	.	.	.	.	0.33	.	.
Cynosurus cristatus	.	.	.	.	.	.	0.32	.	.
Arabis hirsuta	.	.	.	.	.	.	0.27	.	.
Stachys officinalis	.	.	.	.	.	.	0.27	.	.
Agrostis capillaris	.	.	.	.	.	.	0.22	.	.
Echium vulgare	.	.	.	.	.	.	0.22	.	.
Lathyrus pratensis	.	.	.	.	.	.	0.22	.	.
Bromus erectus	.	.	.	.	.	.	.	0.90***	.
Lotus corniculatus	.	.	.	.	.	.	.	0.89***	.
Pimpinella saxifraga	.	.	.	.	.	.	.	0.89***	.
Galium verum	.	.	.	.	.	.	.	0.88***	.
Plantago lanceolata	.	.	.	.	.	.	.	0.88***	.
Sanguisorba minor	.	.	.	.	.	.	.	0.88***	.
Achillea millefolium	.	.	.	.	.	.	.	0.87***	.
Festuca ovina agg.	.	.	.	.	.	.	.	0.86***	.
Agrimonia eupatoria	.	.	.	.	.	.	.	0.82***	.
Brachypodium pinnatum	.	.	.	.	.	.	.	0.82***	.
Euphorbia cyparissias	.	.	.	.	.	.	.	0.82***	.
Medicago lupulina	.	.	.	.	.	.	.	0.81***	.
Plantago media	.	.	.	.	.	.	.	0.76***	.
Trifolium repens	.	.	.	.	.	.	.	0.74***	.
Prunus spinosa	.	.	.	.	.	.	.	0.72***	.
Leontodon hispidus	.	.	.	.	.	.	.	0.68**	.
Centaurea jacea	.	.	.	.	.	.	.	0.61**	.
Ononis spinosa	.	.	.	.	.	.	.	0.5	.
Juniperus communis	.	.	.	.	.	.	.	0.47	.
Origanum vulgare	.	.	.	.	.	.	.	0.43	.
Sorbus aria	.	.	.	.	.	.	.	0.39	.
Trifolium media	.	.	.	.	.	.	.	0.34	.
Potentilla reptans	.	.	.	.	.	.	.	0.32	.
Geranium sanguineum	.	.	.	.	.	.	.	0.29	.
Trifolium striatum	.	.	.	.	.	.	.	0.29	.
Onobrychis viciifolia	.	.	.	.	.	.	.	0.26	.
Thymus pulegioides agg.	.	.	.	.	.	.	.	.	0.96***
Prunella grandiflora	.	.	.	.	.	.	.	.	0.91***
Potentilla neumanniana	.	.	.	.	.	.	.	.	0.88***
Ranunculus bulbosus	.	.	.	.	.	.	.	.	0.87***
Linum catharticum	.	.	.	.	.	.	.	.	0.86***
Scabiosa columbaria	.	.	.	.	.	.	.	.	0.86***
Trifolium pratense	.	.	.	.	.	.	.	.	0.85***
Briza media	.	.	.	.	.	.	.	.	0.85***
Pilosella officinarum	.	.	.	.	.	.	.	.	0.82***
Teucrium chamaedrys	.	.	.	.	.	.	.	.	0.81***
Thuidium abietinum	.	.	.	.	.	.	.	.	0.80***
Daucus carota	.	.	.	.	.	.	.	.	0.78***
Koeleria pyramidata	.	.	.	.	.	.	.	.	0.77***
Leucanthemum vulgare	.	.	.	.	.	.	.	.	0.76***
Asperula cynanchica	.	.	.	.	.	.	.	.	0.71***

Species	W+SOH	W+SOH +SOL	W+SOH +O	W+SOL	W+SOL +O	SOH+ SOL	O+SOH	O+SOH +SOL	O+SOL
Rhytidium rugosum	.	.	.	.	.	.	.	.	0.68***
Euphrasia officinalis	.	.	.	.	.	.	.	.	0.67***
Polygala comosa	.	.	.	.	.	.	.	.	0.63***
Teucrium montanum	.	.	.	.	.	.	.	.	0.62***
Cirsium vulgare	.	.	.	.	.	.	.	.	0.57**
Dianthus carthusianorum	.	.	.	.	.	.	.	.	0.57**
Helianthemum	.	.	.	.	.	.	.	.	0.57**
Hippocrepis comosa	.	.	.	.	.	.	.	.	0.56**
Carex flacca	.	.	.	.	.	.	.	.	0.54**
Entodon concinnus	.	.	.	.	.	.	.	.	0.51*
Salvia pratensis	.	.	.	.	.	.	.	.	0.50*
Anthyllis vulneraria	.	.	.	.	.	.	.	.	0.47*
Hypericum perforatum	.	.	.	.	.	.	.	.	0.47*
Senecio jacobaea	.	.	.	.	.	.	.	.	0.46*
Campanula patula	.	.	.	.	.	.	.	.	0.44*
Polygala amarella	.	.	.	.	.	.	.	.	0.44*
Cirsium acaule	.	.	.	.	.	.	.	.	0.41
Thuidium philibertii	.	.	.	.	.	.	.	.	0.35
Carlina vulgaris	.	.	.	.	.	.	.	.	0.22
Chamaespartium sagittale	.	.	.	.	.	.	.	.	0.22
Ophrys apifera	.	.	.	.	.	.	.	.	0.22
Phleum phleoides	.	.	.	.	.	.	.	.	0.22
Dicranum bonjeanii	.	.	.	.	.	.	.	.	0.22

3.6.6 Appendix S6: Constancy table of the plant communities of the Swabian Jura.

(0%<r<=5%, 5%<+<=10%, 10%<I<=20%, 20%<II<=40%, 40%<III<=60%, 60%<IV<=80%, 80%<V<=100%; woodland (W); semi-open habitat with high canopy closure (SOH) and low canopy closure (SOL); open habitat (O))

	Habitat type	W	SOH	SOL	O
1	*Asarum europaeum*	V	r	.	.
1	*Galium odoratum*	V	.	.	.
1	*Acer pseudoplatanus (Sh)*	IV	.	.	.
1	*Galeobdolon luteum*	III	.	.	.
1	*Anemone nemorosa*	III	.	.	.
1	*Ulmus glabra (H)*	III	.	.	.
1	*Hordelymus europaeus*	III	r	.	.
1	*Oxalis acetosella*	III	.	.	.
1	*Poa chaixii*	III	r	r	.
1	*Viola reichenbachiana*	III	.	.	.
1	*Adoxa moschatellina*	II	.	.	.
1	*Aegopodium podagraria*	II	.	.	.
1	*Lamium maculatum*	II	.	.	.
1	*Paris quadrifolia*	II	.	.	.
1	*Ajuga reptans*	I	.	.	.
1	*Euonymus europaeus (H)*	I	r	.	.
1	*Lathyrus vernus*	I	.	.	.
1	*Polygonatum multiflorum*	I	.	.	.
1	*Aconitum lycoctonum*	I	.	.	.
1	*Mycelis muralis*	I	r	.	.
1	*Phyteuma spicatum*	I	.	.	.
1	*Carex digitata*	+	.	.	.
1	*Carex sylvatica*	+	.	.	.
1	*Dryopteris filix-mas*	+	.	.	.

	Habitat type	W	SOH	SOL	O
1	*Geranium robertianum*	+	.	.	.
1	*Impatiens noli-tangere*	+	.	.	.
1	*Neottia nidus-avis*	+	.	.	.
1	*Viola mirabilis*	+	.	.	.
2	*Fraxinus excelsior (Sh)*	IV	III	r	.
2	*Mercurialis perennis*	IV	I	.	.
2	*Acer campestre (Sh)*	III	II	.	.
2	*Fagus sylvatica (Sh)*	IV	III	r	.
2	*Crataegus monogyna (H)*	II	II	r	r
2	*Geum urbanum*	II	III	r	.
2	*Hedera helix*	II	+	.	.
2	*Lonicera xylosteum (H)*	II	II	r	.
2	*Sambucus nigra*	II	+	.	.
2	*Helleborus foetidus*	I	I	r	.
2	*Vicia sepium*	I	II	r	.
2	*Acer platanoides (H)*	I	r	.	.
2	*Brachypodium sylvaticum*	I	II	.	.
2	*Crataegus rhipidophylla (H)*	+	II	.	.
2	*Galium aparine*	+	I	.	.
2	*Primula elatior*	+	I	.	.
2	*Cephalanthera damasonium*	r	I	.	.
3	*Cornus sanguinea (H)*	I	III	II	r
5	*Dactylis glomerata*	.	III	I	I
5	*Helleborus viridis*	.	II	.	.
5	*Veronica chamaedrys*	.	II	r	.
5	*Prunella vulgaris*	.	II	+	r
5	*Rhytidiadelphus triquetrus*	r	II	r	.
5	*Glechoma hederacea*	.	I	.	.
5	*Potentilla erecta*	.	I	.	.
5	*Astragalus glycyphyllos*	.	I	.	.
5	*Festuca pratensis*	.	I	r	.
5	*Ranunculus lanuginosus*	.	I	.	.
5	*Sorbus intermedia (H)*	.	I	r	.
5	*Rhytidiadelphus squarrosus*	.	I	.	.
5	*Scleropodium purum*	.	I	r	+
6	*Viola hirta*	.	III	I	r
6	*Galium album*	.	II	I	r
6	*Knautia arvensis*	.	I	I	r
6	*Poa angustifolia*	.	I	II	r
6	*Thlaspi perfoliatum*	.	I	I	r
6	*Acinos arvensis*	.	I	I	.
6	*Anthericum ramosum*	.	I	r	.
6	*Tragopogon pratensis*	.	I	I	.
6	*Aesculus hippocastanum*	.	r	.	.
7	*Taraxacum officinalis* agg.	.	IV	III	II
7	*Pimpinella saxifraga*	.	IV	V	IV
7	*Lotus corniculatus*	.	III	V	V
7	*Achillea millefolium*	.	III	V	V
7	*Festuca ovina agg.*	.	III	V	IV
7	*Galium verum*	.	III	V	IV
7	*Medicago lupulina*	.	III	IV	IV
7	*Euphorbia cyparissias*	.	III	IV	IV
7	*Prunus spinosa*	.	III	II	IV
7	*Plantago lanceolata*	.	III	V	V

	Habitat type	W	SOH	SOL	O
7	*Sanguisorba minor*	.	III	V	V
7	*Trifolium pratense*	.	III	V	IV
7	*Trifolium repens*	.	III	IV	III
7	*Briza media*	.	II	IV	V
7	*Daucus carota*	.	II	IV	IV
7	*Thymus pulegioides* agg.	.	II	V	V
7	*Leontodon hispidus*	.	II	III	III
7	*Plantago media*	.	II	IV	IV
7	*Ranunculus bulbosus*	.	II	IV	V
7	*Koeleria pyramidata*	.	II	IV	IV
7	*Linum catharticum*	.	II	IV	V
7	*Teucrium chamaedrys*	.	II	IV	IV
7	*Centaurea jacea*	.	II	II	III
7	*Stachys recta*	.	II	I	II
7	*Leucanthemum vulgare*	.	I	IV	III
7	*Ononis spinosa*	.	I	II	II
7	*Polygala comosa*	.	I	II	III
7	*Prunella grandiflora*	.	I	V	V
7	*Rhytidium rugosum*	.	I	II	III
7	*Thuidium abietinum*	.	I	III	IV
7	*Helianthemum nummularium*	.	I	II	II
7	*Hippocrepis comosa*	.	I	II	III
7	*Juniperus communis (H)*	.	I	II	II
7	*Potentilla reptans*	.	+	+	+
7	*Bromus benekenii*	r	.	.	.
7	*Trifolium campestre*	.	.	III	I
8	*Ligustrum vulgare (H)*	+	+	II	r
8	*Campanula rotundifolia*	.	r	I	.
9	*Brachypodium pinnatum*	.	II	V	IV
9	*Potentilla neumanniana*	.	II	IV	V
9	*Scabiosa columbaria*	.	I	IV	V
9	*Pilosella officinarum*	.	I	IV	IV
9	*Dianthus carthusianorum*	.	+	III	II
9	*Asperula cynanchica*	.	+	III	IV
9	*Euphrasia officinalis*	.	.	II	III
9	*Cirsium vulgare*	.	.	II	II
9	*Teucrium montanum*	.	r	II	III
9	*Entodon concinnus*	.	+	II	II
9	*Carex flacca*	r	r	II	II
9	*Hypericum perforatum*	.	+	II	II
9	*Origanum vulgare*	.	+	II	I
9	*Salvia pratensis*	.	.	II	II
9	*Senecio jacobaea*	.	+	II	II
9	*Campanula patula*	.	r	I	I
9	*Cirsium acaule*	.	r	I	I
9	*Polygala amarella*	.	r	I	I
9	*Anthyllis vulneraria*	.	.	I	II
9	*Carex caryophyllea*	.	.	I	II
10	*Festuca rubra*	.	+	+	II
10	*Pinus sylvestris (H)*	.	.	r	I
11	*Corylus avellana (H)*	I	+	+	+
11	*Fragaria vesca*	I	III	I	I
11	*Vincetoxicum hirundinaria*	I	II	II	I
11	*Euphorbia amygdaloides*	I	.	+	.

	Habitat type	W	SOH	SOL	O
11	*Melica nutans*	I	r	.	.
11	*Quercus robur (H)*	I	I	I	II
11	*Daphne mezereum*	+	r	.	.
11	*Lilium martagon*	+	.	.	.
11	*Polygonatum verticillatum*	+	.	.	.
11	*Quercus petraea (H)*	+	I	I	+
11	*Ribes rubrum*	+	.	.	.
11	*Urtica dioica*	+	+	.	.
11	*Valeriana officinalis* agg.	+	.	r	.
11	*Plagiomnium undulatum*	I	+	r	.
11	*Actaea spicata*	r	.	.	.
11	*Alliaria petiolata*	r	.	.	.
11	*Athyrium filix-femina*	r	.	.	.
11	*Carex montana*	r	.	.	.
11	*Clematis vitalba*	r	.	.	.
11	*Heracleum sphondylium*	r	.	.	.
11	*Impatiens parviflora*	r	.	.	.
11	*Melampyrum pratense*	r	.	.	.
11	*Picea abies (H)*	r	+	.	.
11	*Poa nemoralis*	r	+	.	.
11	*Primula veris*	r	I	r	I
11	*Pulmonaria obscura*	r	.	.	.
11	*Pulmonaria officinalis*	r	.	.	.
11	*Rhamnus cathartica (H)*	r	.	.	.
11	*Sanicula europaea*	r	.	.	.
11	*Scrophularia nodosa*	r	.	.	.
11	*Stachys sylvatica*	r	.	.	.
11	*Tilia cordata (H)*	r	.	.	.
11	*Viburnum opulus (H)*	r	.	.	.
11	*Brachythecium rutabulum*	r	r	.	.
11	*Ctenidium molluscum*	+	.	+	r
11	*Fissidens taxifolius*	r	.	.	.
11	*Porella platyphylla*	r	.	.	.
11	*Rhizomnium punctatum*	r	.	.	.
11	*Thamnobryum alopecurum*	r	.	.	.
11	*Agrimonia eupatoria*	.	III	IV	IV
11	*Agrostis capillaris*	.	r	.	r
11	*Ajuga genevensis*	.	.	.	r
11	*Alchemilla vulgaris*	.	r	.	.
11	*Anthoxanthum odoratum*	.	.	.	+
11	*Anthriscus sylvestris*	.	+	.	.
11	*Arabis hirsuta*	.	+	.	r
11	*Arrhenatherum elatius*	.	+	.	.
11	*Artemisia vulgaris*	.	+	.	.
11	*Bellis perennis*	.	r	.	.
11	*Berberis vulgaris (H)*	.	r	.	.
11	*Bromus erectus*	.	III	V	V
11	*Bromus sterilis*	.	r	.	.
11	*Calamagrostis epigejos*	.	r	.	.
11	*Calamagrostis varia*	.	.	r	.
11	*Carex muricata*	.	r	.	.
11	*Carlina vulgaris*	.	.	r	r
11	*Carpinus betulus (H)*	.	r	.	.
11	*Centaurea scabiosa*	.	.	.	r

	Habitat type	W	SOH	SOL	O
11	*Cerastium holosteoides*	.	r	.	.
11	*Chamaespartium sagittale*	.	.	r	r
11	*Cichorium intybus*	.	.	.	r
11	*Cirsium eriophorum*	.	.	.	r
11	*Clinopodium vulgare*	.	+	.	.
11	*Convolvulus arvensis*	.	+	.	.
11	*Cynosurus cristatus*	.	+	.	+
11	*Echium vulgare*	.	r	.	r
11	*Equisetum arvense*	.	.	r	.
11	*Euphorbia verrucosa*	.	.	.	r
11	*Fragaria viridis*	.	.	r	.
11	*Galeopsis speciosa*	.	r	.	.
11	*Galeopsis tetrahit* agg.	.	r	.	.
11	*Genista pilosa*	.	.	+	r
11	*Geranium sanguineum*	.	I	r	r
11	*Gymnadenia conopsea*	.	.	r	.
11	*Helictotrichon pubescens*	.	r	r	.
11	*Holcus lanatus*	.	II	r	I
11	*Hypochaeris radicata*	.	+	.	.
11	*Inula hirta*	.	.	.	+
11	*Lathyrus pratensis*	.	r	.	r
11	*Lolium perenne*	.	r	.	.
11	*Lotus maritimus*	.	+	I	r
11	*Molinia arundinacea*	.	r	.	.
11	*Onobrychis viciifolia*	.	r	+	r
11	*Ononis arvensis*	.	.	.	r
11	*Ononis repens*	.	.	.	r
11	*Ophrys apifera*	.	.	r	r
11	*Phleum phleoides*	.	.	r	r
11	*Phleum pratense*	.	.	r	.
11	*Picris hieracioides*	.	+	r	.
11	*Poa pratensis*	.	r	.	.
11	*Polygala vulgaris*	.	.	r	+
11	*Potentilla heptaphylla*	.	.	r	.
11	*Prunus avium*	.	r	.	.
11	*Ribes uva-crispa*	.	r	.	.
11	*Sedum reflexum*	.	r	.	.
11	*Sorbus aria*	.	I	I	+
11	*Sorbus aucuparia*	.	+	.	.
11	*Stachys officinalis*	.	+	.	r
11	*Stellaria graminea*	.	r	.	.
11	*Trifolium media*	.	r	+	I
11	*Trifolium striatum*	.	+	+	r
11	*Trisetum flavescens*	.	+	I	r
11	*Viburnum lantana (H)*	.	r	.	.
11	*Vicia hirsuta*	.	.	.	+
11	*Brachythecium glareosum*	.	r	.	.
11	*Brachythecium velutinum*	.	+	.	.
11	*Calliergonella cuspidata*	.	r	+	I
11	*Dicranum bonjeanii*	.	.	r	r
11	*Eurhynchium hians*	.	r	.	.
11	*Fissidens dubius*	.	r	.	.
11	*Homalothecium lutescens*	.	r	.	.
11	*Homalothecium sericeum*	r	r	.	.

	Habitat type	W	SOH	SOL	O
11	*Plagiochila porelloides*	r	.	.	.
11	*Plagiomnium rostratum*	r	r	.	.
11	*Polytrichum formosum*	r	.	.	.
11	*Thuidium philibertii*	.	r	+	I

3.6.7 Appendix S7: Constancy table of the plant communities of the Lueneburg Heath.

(0%<r<=5%, 5%<+<=10%, 10%<I<=20%, 20%<II<=40%, 40%<III<=60%, 60%<IV<=80%, 80%<V<=100%; woodland (W); semi-open habitat with high canopy closure (SOH) and low canopy closure (SOL); open habitat (O))

	Habitat type	W	SOH	SOL	O
1	*Hypnum cupressiforme*	II	.	.	.
1	*Polytrichum formosum*	II	.	.	r
1	*Scleropodium purum*	II	r	.	r
1	*Dryopteris carthusiana*	I	r	r	.
1	*Frangula alnus (H)*	I	.	.	.
1	*Quercus robur (H)*	I	r	.	.
3	*Vaccinium myrtillus*	IV	II	III	r
3	*Sorbus aucuparia (Sh)*	IV	IV	III	r
3	*Rubus idaeus*	I	I	I	.
4	*Calluna vulgaris*	+	III	V	V
4	*Agrostis capillaris*	+	II	III	I
4	*Carex pilulifera*	.	II	II	I
4	*Pilosella officinarum*	.	I	II	I
4	*Hypericum perforatum*	.	I	I	II
4	*Festuca ovina agg.*	.	+	II	II
4	*Holcus mollis*	r	.	I	+
5	*Rumex acetosella*	.	+	II	+
5	*Festuca rubra*	.	.	II	.
6	*Betula pubescens (H)*	.	.	II	I
6	*Scorzoneroides autumnalis*	.	.	II	I
6	*Hieracium lachenalii*	.	r	I	II
7	*Tanacetum vulgare*	.	.	.	I
7	*Luzula campestris agg.*	.	r	.	I
8	*Pleurozium schreberi*	V	II	I	II
8	*Deschampsia flexuosa*	IV	V	V	IV
8	*Pinus sylvestris (H)*	II	II	IV	IV
8	*Hypnum jutlandicum*	II	II	+	II
8	*Quercus petraea (H)*	I	III	III	II
8	*Betula pendula (H)*	I	r	I	II
8	*Luzula multiflora*	I	I	II	r
8	*Molinia caerulea*	I	I	+	II
8	*Corynephorus canescens*	r	.	.	.
8	*Fagus sylvatica (H)*	r	.	.	.
8	*Prunus serotina (H)*	r	.	.	.
8	*Trientalis europaea*	r	.	.	.
8	*Dicranum scoparium*	r	.	.	.
8	*Rhytidiadelphus squarrosus*	r	+	II	+
8	*Achillea millefolium*	.	+	r	I
8	*Leucanthemum vulgare*	.	.	.	r
8	*Cytisus scoparius*	.	.	r	.
8	*Epilobium angustifolium*	.	r	.	.
8	*Galium saxatile*	I	r	r	r
8	*Gnaphalium sylvaticum*	.	.	r	r
8	*Juncus effusus*	.	.	r	.

	Habitat type	W	SOH	SOL	O
8	*Juncus squarrosus*	.	.	.	r
8	*Plantago lanceolata*	.	+	r	+
8	*Poa pratensis*	.	r	.	.
8	*Prunus spinosa (H)*	.	.	r	.
8	*Taraxacum officinale agg.*	.	r	.	.
8	*Veronica officinalis*	.	r	+	r
8	*Pohlia nutans*	.	.	.	r
8	*Polytrichum juniperum*	.	+	+	+
8	*Polytrichum piliferum*	.	r	.	+

3.6.8 Appendix S8: Plant species list of vegetation surveys in all plots of the Swabian Jura.

See following link for Appendix S8
https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Favsc.12526&file=avsc12526-sup-0008-AppendixS8.pdf

3.6.9 Appendix S9: Plant species list of vegetation surveys in all plots of the Lueneburg Heath.

See following link for Appendix S9
https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1111%2Favsc.12526&file=avsc12526-sup-0009-AppendixS9.pdf

4. Outside the comfort zone: Species traits and environmental factors drive woodland and open habitat plant recruitment in semi-open habitats

Unpublished manuscript:

Travers, E., Fichtner, A., Härdtle, W. & Matthies, D.

Abstract

To counteract the adverse effects of habitat fragmentation such as reduced species dispersal and consequently increased species extinction risk, linear dispersal corridors have been introduced to re-connect isolated habitat patches and allow their re-colonisation. However, by connecting one habitat type, linear dispersal corridors act as a barrier for species dispersal themselves if they intersect other habitat types. Semi-open pasture landscapes feature a mosaic of open habitats, individual trees, and groups of trees and have the potential to act as stepping stones for both open habitat and woodland species at the same time and thus mitigate the effects of habitat fragmentation.

We investigated whether seedlings of open habitat and woodland plants can recruit (including seed germination, seedling establishment and seedling survival) in semi-open habitats by carrying out a seed experiment. We sowed seeds of 5 woodland and 5 open habitat species in semi-open habitats in the Lueneburg Heath and the Swabian Jura, also applying a disturbance treatment (sod-cutting and mowing). Using GLMMs we analysed whether species type or species identity drive recruitment. We also investigated if species characteristics such as seed mass and Ellenberg indicator value for light, or environmental conditions such as canopy closure or the disturbance treatment influence seedling recruitment.

Both woodland and open habitat species were able to recruit seedlings in semi-open habitats, however the recruitment success was clearly driven by species identity. The recruitment success strongly depends on the species characteristics (traits) as well as the environmental setting of the location (e.g. light availability, soil conditions). In the Lueneburg Heath high seed mass had a vital effect on the recruitment of seedlings whereas in the Swabian Jura seedling numbers were less affected by seed mass. The effects of light, either in terms of the species' Ellenberg indicator value for light or the canopy closure of the site, on recruitment mostly played a role at a later stage in both regions. Removal of the topsoil also significantly increased seedling numbers. The results indicate that structurally diverse semi-open habitats offer a variety of microsites which cater for different species requirements. If they are managed accordingly, species of woodlands and open habitats are enabled to use semi-open habitats as interim habitat.

4.1 Introduction

Land use changes over the last decades have led to an increase in habitat fragmentation and have decreased landscape connectivity. Remaining habitat patches are often isolated from each other and as a result, both the movement of animals and the dispersal of plants are limited (Uroy *et al.* 2019). Habitat fragmentation and subsequent isolation have resulted in habitat loss, deterioration of habitat quality and an increased extinction risk of species (Haddad *et al.* 2015; Hadley & Betts 2016; Evans *et al.* 2017). Fragmented populations are more vulnerable to genetic drift and inbreeding which increase the risk of genetic erosion, reduced fitness and make populations less resilient to environmental shifts such as climate change (Fischer and Matthies 1998a,b; Kéry *et al.* 2000; Xiao *et al.* 2016).

Linear stepping stones and dispersal corridors have been introduced as a measure to counteract the adverse effects of habitat fragmentation and isolation (Diamond 1975; Wilson & Willis 1975; Keitt *et al.* 1997; Saura *et al.* 2014; Herrman *et al.* 2016; Kormann *et al.* 2016). These are linear habitat patches that connect isolated habitats and enhance movement and dispersal between them (Rosenberg *et al.* 1997; Tewksbury *et al.* 2002). Populations benefit from increased gene flow between isolated habitat patches and re-colonisation of habitat patches counteracts local species extinctions. Linear dispersal corridors are usually designed to connect habitat patches which are fragmented by adverse areas such as settlements, infrastructure or agricultural fields. However, one of the drawbacks with linear dispersal corridors is their barrier-effect for species dispersal if they intersect other habitat types (Dobson *et al.* 1999; van Dijk *et al.* 2014). By connecting one habitat type, they create new barriers for the habitat type they run through (Eggers *et al.* 2010). This holds especially true for Central European landscapes which feature a tight network of woodlands and open habitats.

Many pasture landscapes in Central Europe have developed from traditional land-use such as extensive grazing and alternate husbandry (Finck *et al.* 2002; Jedicke 2015; Tölgyesi *et al.* 2018). Due to abandonment of traditional husbandry, the onset of succession has created a landscape with a high structural diversity featured with a mosaic of open habitat patches and individual trees, groups of trees or shrubs with different degrees of canopy closure in-between woodlands (Poschlod *et al.* 2005; Bergmeier *et al.* 2010; Popp & Scheibe 2013). Featuring heterogeneous environmental conditions which can accommodate species with different habitat requirements (Bergmeier *et al.* 2010), these so-called semi-open landscapes are among the most species-rich habitats in Europe and host a large proportion of the biodiversity in Europe, including many endangered plant and animal species (Jedicke 2015; Tölgyesi *et al.* 2018). Due to the high structural diversity and the availability of various environmental factors, species of both woodlands and open habitats may be able to colonise these semi-open habitats which could potentially act as stepping stones or corridors. Semi-open corridors could be a promising approach to mitigate the effects of habitat fragmentation and avoid the barrier-effects of linear dispersal corridors (Eggers *et al.* 2010).

So far, it is not known to what extent semi-open corridors may facilitate the dispersal of plants. Due to their sedentary mode of living, plants rely on animal vectors and external dispersal agents for their dispersal (Bonn & Poschlod 1998; Jongman *et al.* 2004). Therefore, the success of plant dispersal is also dependent on the suitability of the corridor for the dispersal vector. In other cases, corridors act as stepping stone habitats where plant diaspores only travel short distances of the corridor and need several generations until they have finally reached their destination habitat (Damschen *et al.* 2008). Hence, the corridor must also act as an interim habitat and has to accommodate for the different life stages of a plant (Brederveld *et al.* 2011; Calçada *et al.* 2013; Lõhmus *et al.* 2014; Saura *et al.* 2014). The stochasticity of plant dispersal limits the extent of research (Murphy & Lovett-Doust 2004) and little is known about the suitability of corridors as stepping stone habitats that allow plant establishment, reproduction and further dispersal.

Acting as an interim habitat means semi-open corridors do not only have to cater for plant traits which facilitate dispersal but also for traits which are important for seedling recruitment. Especially, seed mass and light requirements are important traits to consider during seed germination (Veloso *et al.* 2017). The environmental surrounding drives seed germination by offering the right light availability and appropriate surface conditions (for example, bare soil for soil-seed contact and suitable soil moisture). However, it is unknown to what extent these factors (seed mass, light, surface conditions) affect seedling recruitment of woodland and open habitat species in semi-open habitats.

In the present study we investigated whether semi-open habitats may act as stepping stone habitats for plants of both woodland and open habitats by offering a suitable environment for seedling recruitment, including seed germination, seedling establishment and seedling survival (according to Larson *et al.* 2015). To quantify to which extent plants are able to colonise semi-open habitats, we carried out an experiment by sowing seeds of woodland and open habitat species in semi-open habitats to track their recruitment success. We asked the following questions: (i) Which woodland and open habitat species recruit best in semi-open habitats, (ii) which species traits and environmental factors affect their seedling recruitment in semi-open habitats and (iii) do habitat management techniques such as sod-cutting and mowing have an effect on the recruitment success of woodland and open habitat species in semi-open habitats?

4.2 Materials and methods

4.2.1 Study area and climatic conditions during the study period

Our study sites were situated in the Lueneburg Heath in Northern Germany and in the Swabian Jura in Southern Germany. Semi-open landscapes exist in both regions; however, they differ in soil conditions and plant communities (see Travers *et al.* 2020). The landscapes had been kept open by many centuries of livestock grazing (Beinlich & Plachter 1995; Cordes *et al.* 1997). Changes in habitat management such as reduced grazing have led to an increase of dense vegetation such as shrubs which resulted in large areas of semi-open habitats (see Finck *et al.* 2002). Soils in the Lueneburg Heath are acidic, and the study sites consist of a mosaic of heathlands dominated by *Calluna vulgaris* and small patches of groups of trees composed of *Betula pendula*, *Juniperus communis*, *Quercus* spp. and *Pinus sylvestris*. The study sites in the Swabian Jura are calcareous grasslands alternating with shrubs and trees of *Juniperus communis*, *Prunus spinosa*, *Quercus robur* and *Fagus sylvatica* at different densities and ages.

Data on the climatic conditions in the study years were obtained from Deutscher Wetterdienst for the stations Soltau in the Lueneburg Heath and Münsingen-Apfelstetten in the Swabian Jura, which were close to the study sites. During the study period several periods of drought occurred. In the Lueneburg Heath there was a strong drought during July and August 2013 and again in September 2014 (Figure S1, Supporting Information). Less severe periods of drought occurred in June 2015 and September 2016. In contrast, in the Swabian Jura precipitation was generally higher and there was no drought in 2013 and 2014 (Figure S2, Supporting Information).

4.2.2 Experimental design

In 2013, we randomly chose four study sites of 25 ha each in each region (blocks). At each study site we set up four fenced 5 m x 5 m plots. We set up two plots with high canopy closure under groups of trees and two plots with a low canopy closure under single trees. The light climate in each plot was determined by taking a hemispherical photograph 1 m above ground at the centre of each plot with a fish-eye lens (Nikon, Fisheye Converter FC-E8 0.21x, Japan) and canopy closure was determined with the program Gap Light Analyzer 2.0 (Cary Institute of Ecosystem Studies 1999).

From March to April 2013, we set up twenty 0.25 m x 0.25 m subplots in each plot. To compare the effects of possible management measures to reduce competition by the established vegetation on seedling recruitment, we applied two disturbance treatments: In ten randomly chosen subplots we removed the top 5 cm of soil with a spade ("sod-cutting") and in the other ten subplots we cut the vegetation at a height of 2 cm above ground ("mowing").

4.2.3 Study species

In March and April 2013, we sowed seeds of ten species into the two types of subplots of each plot. Half of the species were from woodlands and half from open habitats, in the following called "species types" (Table 6), which differ in their realised ecological niche with respect to light, as shown by their different Ellenberg indicator values for light (Table 6). The species were selected to be typical representatives of these habitats in the two regions and were obtained from commercial suppliers (Appels Wilde Samen, Darmstadt; Jelitto, Schwarmstedt; Rieger-Hofmann, Blaufelden). In each plot there was one subplot for each combination of species and disturbance treatment (sod-cutting and mowing). The number of seeds for each species sown into a subplot depended on its seed mass, as smaller seeds were expected to have a lower chance of producing a seedling. For species with a seed mass of < 0.05 mg we used 5000 seeds per subplot, while for the others we used 2000 seeds.

Table 6: Habitat preference and traits of the study species in the two regions Lueneburg Heath and Swabian Jura (nomenclature based on Müller et al. 2021). L: Ellenberg indicator value for light according to Müller et al. 2021. Seed mass as listed by Kleyer et al. (2008).

Region	Species type	Habitat type	Species	Seed mass (mg)	L
Lueneburg Heath	Woodland	*Betulo-Quercetum* woodlands	*Hieracium murorum*	0.4	4
			Luzula multiflora	0.4	7
			Solidago virgaurea	0.61	5
			Vaccinium myrtillus	0.27	5
			Veronica officinalis	0.12	4
	Open habitat	*Genisto-Callunetum* heathlands	*Arnica montana*	1.47	9
			Calluna vulgaris	0.03	8
			Jasione montana	0.03	7
			Luzula campestris	0.68	7
			Thymus serpyllum	0.2	7
Swabian Jura	Woodland	*Galio odorati-Fagetum* woodlands	*Astrantia major*	2.98	6
			Galium sylvaticum	1.1	5
			Melica nutans	2.49	4
			Primula elatior	0.45	6
			Ranunculus auricomus	2.32	5
	Open habitat	*Gentiano-Koelerietum* grasslands	*Betonica officinalis*	1.4	7
			Briza media	0.4	8
			Filipendula vulgaris	0.79	7
			Pimpinella saxifraga	1.15	7
			Prunella grandiflora	0.86	7

We recorded seedling recruitment in each subplot by counting the surviving seedlings in autumn 2013 and 2014, and in the Lueneburg Heath additionally in the years 2015 and 2016. Because of lack of permission, it was not possible to continue the study after 2014 in the Swabian Jura. One plot with low canopy closure had to be abandoned in the Swabian Jura at the end of the growing season in 2013 as fencing was no longer allowed. The experiment was repeated in 2014 in both regions using a new set of subplots in the same plots, and the plot which had to be removed in

2013 in the Swabian Jura was replaced by another one at the same site. However, due to seed shortage *Melica nutans* was not re-sown in 2014.

4.2.4 Statistical analyses

All analyses were conducted in R version 4.2.2 (R Core Team 2022). To study the development of the experimental populations of the various species over time, we calculated for each species and year, separately for the plants sown in 2013 and 2014 (sowing date (cohort)), the number of seedlings alive as a proportion of the number of seeds sown (recruitment). The proportion of seedlings recruited over time was plotted on a log-scale, so that the slopes of the curves indicated mortality, or in the case of population increase, the specific population growth rate (r).

Differences among the species sown in their recruitment in the first year after sowing was analysed with generalised linear mixed-effects models (GLMMs; package glmmTMB, Brooks *et al.* 2017) with a logit-link and beta-binomial error distribution to account for overdispersed binominal data (Zuur *et al.* 2013). Plots nested within blocks were included as random effects. Models were fitted for each region and sowing date (cohort) separately.

To study potential differences between species from open and woodland habitats, we investigated the effect of that factor together with that of the disturbance treatment and the environmental variable canopy closure on seedling recruitment in the different years with analogous GLMMs but included species identity as a random instead of a fixed effect. Models were fitted for each region, sowing date (cohort) and year separately. We initially included all two-way interactions and then determined the best models using the sample size corrected Akaike Information Criterion (AICc) with the dredge function of the MuMIn package (Bartoń 2020). Model assumptions were tested using the DHARMa package (Hartig 2020). To investigate the effects of functional traits of the species (seed mass and the Ellenberg indicator value for light (Ellenberg *et al.* 1992); see Table 6), disturbance treatment and canopy closure on seedling recruitment in the different years, we used analogous GLMMs and also selected the best models according to the lowest AICc. The significance of terms was determined with Wald-tests with the Anova function of the package car (Fox & Weisberg 2019).

4.3 Results

4.3.1 Demography of the experimental populations

Seedling recruitment from the seeds sown in the spring of 2013 in the Lueneburg Heath was generally low for all species in the first year, but varied strongly among species ($Chi^2 = 72.5$, $p < 0.001$; Figure 5). While 0.8% of the seeds of *Luzula multiflora* produced a seedling that survived until autumn 2013, recruitment was less than 0.1% for most other species. There was some evidence that the mean seedling recruitment of woodland species was higher than that of open habitat species (logit = 1.53; p = 0.079; Figure 5a,b; Table S1 in Supporting Information). However, this difference was transient and in the next year no longer observed. The number of individuals of all species, except for *Luzula multiflora* and *Veronica officinalis*, increased from 2013 to 2014, indicating that additional seeds germinated after the winter in spring 2014 (Figure 5). Seedlings of *Calluna vulgaris* were first observed in 2014. From 2014 to 2016 the number of individuals of species from open habitats (Figure 5) decreased much more strongly than that of woodland species (Figure 5b), and *C. vulgaris* became even extinct in the study plots in 2016. In 2016, recruitment of species from open habitats had declined strongly with canopy closure, while that of woodland species had hardly been influenced (Figure 6; Table S1 in Supporting Information).

The first year of recruitment of seedlings from seeds sown in spring 2014 in the Lueneburg Heath varied strongly among species ($Chi^2 = 73.9$, $p < 0.001$) and was generally higher than that of seedlings from seeds sown in 2013 (Figure 5c,d), but seedlings of *Vaccinium myrtillus* were only found in 2015. Similar to the recruited seedlings from seeds sown in 2013, the new cohort of seedlings from open habitats suffered heavy mortality from 2014 to 2015. In contrast to the old cohort, their mortality from 2015 to 2016 was rather low.

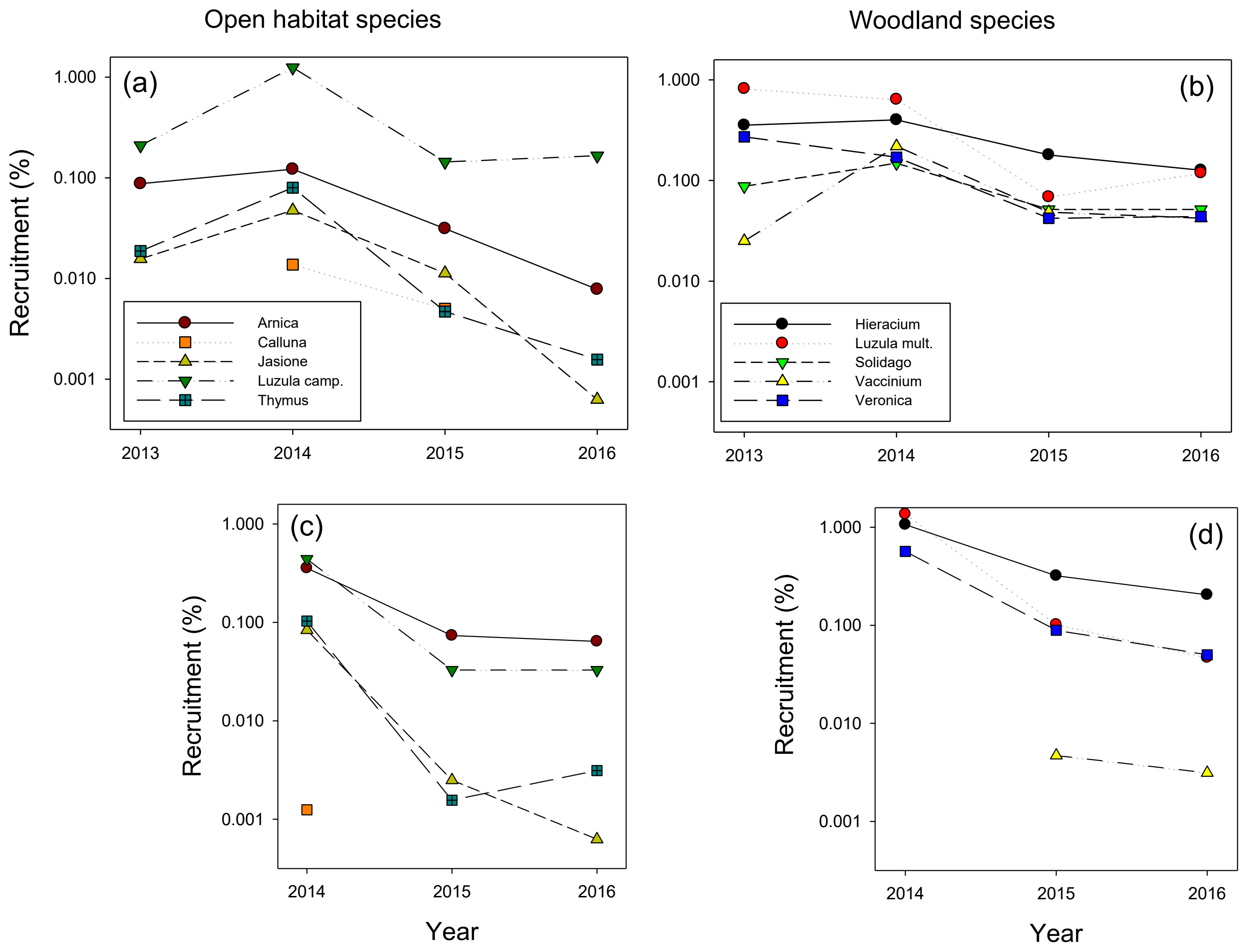


*Figure 5: Changes in the relative number of recruited individuals over time for the species sown in the Lueneburg Heath in (a,b) 2013 or (c,d) 2014. (a,c) Open habitat species: Arnica montana, Calluna vulgaris, Jasione montana, Luzula campestris, Thymus serpyllum. (b,d) Woodland species: Hieracium murorum, Luzula multiflora, Solidago virgaurea, Vaccinium myrtillus, Veronica officinalis***.**

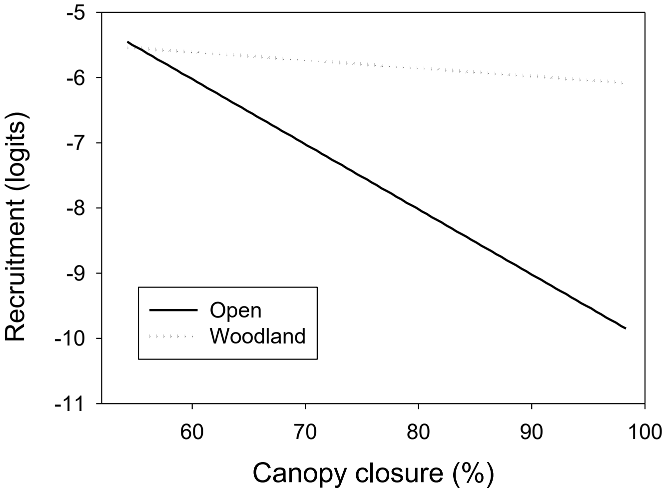


Figure 6: The effects of canopy closure on the recruitment of seedlings in the Lueneburg Heath in 2016 from seeds sown in 2013, for species from open and woodland habitats.

The number of recruited seedlings from the seeds sown in 2013 in the Swabian Jura was also low and less than 1%, except for *Prunella grandiflora* (1.2%; Figure 7a), but varied strongly among species ($Chi^2 = 81.9$, $p < 0.001$). Mean recruitment was lower for woodland species than for open habitat species (logit = -1.54, p = 0.031). However, this effect was transient and in 2014 there was no longer a difference between the two types of species. The number of individuals of all species from open habitats declined from 2013 to 2014, indicating that there was no further recruitment, or that mortality was much higher than additional recruitment. The decline in numbers was similar for four of the species, but much stronger for *Briza media*. Two of the woodland species (*Primula elatior* and *Astrantia major*) increased in numbers from 2013 to 2014, indicating further recruitment in 2014 from the seeds sown in 2013 (Figure 7b). The number of *P. elatior* increased very strongly, because many seeds germinated in the second spring and survived until autumn. In contrast, *Melica nutans* slightly declined, and *Ranunculus auricomus* and in particular *Galium sylvaticum* declined strongly from 2013 to 2014.

The first year of recruitment of seedlings from seeds sown in spring 2014 varied strongly among species ($Chi^2 = 92.0$, $p < 0.001$) and was similar to that of those sown in 2013 for most of the species, except for *B. media*, whose recruitment in 2014 was much lower (Figure 7a) and for *P. elatior* that showed much higher recruitment success in 2014 than in 2013 (Figure 7b).

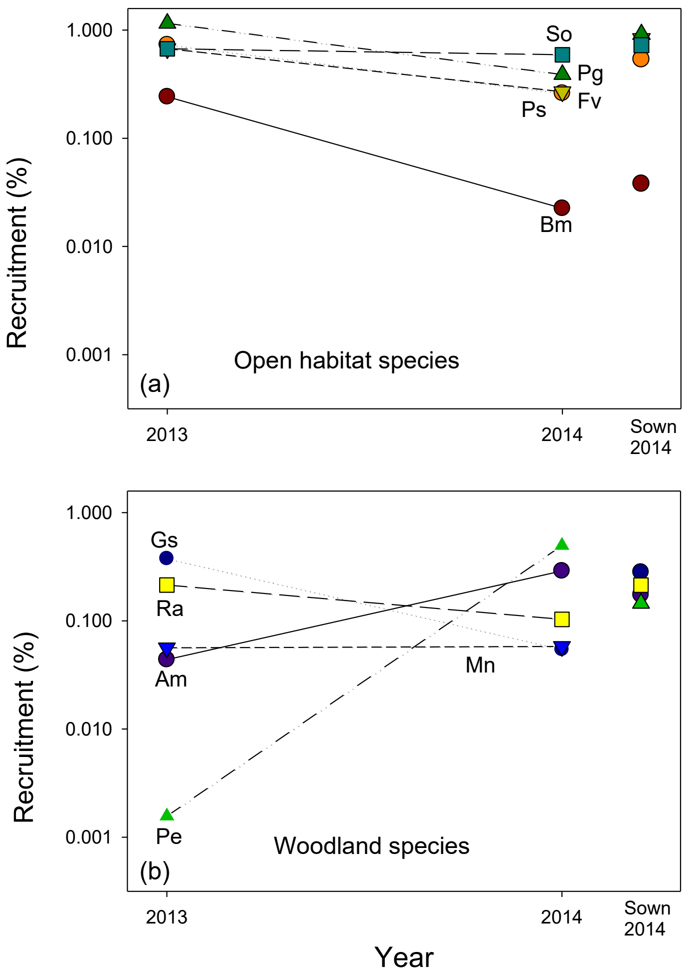


Figure 7: Changes in the relative number of recruited individuals over time for the species sown in the Swabian Jura. (a) Open habitat species: Bm, Briza media; Fv, Filipendula vulgaris; Pg, Prunella grandiflora; Ps, Pimpinella saxifraga; So, Betonica officinalis; (b) Woodland species: Am, Astrantia major; Gs, Galium sylvaticum; Mn, Melica nutans; Pe, Primula elatior; Ra, Ranunculus auricomus. Seeds were sown in 2013 and again in 2014.

4.3.2 Effects of species traits, canopy closure and disturbance treatment on seedling recruitment

Sod-cutting increased the proportion of recruited seedlings in comparison to simulated mowing observed in most years in both regions (Table 7), but effects varied strongly among years. While sod-cutting increased the odds of recruitment by only 1.40 in the Lueneburg Heath, the effect was much stronger in the Swabian Jura in 2014 (+21.8). However, the positive effect was transitory in the Lueneburg Heath, as after three years in 2016 the effect of disturbance by sod-cutting was still positive, but no longer significant for seeds sown in 2013, probably due to the overall very low number of surviving plants (Figure 5). In the Swabian Jura, the effects of sod-cutting depended in 2014 for seedlings from seeds sown in 2013 on the indicator value for light of a species (Figure 8a) and on its seed mass (Figure 8b).

*Table 7: Results of generalised linear mixed-effects models with betabinomial errors with most support (lowest AICc) for the effects of disturbance treatment (sod-cutting vs. mowing), the $\log_{10}$ seed mass of a species, its Ellenberg indicator value for light (L), and of canopy closure on the recruitment of seedlings from seeds sown in 2013 or 2014 in the Lueneburg Heath and Swabian Jura in different years. Recruitment consists of germination of seeds and subsequent survival. Shown are the regression coefficients (logits) of the predictors. The interactions between disturbance and L and between seed mass and canopy closure were never part of a best model.***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; (*), $p < 0.1$; ns, $p > 0.10$.*

Period Sown - Obser.	Intercept	Sod-cut	Seed mass	L	
Lueneburg Heath					
2013 - 2013	-6.548***	0.653**	1.987**		
2013 - 2014	-5.887***	0.334$^{(*)}$	1.358*		
2013 - 2015	-6.242***	0.432$^{(*)}$	1.368**	-0.221$^{(*)}$	
2013 - 2016	-15.03***	0.391 ns	2.270**	1.822**	+ Canopy closure: 0.138*
					+ L x Canopy closure: -0.031***
2014 - 2014	-7.818***	1.493***			
2014 - 2015	-8.764***	1.465***	1.823$^{(*)}$		
2014 - 2016	-6.792***	1.109***	2.151*	-0.293 ns	
Swabian Jura					
2013 - 2013	-6.835***	1.045***			
2013 - 2014	-10.89***	3.083*	1.965$^{(*)}$	0.599*	+ Sod-cut x L: -0.380$^{(*)}$
					+ Sod-cut x Seed mass: -1.307$^{(*)}$
2014 - 2014	-6.351***	-0.264 ns			+ Canopy closure: -0.007 ns
					+ Sod-cut x Canopy: 0.018**

Canopy closure rarely had an effect. In 2016, seedling recruitment of seeds sown in 2013 in the Lueneburg Heath was influenced by the interactive effects of canopy closure and the light indicator value of a species (Figure 8c). The odds of recruitment increased with canopy closure for species from shaded habitats, while they decreased with canopy closure for species from open habitats. In 2014, recruitment of seedlings in the Swabian Jura from seeds sown in spring of the same year decreased with canopy closure in plots that were mown, but increased in plots that were sod-cut (Figure 8d).

The general effects of the indicator values for light (L) of a species varied between years and region from negative to positive and also sometimes depended on sod-cutting. In the Swabian Jura in 2014, seedling recruitment of seeds sown in 2013 was higher for species from high light than from low light habitats, but this effect was stronger if plots were only mown and not sod-cut (Figure 8a).

In most of the years, recruitment increased with the seed mass of a species, especially in the Lueneburg Heath (Table 7). Effects varied from an increase of the odds of recruitment of 3.9 for the Lueneburg Heath in 2014 to one of 9.7 in 2016 with each increase of seed mass by one order of magnitude. In the Swabian Jura in 2014, seedling recruitment of seeds sown in 2013 increased more strongly with seed mass in plots that were mown than sod-cut (Figure 8b).

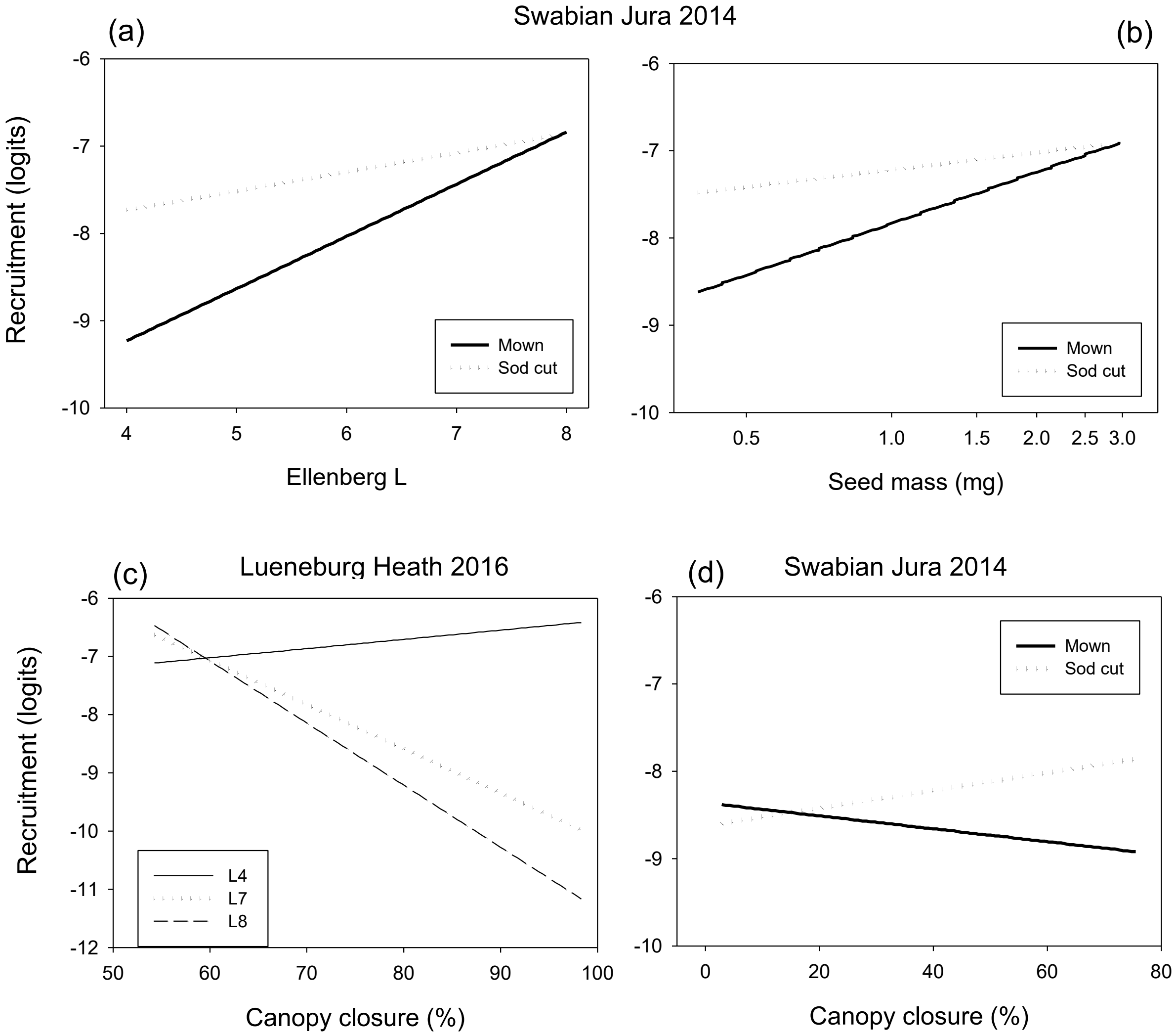


Figure 8: Interactive effects on seedling recruitment. (a) Interactive effects the Ellenberg indicator value for light (L) of a species and the disturbance treatment (mowing or sod-cutting), and (b) interactions between the seed mass of a species and the disturbance treatment on the recruitment of seedlings in 2014 from seeds sown in spring 2013 in the Swabian Jura. (c) Effects of canopy closure on the recruitment of species with different indicator value for light (L) in the Lueneburg Heath in 2016 for seedlings that were sown in spring 2013. (d) Effects of canopy closure on the recruitment of seedlings in 2014 that were sown in spring 2014 in plots that were mown, or sod-cut in the Swabian Jura.

4.4 Discussion

4.4.1 Recruitment success of woodland and open habitat species in semi-open habitats

Our results demonstrate that both species from woodlands and open habitats were able to recruit seedlings in the semi-open habitats of both study regions. In this context it is important to note that seedling recruitment describes the process of seed germination, seedling establishment and seedling survival (Eriksson & Ehrlén 2008; Larson *et al.* 2015) and thus integrates different ontogenetic stages of a plant from being present as a seed to a fully developed seedling. The number of seedlings in our experimental setup therefore mirrors the effects of both germination and seedling survival.

While there was some evidence that the recruited seedlings were affected by a species type effect in the first year in both regions for seeds sown in 2013, the effect was not persistent and no longer observed in further years or for the seeds sown in 2014.

Recruitment success was much more driven by a species identity effect. In the Lueneburg Heath, for both species of woodlands and open habitats, numbers strongly varied for seedlings from seeds sown in 2013 and in 2014. However, the tendency of seedling recruitment was very similar. Seedlings from seeds sown in 2013 increased in the first two years and then showed a decline in numbers in 2015. While the seedling numbers from seeds sown in 2014 produced a high number of seedlings in the first year, all species declined in numbers in the second year in 2015. This is in line with the seedling numbers from seeds sown in 2013 indicating external factors such as the weather conditions in 2015 may have affected seedling survival. As mentioned above, in the Lueneburg Heath September 2014 (seedling numbers for 2014 were counted just before the drought started) and June 2015 were affected by droughts and may have had a negative effect on the seedling numbers counted in autumn 2015. Individual species such as *C. vulgaris* and *V. myrtillus* showed delayed seedling recruitment with less seedling numbers than the other species, and seedlings of *C. vulgaris* of both cohorts even failed to survive until the end of the experiment.

In the Swabian Jura, the numbers also strongly varied for seedlings from seeds sown in 2013 and in 2014. However, while all open habitat species and most woodland species from seeds sown in 2013 declined in numbers in the second year, *P. elatior* and *A. major* showed an increase in numbers in the second year. Both species are cold germinators (Ten Brink *et al.* 2013) and need to be exposed to cold conditions to break seed dormancy in the first year. This supports the conclusion that species type played less of a role for seedling recruitment. Instead, recruitment success in both species types was strongly mediated by species identity effects (which in turn are partly attributable to individual life-history traits; see below). Our results suggest that semi-open habitats have the potential to support recruitment of species from both open habitats and woodlands, but that species identity drives the recruitment success. This is supported by our finding that both woodland and open habitat species recruited seedlings in semi-open habitats, and that species type proved to be a weak predictor for seedling recruitment in our models. Thus, semi-open habitats with their wide range of light conditions and a variety of microclimates (Tölgyesi *et al.* 2018) may fulfil recruitment requirements for a broader spectrum of plant species. These results correspond to findings of Eggers *et al.* (2010), according to which also both woodland and open habitat ground beetle species were recorded in semi-open habitats at the same time.

Our finding that more woodland species showed higher numbers of seedlings in the Lueneburg Heath and open habitat species were more successful in the Swabian Jura is in agreement with Travers *et al.* (2020). In that study, woodland species were recorded in higher numbers in semi-open habitats of the Lueneburg Heath compared to the Swabian Jura. In contrast, open habitat species featured higher numbers in semi-open habitats in the Swabian Jura than in the Lueneburg Heath. Therefore, recruitment of woodland and open habitat species may also show a region-specific effect, obviously depending on the prevailing plant communities, i.e. Fagion- vs. Quercion robori-petraeae-communities and related site conditions (see below). We hypothesise that Lueneburg Heath woodland species (i.e. species of the alliance Quercion robori-petraeae) have a lower habitat specificity to woodlands (i.e. are to a lesser extent stenoecious) than woodland species of the Swabian Jura (i.e. species of the alliance Fagion) with regards to life-history traits and environmental requirements (Travers *et al.* 2020). This suggests that woodland species of the Lueneburg Heath might be less demanding in terms of recruitment conditions such as light availability or soil moisture. Therefore, semi-open habitats of the Lueneburg Heath may cater better to recruitment requirements of the corresponding woodland species than semi-open habitats of the Swabian Jura do. This indicates that the establishment of semi-open corridors may lead to differing recruitment success across species types depending on the geographical location and the prevailing plant communities.

Interestingly, in the Lueneburg Heath the highest numbers of seedlings of many woodland and open habitat species occurred in the second year after sowing for the seeds sown in 2013. The increased seedling numbers in 2014 suggests that some seeds only germinated in the second year after sowing. This would indicate that seeds of these species irrespective of species type were able to persist in the soil and germinate at a later date (Thompson *et al.* 1998). In the Swabian Jura, many of the open habitat and woodland species already showed a decreased seedling number after the first year. Even taking into account that germinated seeds from 2013 died off, it can be assumed that less seeds germinated in the second year. This corresponds to the results of Bossuyt *et al.* (2006) according to which seeds of calcareous grassland species are mostly transient and thus cannot not persist in the soil for a longer period of time. Similarly, woodland species do not feature persistent seeds (Bossuyt *et al.* 2008). Only species such as *Betula pendula* and *Calluna vulgaris*, that also make up the woodlands of the Lueneburg Heath, were found in the seed banks of woodlands (Bossuyt *et al.* 2008). These are species of early successional stages which are adapted to and thus benefit from stochastic disturbance processes. Therefore, species' seed persistence is something to have in mind when planning the establishment of semi-open corridors. Even if calcareous grassland or woodland species of the Swabian Jura may be able to disperse into semi-open corridors (Travers *et al.* 2020), it might take a long time for them to recruit seedlings given that suitable recruitment conditions are not available. In addition, it may also take a long time for plants to reproduce in the semi-open corridors, which in turn delays the further dispersal process. In contrast, species of the Lueneburg Heath are able to persist in the soil seed bank for longer and can, therefore, recruit seedlings whenever the conditions are suitable, reproduce and, thus, disperse faster.

The decrease of seedling numbers in the third and fourth year after sowing for the seeds sown in 2013 in the Lueneburg Heath suggests that some individuals did not survive more than two years and that the initial recruitment burst is also slowed down. It can be assumed that intra-specific competition has at least partly contributed to limiting constant recruitment. After two years, seedling numbers reached an equilibrium between recruitment of leftover seeds and survival of already recruited seedlings.

4.4.2 The effects of life-history traits and environmental factors on recruitment success

In the Lueneburg Heath high seed mass had a strong effect on the recruitment of the sown seeds of species in semi-open habitats, especially after the first year. Seed mass plays an important role during seedling development immediately after germination (Moles & Leishman 2008; Kołodziejek 2017). Larger seeds develop taller seedlings which have better access to water and light (Leishman *et al.* 2000) and better withstand competition (Westoby *et al.* 2002; Kołodziejek 2017). As a result, species with large seeds show a lower initial mortality rate than small-seeded species (Moles & Westoby 2004), and therefore an increased seedling survival rate (Bruun & Ten Brink 2008). This seems to apply to the species with the highest seedling numbers in the Lueneburg Heath, i.e. *Luzula multiflora*, *Hieracium murorum*, and *Luzula campestris*. These species exhibited some of the highest seed mass of the species of the Lueneburg Heath (Table 1). Considering that open habitat species often have light seeds and woodland species usually have heavier seeds (Salisbury 1974; Hodkinson *et al.* 1998; Thompson & Hodkinson 1998; Turnbull *et al.* 2012), the seed mass of species of the Lueneburg Heath differed little between both species types.

While in the Swabian Jura there was only a marginal significant increase in recruitment with increasing seed mass in 2014 for seeds sown in 2013, especially when the plots were mown than sod-cut, woodland and open habitat species display a noticeable difference in seed mass between species type (Table 1). The results indicate that woodland species were more likely to recruit more seedlings and they were also at an advantage recruiting seedlings in the surrounding vegetation. This corresponds to Westoby *et al.* (2002) and Kołodziejek (2017) emphasizing that seeds with high seed mass are able to better resist competition by other plants. Ground covered by vegetation may also mimic the woodland floor and features a moister environment e.g. retain more moisture than sod-cut soil which enhances the recruitment of woodland species.

The influence of light on the recruitment also played an important role in the Lueneburg Heath in later years. In the fourth year after sowing of seeds sown in 2013, species with low indicator values for light showed lower seedling numbers in lighter areas, but higher seedling numbers in more shaded areas with higher canopy cover. On the contrary, species with high indicator values for light showed higher seedling numbers in lighter areas with less canopy cover than in darker areas. While the indicator values for light generally had an effect on recruitment in the second year of seedling recruitment of seeds sown in 2013 in the Swabian Jura, there were no interactive effects with canopy closure. These results indicate that the effects of canopy cover and therewith light conditions are an important factor mediating the species' recruitment success in the medium term (Rüger *et al.* 2009;

Yan & Chen 2020). Once the seedlings have emerged, the effect of canopy cover in semi-open habitats proved to be critical to their survival. Results of the Lueneburg Heath and Swabian Jura also indicate that light intensity might not be essential for germination but only becomes relevant at later stages of recruitment (Simão *et al.* 2007; Veloso *et al.* 2017). As to be expected, species with higher shade tolerance (e.g. woodland species) exhibited higher seedling numbers in semi-open habitats with a denser canopy (e.g. groups of trees), whereas species with higher light requirements (e.g. open habitat species) preferred areas that featured little to no canopy cover. These results show that although recruitment of open habitat and woodland species in semi-open habitats is generally possible, abiotic factors such as light play a crucial role to their emergence and survival (González-Varo *et al.* 2012). They also emphasize the importance of the development of structural diversity with different niches (e.g. open space, single trees, shrubs, groups of trees) as part of habitat management of semi-open corridors.

4.4.3 The influence of habitat management on seedling recruitment in semi-open habitats

Besides environmental factors, habitat management must also consider the establishment of suitable surface and soil conditions for seedling recruitment to take place. In both regions, recruitment was significantly more successful on sod-cut than on mown subplots. This effect has been observed before (Röder 2009, Drobnik 2011; Poschlod *et al.* 2013). Although contact with the upper mineral soil surface layer is not essential for germination as seeds are able to absorb enough water through vapour (Wuest 2002), disturbed soil increases soil-seed contact and therefore, the likelihood of germination (Isselstein *et al.* 2002). Seedlings also need to compete less for light and other resources on sod-cut than on mown subplots. This is also underpinned by the interactive effects in the Swabian Jura in 2014 for seeds sown in 2013 where species which require more light featured higher seedlings numbers on sod-cut than on mown subplots. The decline of seedling numbers after a few years may be explained by an increasing vegetation cover and therefore increased competition for light and water (Jacquemyn *et al.* 2011). These results suggest that it is important to manage semi-open corridors accordingly, i.e. creating patches of bare soil where seeds might get into contact with the upper mineral soil surface layer and thus experience more appropriate conditions for germination (e.g. vegetation removal and creation of small patches of bare soil due to hoof trampling during grazing) but also leaving vegetated patches to allow for microhabitats with different microclimates (Drobnik 2011; Poschlod *et al.* 2013).

Although our results showed that several species were able to recruit in semi-open habitats, their recruitment was very low (< 1%). This has also been observed in other studies (Röder 2009; Durbecq *et al.* 2021). Since our experiment used a higher number of seeds than would be expected during natural seed dispersal processes, it is likely that seed availability of open habitat or woodland species might be a limiting factor for dispersal processes of species by means of semi-open corridors, particularly in fragmented landscapes with extremely isolated habitat patches. It is, therefore, necessary to establish a dense net of structurally diverse semi-open corridors to increase the probability of dispersal and recruitment events of species in semi-open corridors and to counteract biodiversity loss in fragmented landscapes.

4.4.4 Conclusions

Our findings demonstrate that semi-open habitats have the potential to serve as stepping stone habitats for species of both woodlands and open habitats. The recruitment success strongly depends on the species characteristics (traits) as well as the environmental setting of the location (e.g. light availability, soil conditions). This indicates that once species have reached the semi-open habitats, they are able to persist in semi-open habitats and thus propagate further through the corridor.

However, the recruitment success of seeds is also highly affected by external factors. For example, thick leaf litter layers in densely vegetated areas may inhibit the germination of seeds (Dalling & Hubbell 2002; Dzwonko & Gawroński 2002). Seed predation also plays an important role reducing recruitment success (Drobnik 2011; Poschlod *et al.* 2013). Considering that the number of seeds reaching the stepping stone habitat during natural plant dispersal will be much lower than the amount we used during our study, these germination obstacles can significantly delay or decrease the recruitment success.

To promote increased seedling recruitment of as many woodland and open habitat species as possible in semi-open corridors, we need to design semi-open habitats in such a way that both species types are offered a structurally diverse habitat with a variety of microsites to facilitate recruitment success for a broad spectrum of ecologically different species (Turnbull *et al.* 2000). This means managing shrubs and trees to develop a mosaic of different vegetation densities and light gradients but also creating different topsoil conditions such as patches of bare soil or short vegetation to enhance microclimate and seedbed variability.

In summary, by managing semi-open habitats accordingly, we enable species of woodlands and open habitats to use semi-open habitats as interim habitat to establish themselves and reproduce for further dispersal once they have entered them. This way, semi-open habitats have the potential to facilitate plant species dispersal on a large scale and thus mitigate the effects of habitat fragmentation.

4.5 References

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4.6 Supporting Information

*Table S1: Results of generalised linear mixed-effects models with betabinomial errors with most support (lowest AICc) for the effects of species type (from woodland or open habitat), disturbance treatment (sod-cutting vs. mowing), and of canopy closure on the recruitment of seedlings from seeds sown in 2013 or 2014 in the Lueneburg Heath and Swabian Jura in different years. Recruitment consists of germination of seeds and subsequent survival. Shown are the regression coefficients (logits) of the predictors. The interactions between disturbance and species type and between disturbance and canopy closure were never part of a best model.***, p < 0.001; **, p < 0.01; *, p < 0.05; (*), p < 0.1; ns, p > 0.10.*

	Year of sowing	Observation year	Intercept	Woodland species	Sod-cutting	Canopy closure	Woodland species x canopy closure
Lueneburg Heath	2013	2013	-8.551***	1.530$^{(*)}$	0.648**		
		2014	-6.746***		0.335$^{(*)}$		
		2015	-8.485***		0.426$^{(*)}$		
		2016	-2.217 ns	-4.931*		-0.101**	0.089**
	2014	2014	-7.818***		1.493***		
		2015	-9.566***		1.465***		
		2016	-9.975***		1.108***		
Swabian Jura	2013	2013	-5.988***	-1.541*	1.035***		
		2014	-6.977***		0.548***		
	2014	2014	-6.630***		0.460**		

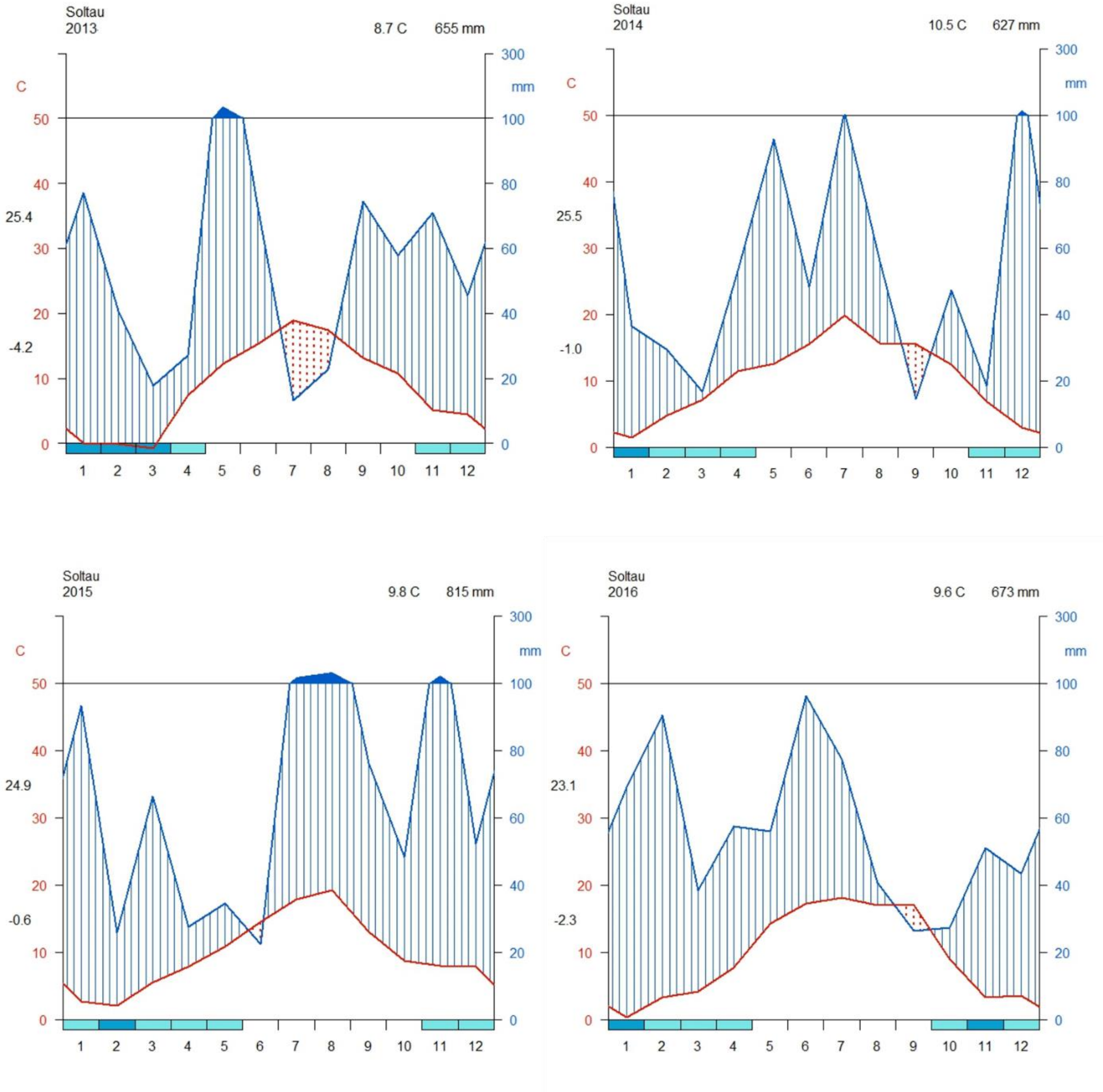

Figure S1: Walter and Lieth climate diagrams of the yearly climatic conditions in the Lueneburg Heath from 2013 to 2016 based on data from Deutscher Wetterdienst (2024)

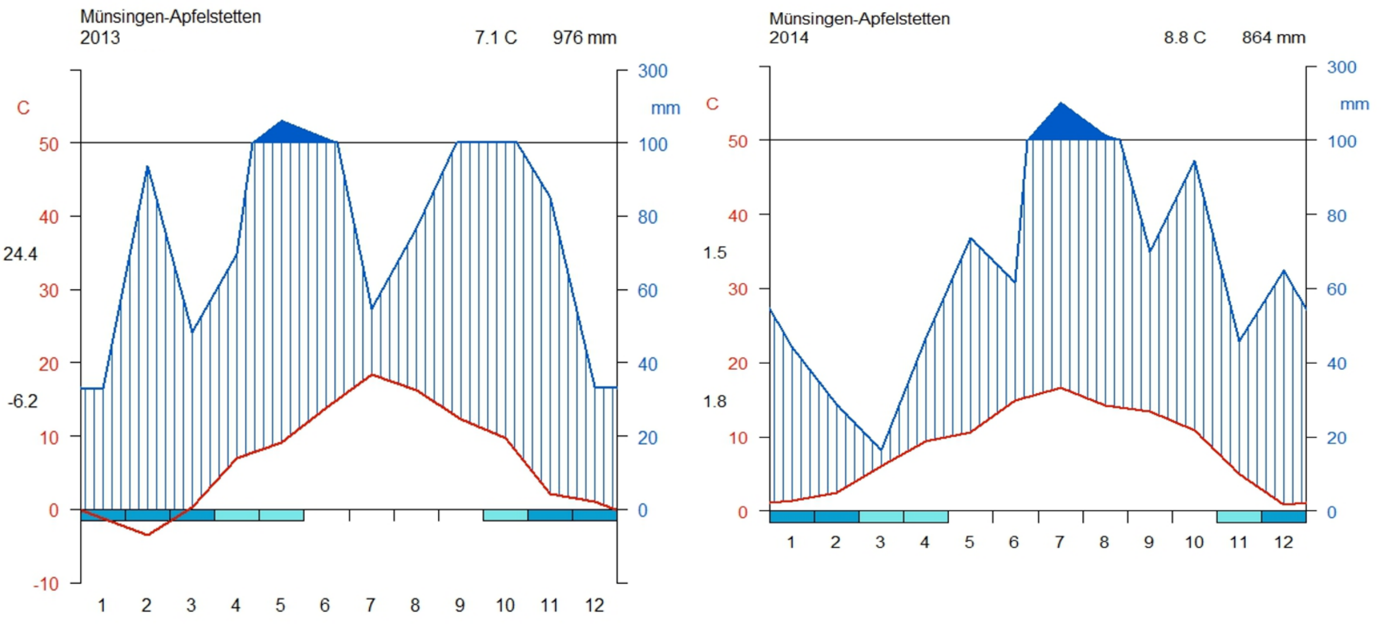

Figure S2: Walter and Lieth climate diagrams of the yearly climatic conditions in the Swabian Jura from 2013 to 2014 based on data from Deutscher Wetterdienst (2024)

5. Synthesis and Conclusion

5.1 Main findings

Increasing land use changes accelerate habitat fragmentation, which results in extinction of many plant species and hence, loss of plant diversity (Aguilar *et al.* 2019; González *et al.* 2020). To counteract the adverse effects of habitat fragmentation on biodiversity, several approaches have been adopted, for example the establishment of linear dispersal corridors or stepping stones (Battisti *et al.* 2022; Resasco 2019; Xu *et al.* 2019), but also technical solutions such as wildlife crossings ("Grünbrücken"; Lister *et al.* 2015; Martínez-Medina *et al.* 2022). However, most of these solutions work only on a small scale, connect equal habitat types and are mostly designed to support the dispersal of animals, not plants. Solutions for large-scale habitat networks, where a dispersal corridor for one habitat type does not create a new barrier for another habitat type and thereby obstruct species dispersal, are lacking, particularly with regard to plant species (see Chapter 2).

Based on this situation, the present thesis investigated whether the establishment of semi-open pasture landscapes as semi-open corridors facilitates the simultaneous dispersal of plant species that are typical of woodlands and open habitats and therefore may act as a stepping stone for plant species of different habitat types. The findings provide evidence, that – depending on prevailing plant communities and soil conditions – semi-open habitats have the potential to act as a stepping stone for both woodland and open habitat plant dispersal and therefore, act as link for connecting isolated habitats patches in large-scale habitat networks. The results of the thesis suggest that:

a) Semi-open habitats provide a suitable interim habitat for open habitat plant species and to a lesser extent for woodland plant species.
b) Species identity plays a more important role for seedling recruitment in semi-open habitats than the species type.
c) Dispersal traits, species site requirements, environmental setting and site management drive the occurrence and recruitment success of both species types in semi-open habitats.

5.2 Mechanisms supporting plant species dispersal in semi-open habitats

In contrast to animals which can move independently within their range, plant dispersal is a process which is highly dependent on chance. Because of their sedentary mode of living, plants mainly depend on external vectors to distribute their seeds (Bonn & Poschlod 1998; Jongman *et al.* 2004). For long-distance dispersal, either the external vector must travel long distances (e.g. wind, water, migratory animals) or plants rely on "stepping stone habitats" to reproduce and create new seeds for further dispersal (Figure 1). Going through the process of recruitment in a stepping stone habitat, it may take several generations for a plant species to reach the destination habitat (Damschen *et al.* 2008). To study whether woodland or open habitat plant species can use semi-open habitats as stepping stone and therefore as dispersal corridor, the dispersal process must be broken down into the individual phases of dispersal and recruitment. Two approaches, an observational (see Chapter 3) and an experimental study (see Chapter 4), were adopted to investigate these further.

To prove plant dispersal into semi-open habitats, I carried out an observational study of the species occurring in (1) semi-open habitats and their surrounding (2) woodlands and (3) open habitats of the Lueneburg Heath and the Swabian Jura (see Chapter 3). By comparing the vegetation of woodlands and open habitats with semi-open habitats, my analyses provided evidence that species of both woodlands and open habitats occur in semi-open habitats in differing frequencies. Plant communities of semi-open habitats were more similar to open habitats (81% in the Swabian Jura and 64% in the Lueneburg Heath) than to plant communities of woodlands (29% in the Swabian Jura and 48% in the Lueneburg Heath), particularly in the Swabian Jura. However, semi-open habitats still offered shelter to at least one third of the woodland species. Therefore, this study confirms that woodland and open habitat plants can occupy semi-open habitats, and semi-open habitats provide a stepping stone habitat to a certain extent (see Chapter 3). This is in agreement with Eggers *et al.* (2010) who already identified that woodland and open habitat ground beetles were able to disperse into semi-open habitats.

The presence of woodland and open habitat plant species was driven by traits which determine and impact seed dispersal and recruitment (see Chapter 3). Especially woodland species of the Swabian Jura such as *Polygonatum multiflorum* and *Actaea spicata*, which were mainly characterised by a high seed mass together with short-distance dispersal mechanisms such as vegetative reproduction, autochory or zoochory by small vertebrates and invertebrates, were limited to woodlands (see Chapter 3). The poor dispersal ability of woodland species explains the low number (e.g. *Helleborus foetidus*, *Primula elatior*) recorded in semi-open habitats and is supported by other studies as well (Brunet & von Oheimb 1998; Heinken 2004; Kimberley *et al.* 2013). Verheyen *et al.* (2003) even highlights that low dispersability is the key factor for limited dispersal of woodland species. Seeds of open habitat species, on the other hand, were characterised by a low seed mass. This facilitates more effective long-distance dispersal, for example, via wind (see Chapter 3). Given that wind dispersal is most effective when corridors are aligned to the prevailing wind direction (Damschen *et al.* 2014), it can be assumed that the mosaic of semi-open habitats provides enough opportunities for seeds to settle in open areas (Purschke *et al.* 2012), especially if the open areas are aligned along the edges. Many open habitat species are also distributed via zoochory by large vertebrates. As semi-open habitats are mainly grazed by domestic animals, they potentially transport seeds through adhesion and endozoochory over large distances (Manzano & Malo 2006; Albert *et al.* 2015). These distinct differences of dispersal mechanisms between woodland and open habitat species clearly allows open habitat species to travel further faster and gives them a dispersal advantage. This explains why open habitat species (e.g. Lueneburg Heath: *Festuca ovina* agg., *Pilosella officinarum*; Swabian Jura: *Salvia pratensis*, *Centaurea jacea* agg.) were recorded in both open and semi-open habitats in higher numbers than woodland species (see Chapter 3)

In addition, most woodland species (Lueneburg Heath: 77%; Swabian Jura: 87%) were characterised by having a transient seed bank, so seeds do not last more than a year in the ground (Verheyen *et al.* 2003; Hopfensperger 2007; Bossuyt & Honnay 2008). This affects future seed production and recruitment, as low seed persistence means that if the environmental conditions are not favourable for germination in the first year, seeds cannot outlive and wait for more favourable conditions, but they die off. On top of that, a high proportion of the woodland species of the Swabian Jura take one to five years (88%) or more than 5 years (6%) to flower (see Chapter 3). So, if seeds survive and germinate within the first year, they will not be able to produce seeds themselves within the first few years. The delay of new seed production, and therefore the recruitment of the next generation, reduces the dispersal speed considerably. A large proportion of the open habitat species of the Swabian Jura also featured a transient seed bank persistence (83%), but they also exhibited a higher proportion of species with a short-lived seed bank (12%), so seeds which survive up to 5 years in the ground. In contrast, large proportions of open habitat species of the Lueneburg Heath can outlast up to 5 years (38%) or more than 5 years (34%) in the ground. Only 28% of the species become non-viable after a year. Up to 99% of the open habitat species of both regions are able to flower within the first five years after germination, about one third may already flower in the first year in the Swabian Jura. This means open habitat species can "wait" for favourable environmental conditions until they germinate, and subsequent propagation takes place within five years (Bazzaz 1979; Bossuyt & Honnay 2008). Similarly, ten Brink *et al.* (2013) have shown that the germination strategies of woodland species are adapted to short time windows such as springtime where the tree canopy cover has not developed yet. In contrast, open habitat species are less constrained and can germinate readily at any time when the environmental conditions are favourable. While in woodlands the limited germination window for woodland species secures their propagation in a favourable environment, in semi-open habitats, these traits limit their recruitment and therefore, their dispersal, and give open habitat species an advantage. Quick seed germination, seedling establishment and propagation will also increase the success rate of species persistence within the semi-open corridors. Otherwise, seeds may be prone to seed predation, seed or seedling mortality (e.g. because of desiccation, unfavourable environmental conditions, trampling etc.; Studer 2000; Bricker *et al.* 2010; Franchi *et al.* 2011) before they can propagate.

While species traits such dispersal mechanisms, seed persistence and flowering age obviously seem to affect dispersal and propagation success, their requirements towards the site conditions must be considered as well (see Chapter 3). Species, which were recorded in semi-open habitats, featured similar realised ecological niches in terms of light and soil moisture to open habitat species, whereas the site requirements of woodland species clearly differed from species recorded in semi-open habitats. Especially in the Swabian Jura, woodland species are clearly adapted to woodlands with low light input and a dense canopy cover (mean Ellenberg indicator value for light: 3.3). Although woodland species of the Lueneburg Heath also showed similar trends in comparison to species recorded in semi-open habitats, they are not adapted to very shady conditions (mean Ellenberg indicator value for light: 5.6). This means, environmental conditions of semi-open habitats also drive the suitability for species in terms of recruitment and propagation. Especially woodland species will be limited in their dispersal range, if semi-open habitats do not cater for their needs.

Although woodland species in both regions were clearly limited by their dispersal and recruitment traits, woodland species of the Lueneburg Heath were less confined to woodlands and their traits showed a less clear pattern of adaption or restriction to woodlands. The differences in the species distribution as well as the species traits between the Swabian Jura and the Lueneburg Heath may be explained by the prevailing plant communities (Chapter 3), soil conditions and site management history (e.g. *Fagion* vs. *Quercion* woodlands and *Mesobromion* vs. *Genistion* grass-/heathlands in the Swabian Jura and the Lueneburg Heath, respectively; Leuschner & Ellenberg 2018). Therefore, using semi-open habitats as corridors has high potential, however, the success of species dispersal is primarily dependent on the environmental setting and the site history which both determine the species assemblages and their species characteristics.

5.3 Surviving outside the comfort zone?

By comparing the vegetation of the different habitat types with each other, this thesis was able to provide evidence that woodland and open habitat species occur in semi-open habitats (see Chapter 3). However, to prove that these plant species were not just remnants, but that they can also serve as sources for further dispersal, therefore, can also recruit and propagate in semi-open habitats, I sowed woodland and open habitat species into semi-open habitats as part of an experimental setup (see Chapter 4). The findings of this experimental study showed that both woodland and open habitat species were able to recruit seedlings in semi-open habitats (see Chapter 4). Although recruitment rate across species was generally very low (< 1%), most woodland species of the Lueneburg Heath recruited a higher number of seedlings than open habitat species. In contrast, in the Swabian Jura, woodland species recruited less seedlings than open habitat species. However, the recruitment success was more driven by a species identity effect and to a lesser extent by a species type effect. Lueneburg Heath species such as *Luzula campestris*[3], *Hieracium murorum*[4], *Luzula multiflora*[4] and *Veronica officinalis*[4] showed a clear increase in seedling numbers. In the Swabian Jura, *Betonica officinalis*[3], *Filipendula vulgaris*[3], *Galium sylvaticum*[4], *Pimpinella saxifraga*[3], *Prunella grandiflora*[3] and *Ranunculus auricomus*[4] also recruited a distinct number of seedlings. Looking at these species, species of both woodlands and open habitats were able to recruit in semi-open habitats, but species type proved to be a weak predictor for seedling recruitment. Nonetheless, more woodland species successfully recruited seedlings in the Lueneburg Heath whereas more open habitat species successfully recruited seedlings in the Swabian Jura. This is in agreement with Chapter 3 where a

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[3] Open habitat species
[4] Woodland species

higher number of woodland species was recorded in semi-open habitats of the Lueneburg Heath compared to the Swabian Jura, and on the other hand, slightly more open habitat species were recorded in semi-open habitats in the Swabian Jura than in the Lueneburg Heath. But what is it that drives these species' recruitment?

I investigated the effects of functional species traits such as seed mass and Ellenberg indicator value for light as well as the effect of the canopy closure on species recruitment (see Chapter 4). On top of that, I analysed two types of disturbance treatment (mowing and sod-cutting) on recruitment. High seed mass had a significant effect on the recruitment of the species sown especially in the Lueneburg Heath. This means the heavier the seeds, the higher the number of recruited seedlings. In contrast, in the Swabian Jura, seed mass only slightly increased recruitment in 2014, especially on mown subplots. As seed mass plays an important role for seedling development (Moles & Leishman 2008; Kołodziejek 2017), heavier seeds may be able to provide their seedling with more minerals and nutrients to start out (Kołodziejek 2017) and enable seeds to develop taller seedlings with better access to water and light (Leishman *et al.* 2000) and to better withstand competition (Westoby *et al.* 2002; Kołodziejek 2017). Other studies confirmed that large-seeded species have a lower initial mortality rate than species with small seeds (Moles & Westoby 2004), and therefore, are more likely to survive as seedlings (Bruun & Ten Brink 2008). However, while Larson *et al.* (2015) confirm that seed mass has a vital effect on germination rates, they point out that it plays a secondary role during emergence, so the phase where a germinated seed transitions to a seedling. It was not possible to distinguish between those phases during my experiment.

In the Lueneburg Heath *Luzula multiflora*[4], *Hieracium murorum*[4], and *Luzula campestris*[3]. exhibited some of the highest seed masses (see Chapter 4). While it is often assumed that open habitat species often have small and light seeds and woodland species usually have large and heavy seeds (Salisbury 1974; Hodkinson *et al.* 1998; Thompson & Hodkinson 1998; Turnbull *et al.* 2012), there was little difference between both species types in the Lueneburg Heath. These results coincide with the results from the observational study and the results already stated in Chapter 5.2, where traits of Lueneburg Heath species showed no clear patterns and species were less limited in their habitat specificity with regards to species traits.

Looking at the species requirement for light and the effects of the site's canopy closure, I found that species of the Lueneburg Heath with a low Ellenberg indicator value for light (L) recruited less seedlings in areas with high light levels whereas species with a high L recruited less seedlings in shaded areas with a high canopy cover during the fourth year after sowing (see Chapter 4). In the Swabian Jura, L also showed significant effects on species recruitment in the second year after sowing, especially on mowed subplots (see Chapter 4). This indicates that the species demand for light and the site's light availability only become relevant at a later stage of recruitment. Light availability may play a less significant role for the germination phase and becomes more critical during emergence (Rüger *et al.* 2009; Yan & Chen 2020). Generally, these results emphasize the importance of the structural diversity of semi-open habitats to support woodland and open habitat species by offering different environmental conditions for a variety of species. For species which tolerate more shaded areas (e.g. woodland species) featured higher seedling numbers in semi-open habitats with a denser canopy (e.g. groups of trees) and species with a need for high light levels (e.g. open habitat species) were found more in areas with little to no canopy cover (e.g. open areas).

To study which type of management enhances species recruitment in semi-open habitats, the vegetation was either mowed or topsoil was removed. In both regions, recruitment benefitted from topsoil removal beforehand (see Chapter 4). This has also been observed in other studies (Röder 2009, Drobnik 2011; Poschlod *et al.* 2013). Topsoil removal in this case is supposed to mimic the creation of open soil patches by hoof trampling during grazing. The creation of open soil patches enhances soil-seed contact and increases the likelihood of germination (Isselstein *et al.* 2002). In comparison to mowing, competition with other vegetation for light and resources is reduced and therefore, the number of germinated seeds is higher. Interestingly, in the Lueneburg Heath, the positive effect of sod-cutting compared to mowing decreased with time and had no significant effect on the seedling numbers in the fourth year. This indicates that with time, as the surrounding vegetation starts to grow again, the advantages of topsoil removal decline (Jacquemyn *et al.* 2011). The results show that while the successful application of semi-open habitats as corridors is dependent on species traits and the environmental setting, the site management also drives the capability of seedling recruitment. Again, the results of the experiment emphasize the need for highly structurally diverse semi-open habitats, which offer a variety of site conditions that can shelter species with different habitat requirements.

Verheyen *et al.* (2003) stressed that low dispersability is the key factor for limited woodland species dispersal, not recruitment. I was able to confirm that the dispersal of woodland species is indeed not limited by seedling recruitment. While dispersal traits of woodland species in general limited their distribution into semi-open habitat, successful recruitment was more dependent on individual species traits and could not be generalised. Although their limited germination window may restrict their recruitment temporally (see Chapter 5.2), woodland species are not confined by traits relevant to recruitment. This means once woodland species have reached semi-open habitats, they are able to recruit new generations.

The findings of this thesis have shown that semi-open habitats are able to accommodate juvenile emerging plant life stages (see Chapter 4). However, in the given time frame, the studies conducted were unable to identify whether woodland and open habitat species are able to reproduce in semi-open habitats, a prerequisite for further dispersal through semi-open habitats by using them as stepping stones. From personal observations during the experiment, I noticed that certain species, for example, *Briza media*[3], *Luzula multiflora*[4], *Primula elatior*[4], *Solidago virgaurea*[4] and *Veronica officinalis*[4] were able to flower in semi-open habitats. It is therefore likely that these species may produce seeds in semi-open habitats. In conclusion, semi-open habitats show high potential to function as stepping stone habitats for certain woodland and open habitat species. To explore their effectiveness in more detail, it is recommended to carry out genetic analyses to identify whether the species found in the semi-open habitats originate from parents in the surrounding woodland and open habitats (Cain *et al.* 2000).

5.4 Establishment of semi-open corridors: landscape suitability and management

In the face of global change, solutions are urgently needed to counteract biodiversity losses attributable to habitat fragmentation (Leimu *et al.* 2010; Banks-Leite *et al.* 2020). Plants, particularly stenoecius plant species with low dispersal power, are threatened by habitat fragmentation on a large scale (Vranckx *et al.* 2011; McConkey *et al.* 2012; Aguilar *et al.* 2019). Semi-open corridors provide a tool to connect different types of habitats simultaneously and to overcome the effects of habitat fragmentation. Considering the potential that semi-open corridors have for plant dispersal as well as biodiversity protection, this thesis advocates their implementation in conservation management.

However, establishing semi-open corridors to simultaneously connect different habitat types and reduce the barrier effect of one habitat type onto another is not a solution for all types of landscapes. Especially in Central Europe, historic pasture landscapes (including semi-open pastures, wood pastures) and natural woodland-open habitat ecotones in particular, qualify for linking up habitats on a landscape level and increase the resilience of biodiversity to global change. These European landscapes are characterised, for example, by a mosaic of alternating open and wooded patches, structural diverse woodland edges or wood pastures (Bergmeier *et al.* 2010, Plieninger *et al.* 2015). In addition, these landscapes feature a large number of plant species and serve as a refuge for a high phytodiversity (see Chapter 3; Tölgyesi *et al.* 2018). The successful application of semi-open corridors will probably differ between regions. The results of this thesis showed that the geographical location and the environmental setting of the pasture landscapes and therefore, semi-open habitats, are important drivers of the dispersal success.

On the other hand, as semi-open habitats are often grazed pastures or need some kind of management, the development of semi-open corridors may not be adequate in habitats which are left to dynamic natural processes (e.g. wet woodlands, peat bogs; Graf *et al.* 2022). On top of that, as semi-open habitats should not enhance the dispersal of unwanted or invasive species, they should also not be established in habitats which are characterised by ubiquitous, euryoecious or invasive species. These limitations show that the choice of the suitable landscape must be carefully considered.

Ideally, semi-open corridors are managed by low intensity year-round grazing (von Oheimb *et al.* 2006). Livestock grazing keeps the herbaceous vegetation low and limits shrub encroachment. Grazing allows a patchy structure to develop and enhances a vegetation mosaic (Henning 2017). The grazing animals and stocking density need to be chosen according to the prevailing site conditions. Cattle and sheep graze predominantly on grasses and herbaceous species while horses or goats browse additionally on woody vegetation such as shrubs and trees. Next to containing the vegetation, the large herbivores will also transport seeds in their fur over large distances and therefore, serve as seed dispersers (Manzano & Malo 2006). Hoof trampling provides patches of bare soil as micro-habitats for the germination of seeds (Henning 2017). As grazing is usually not enough to manage the shrub density, shrub removal should be conducted as an accompanying measure on a rotational basis to allow enough suitable micro-habitats for woodland species (Olmeda *et al.* 2019). Monitoring semi-open corridors ensures to achieve adequate structural and species diversity and helps to counteract excessive shrub encroachment (de Bello *et al.* 2010; Madsen *et al.* 2020). If the aimed species diversity cannot be implemented, or to speed up species dispersal, it may be assisted by transferring seeds or seedlings from surrounding local sites (e.g. by hay transfer or seed addition for open habitat species; soil translocation for woodland species; Török *et al.* 2012; Craig *et al.* 2015). The seeds need to be added in sufficient high numbers to compensate for the low recruitment rate. Due to their lack of seed persistence in the soil, woodland species in particular may need to be introduced as seedlings to ensure successful establishment within semi-open corridors (Lamb *et al.* 2022).

At present, the implementation of semi-open corridors as a connectivity tool in European landscapes proves to be difficult. On the one hand, the abandonment of extensive grazing practices due to low productivity, low subsidies and low income makes managing pasture landscapes on the same lines as they have been for the last centuries increasingly difficult (Terres *et al.* 2015; Steinshamn *et al.* 2018). Consequently, many pastures are being abandoned and are subject to increasing shrub encroachment (Pietzsch *et al.* 2013). Semi-open habitats would be a cost-effective way to secure those pasture landscapes with the available resources. However, to secure the grazing activity in the long-term, farmers must be remunerated for this landscape conservation service (Pietzsch *et al.* 2013; Batáry *et al.* 2015). Agri-environment schemes must value these services with adequate compensation which cover the necessary equipment (e.g. fencing, water troughs) and secure the farmers' income.

On the other hand, next to practical questions on the implementation, the current regulatory framework also impedes the realisation of semi-open habitats. Already the term 'semi-open habitat' comprises a wide variety of habitat types such as wood pastures, pasture woodland, semi-open pastures, and other landscape types, which makes it difficult to classify the habitat type and choose the right category of legislation. Some of these semi-open habitats are not even represented or described by European legislation. For example, wood pastures are either categorised as forest or pasture habitats or not described at all (Bergmeier *et al.* 2010; Tölgyesi *et al.* 2018). Wood pastures as such are hardly found as a legal category. Other habitats, which have the potential to develop into semi-open habitats, are described by the "Annex I habitat types" of the Habitat Directive of the European Union. Semi-natural dry grasslands and scrubland facies on calcareous substrates (6210), for example, includes scrub and woody vegetation as well as the transitions from woody to grassland vegetation as part of the habitat description. The habitat description recognises that these grassland-shrub transitions are important habitats for certain species (e.g. orchids) and feature a high species richness (Calaciura & Spinelli 2008). However, it is suggested that the amount of shrub is to be limited to up to 30% (Olmeda *et al.* 2019). For European dry heathlands (4030), it is suggested that the structural diversity is to be enhanced by allowing bare ground, dwarf shrubs of different age classes as well as shrubs and single trees (Olmeda *et al.* 2020) but the cover of trees and scrub should be limited to less than 10%. The "Annex I habitat types" are part of the Natura 2000 network of the European Union – a network to provide connectivity on a large transnational scale. Promoting and facilitating the establishment of semi-open corridors within this network could help to connect many of the different habitat types with each other. Encouraging a transition between open habitats and wooded vegetation by managing shrub encroachment accordingly and allowing single trees to mature increases the structural diversity and a mosaic with different environmental conditions for open habitat and woodland species will develop.

However, from personal observation, it is noted that the shrubs are often completely removed. There are a variety of reasons for this. Firstly, in Germany woodland and open habitats are managed by different government agencies. Woodlands are operated by forestry agencies and open habitats are managed by nature conservation or agricultural agencies. Both agencies pay a lot of attention that the canopy cover of the shrub encroachment does not exceed the area which will turn the area legally into woodland and *vice versa*. Shrub clearance will become increasingly difficult if the canopy cover turns too high due to regulations regarding woodland compensation. Therefore, keeping the canopy cover of shrubs and trees low or non-existent ensures that open habitats will not be lost in the long-term. Secondly, already existing woody vegetation will enhance future shrub encroachment which in turn needs to be maintained or removed again. Removing the shrubs completely at once will lower the frequency of future shrub removal, therefore lower the long-term workload and costs. And thirdly, to receive funding for conservation management, it is often necessary to comply to certain shrub limitations (for example, max. 25% in Lower Saxony (Assmann *et al.* 2016); 5% in Thuringia (Klaus 2022)). Government agencies conduct checks and non-compliance will result in the deduction of funds. So, as it is difficult to control the shrub limitation in the field, it is easier to remove all the vegetation at once. Therefore, although some regulations allow and even support different successional stages to a certain extent, in practice this is hardly realised (Olmeda *et al.* 2019). For this, there is a need to think about a more dynamic management approach rather than a static approach in nature conservation. The decline of suitable farming practices will make managing pasture landscapes in a static manner increasingly difficult and is not cost-effective.

It is important to emphasize that this thesis does not advocate the abandonment and subsequent shrub encroachment of open habitats. However, the establishment of semi-open corridors should be considered on suitable sites which cross-link woodlands and open habitats, and which are already subject to shrub encroachment or where an open habitat management cannot be secured in the long term.

As the concept of semi-open habitats can be applied to different plant communities, future research needs to look further into the management of the different types of semi-open corridors to allow both woodland and open habitat species to flourish. For example, which effect does rotational shrub removal have on woodland species? Do woodland species rely on mature tree stands to establish in semi-open habitats? How much shrub encroachment is acceptable for the establishment of open habitat species? The implementation of semi-open corridors has to be closely monitored to be able to react accordingly when shrub encroachment takes over.

5.5 Conclusion

This thesis provides evidence that semi-open corridors allow to mitigate habitat fragmentation for open habitat and woodland plant species by offering stepping stone habitats for their dispersal. Open habitat and woodland species were both present and able to germinate and recruit in semi-open habitats, showing different success rates regarding presence and seedling recruitment in semi-open habitats, also depending on the local setting. Therefore, both are able to use semi-open habitats as stepping stone to a certain extent.

However, many questions are still unanswered and need to be further investigated. For example, to what extent are open habitat and woodland species able to reproduce in semi-open habitats? Only if reproduction is successful, can semi-open habitats act as stepping stone for the complete life cycle of plant species and seeds will be able to travel further. In addition, questions regarding the kind of management for the different habitat types in different geographical locations need to be answered to enable both species types to get the best out of semi-open corridors.

Although this research has not been able to show if the species are actually arriving at their destination, the results have shown that open habitat and woodland species are able to use semi-open habitats during certain life stages (e.g. seedlings). The seedling stage is a particular vulnerable stage for plants. Therefore, there is a high probability that these species are also able to survive in semi-open habitats at later life stages. Consequently, semi-open habitats are suitable alternatives to linear corridors to overcome dispersal limitations and with it, biodiversity loss.

5.6 References

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Appendix

Article overview and authors' contribution to articles

This thesis includes three articles that have either been published or are close to submission for publication in international peer-reviewed journals. The articles are the result of the collaborative work of several authors. Table 8 features a summary of my and the co-authors' contributions to each article presented in this thesis (in accordance with the Doctoral Regulations of 20 July 2023 § 8 Section 3 and the Guideline for Cumulative Dissertations enacted at the Faculty of Sustainability in January 2012).

Table 8: Overview of the authors' contributions to each article

Article	I	II	III
Title	Corridors as a tool for linking habitats – shortcomings and perspectives for plant conservation	The role of semi-open habitats as dispersal corridors for plant species of woodlands and open habitats.	Outside the comfort zone: Species traits and environmental factors drive woodland and open habitat plant recruitment in semi-open habitats
Journal	Journal for Nature Conservation	Applied Vegetation Science	-
Publication status	published	published	preparing for submission
Weighting factor of my contribution	predominant contribution (1.0)	predominant contribution (1.0)	predominant contribution (1.0)
Specific contribution* of all authors			
Conceptualisation	ET, WH, DM	ET, WH, DM	ET, WH, DM
Methodology	-	ET, WH, DM	ET, WH, DM
Investigation	ET	ET, WTP	ET
Formal analysis	-	ET, AF	ET, AF, DM
Writing – original draft	ET	ET	ET
Writing – review & editing	ET, WH, DM	ET, WH, DM, AF	ET, WH, DM, AF

*Contributor roles according to CRediT
Authors: ET: Eliane Travers[1]; WH: Werner Härdtle[1]; DM: Diethart Matthies[2]; AF: Andreas Fichtner[1]; WTP: Witja Till Pitz[1]

Authors' affiliations:

[1]Institute of Ecology, Leuphana University Lueneburg, Universitätsallee 1, 21335 Lueneburg, Germany
[2]Department of Biology, University of Marburg, Karl-von-Frisch-Straße 8, 35043 Marburg, Germany

Explanatory Notes:

Specific contribution of PhD candidate submitting the doctoral thesis / Author status according to § 12 of the guideline for cumulative dissertations

- Single author = own contribution amounts to 100%.
- Co-author with predominant contribution = own contribution is greater than the individual share of all other co-authors and is at least 35%.
- Co-author with equal contribution = (1) own contribution is as high as the share of other co-authors, (2) no other co-author has a contribution higher than the own contribution, and (3) the own contribution is at least 25%.
- Co-author with important contribution = own contribution is at least 25%, but is insufficient to qualify as single authorship, predominant or equal contribution.
- Co-author with small contribution = own contribution is less than 20%.

Weighing Factor according to § 14 of the guideline for cumulative dissertations

Single author	1.0
Co-author with predominant contribution	1.0
Co-author with equal contribution	1.0
Co-author with important contribution	0.5
Co-author with small contribution	0

Declaration

I avouch that all information given in this appendix is true in each instance and overall.

Oberpframmern, 10th May 2024

Eliane Travers

List of Publications

Peer-reviewed journals

Travers, E., Pitz, W. T., Fichtner, A., Matthies, D., & Härdtle, W. (2021). The role of semi-open habitats as dispersal corridors for plant species of woodlands and open habitats. *Applied Vegetation Science*, 24, e12526.

Travers, E., Härdtle, W., & Matthies, D. (2021). Corridors as a tool for linking habitats–Shortcomings and perspectives for plant conservation. *Journal for Nature Conservation*, 60, 125974.

Book publication

Assmann, T., Boutaud, E., Finck, P., Härdtle, W., Matthies, D., Nolte, D., Von Oheimb, G., Riecken, U., **Travers, E.** & Ullrich, K. (2016). Halboffene Verbundkorridore: Ökologische Funktion, Leitbilder und Praxis-Leitfaden. *Naturschutz und Biologische Vielfalt*, 154. Bonn - Bad Godesberg. DOI: 10.19213/973154

Conference contributions and talks

Travers, E. (2013). *Halboffene Lebensräume: eine besondere Chance für den Naturschutz?*, NNA, Schneverdingen (2013) | Talk.

Travers, E., Härdtle, W., von Oheimb, G. & Matthies, D. (2014). *Building interchanges instead of highways - Use of semi-open corridors to simultaneously connect woodland and grassland habitats.* 99th ESA *(Ecological Society of America)* Annual Meeting, Sacramento | Poster.

Travers, E. (2016). *Vegetation und Gehölzstrukturen von halboffenen Lebensräumen und ihre Bedeutung für Offenland- und Waldflora*. Fachtagung zur ökologischen Funktion von halboffenen Verbundkorridoren, NNA, Schneverdingen | Talk.

Travers, E. (2016). *Using semi-open corridors to simultaneously connect open landscapes and woodlands – from a plant perspective*, 45th Annual Meeting of the GfÖ *(Gesellschaft für Ökologie)*, Marburg | Talk.

Assmann, T. & **Travers, E**. (2016). *F+E-Vorhaben: Ökologische Funktion von halboffenen Verbundkorridoren*, 3. Fachtagung zum Management des Grünen Bandes, BUND, Salzwedel | Talk.