HEDGEROWS HAVE A BARRIER EFFECT AND CHANNEL POLLINATOR MOVEMENT IN THE AGRICULTURAL LANDSCAPE

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ABSTRACT

Agricultural intensification and the subsequent fragmentation of semi-natural habitats severely restrict pollinator and pollen movement threatening both pollinator and plant species. Linear landscape elements such as hedgerows are planted for agricultural and conservation purposes to increase the resource availability and habitat connectivity supporting populations of beneficial organisms such as pollinators. However, hedgerows may have unexpected effects on plant and pollinator persistence by not just channeling pollinators and pollen along, but also restricting movement across the strip of habitat. Here, we tested how hedgerows influence pollinator movement and pollen flow. We used fluorescent dye particles as pollen analogues to track pollinator movement between potted cornflowers *Centaurea cyanus* along and across a hedgerow separating two meadows. The deposition of fluorescent dye was significantly higher along the hedgerow than across the hedgerow and into the meadow, despite comparable pollinator abundances. The differences in pollen transfer suggest that hedgerows can affect pollinator and pollen dispersal by channeling their movement and acting as a permeable barrier. We conclude that hedgerows in agricultural landscapes can increase the connectivity between otherwise isolated plant and pollinator populations (corridor function), but can have additional, and so far unknown barrier effects on pollination services. Functioning as a barrier, linear landscape elements can impede pollinator movement and dispersal, even for highly mobile species such as bees. These results should be considered in future management plans aiming to enhance the persistence of threatened pollinator and plant populations by restoring functional connectivity and to ensure sufficient crop pollination in the agricultural landscape.

Key words: Fragmentation, Linear Landscape Elements, Functional connectivity, Corridor, Pollen flow

INTRODUCTION

Pollinators provide a crucial ecosystem service in the agricultural landscape by contributing to crop production (Gallai *et al*., 2009) and quality (Klatt *et al*., 2014). Today, various threats associated with intensive agriculture such as habitat loss and fragmentation lead to a decline of many pollinator species (Benton *et al*., 2003; Potts *et al*., 2010). In particular, the fragmentation of habitats, coupled with intensified land use between habitat remnants decreases functional connectivity (Taylor *et al*., 1993; Tischendorf & Fahrig, 2000). Fragmentation causes limitations in species dispersal, which leads to a reduced gene flow between populations of pollinators and plants and threatens sufficient pollination of crops (Forman & Godron, 1981; Klein *et al*., 2007).

To restore connectivity and facilitate movement of pollinators through agricultural landscapes, linear landscape elements such as hedgerows are planted alongside crop fields (Fahrig & Merriam, 1994; Tischendorf & Wissel, 1997). Hedgerows are narrow bands of vegetation, such as trees and shrubs providing habitat and food resources for wildlife (Forman & Baudry, 1984; Hannon & Sisk, 2009). As one of the most important non-crop habitats in the agricultural landscape, they host arthropods, which provide ecosystem services such as biological control of pest species, as well as crop pollination (Pollard & Holland, 2006). Fluxes of wind speed, soil desiccation, soil erosion, as well as nutrient runoff are also important factors for agriculture, which are affected by hedgerow networks (Forman & Baudry, 1984). Furthermore, hedgerows serve as corridors for various plants and animals increasing the connectivity of habitat patches and facilitating the movement between habitats, which are separated by an otherwise inhospitable matrix (Forman & Baudry, 1984; Joyce *et al*., 1999).

Those corridor effects have been observed for different insect taxa. Dipterans, for example, were shown to follow closed edges, which may direct them along corridors and into connected patches (Fried *et al.*, 2005). Furthermore, Berggren *et al*. (2002) showed how the dispersal of an orthopteran species was facilitated by linear landscape elements in the form of corridors. The movement of various species of butterflies was observed to be directed by corridors as well (Haddad *et al.*, 2003).

However, there might be unexpected effects of hedgerows affecting insect dispersal when they act not just as corridors, but also as barriers for movement. A barrier effect was for example shown for three butterfly species with hedgerows impeding their movement through the landscape (Dover & Fry, 2001). Similarly, Mauremooto *et al*. (1995) showed that hedgerows slow the movement of carabid beetles. Especially those hedgerows that are tall and dense are likely to act as a barrier to arthropods (Mauremooto *et al*., 1995).

Hedgerows can benefit pollinating insects by supporting high densities of flowering shrubs and trees, which makes them attractive foraging habitat for pollinators (Hannon & Sisk, 2009). This can benefit threatened species of pollinators, as well as ensure the pollination of agricultural crops (Hannon & Sisk, 2009). Furthermore, pollinator-dependent plants rely on pollen transfer mediated by insects ensuring sufficient gene flow (Garibaldi *et al*., 2011; Sun *et al*., 1998). Isolated populations in highly fragmented landscapes are more threatened by inbreeding with insufficient outcrossing (Osborne & Williams, 2001; Severns, 2003). Generally, linear landscape elements such as hedgerows are thought to act as corridors facilitating migration and thereby reconnecting isolated patches of habitat (Townsend & Levey, 2005).

For pollinators in general however, there still is a lack of knowledge regarding the effect of linear landscape elements on their movement and dispersal (Zurbuchen *et al*., 2010). Townsend and Levey's (2005) results support the traditional corridor hypothesis for pollinators. Pollen transfer by butterflies, bees, and wasps between isolated patches was found to be significantly higher when patches were connected by a corridor. Regarding a possible barrier effect, one study by Krewenka *et al*. (2011) found the movement of foraging bees not to be confined by hedgerows. On the contrary, Campagne (2009) showed how *Bombylius* sp. activity impeded pollen flow in a dense hedgerow network. Further knowledge about the movement and dispersal of pollinators in the landscape can help to better manage pollinating insects for agriculture. Besides crop pollination, a main target in conservation is ensuring the connectivity of rare plant species populations by ensuring their connectivity via pollen and therewith gene flow.

Therefore, in this study, we focus on the effect of hedgerows on pollinator movement and animal mediated pollen transfer. We investigated possible channeling and barrier effects of hedgerows for pollen dispersal. Pollen flow was tracked using fluorescent powder acting as a pollen analog. Dispersal via pollinating insects between patches of corn flowers (*Centaurea cyanus*) across and along a hedgerow compared to into a meadow was measured. To ensure similar levels of pollination, the number of pollinators was recorded for each patch of flowers. *Centaurea cyanus*, once a common weed in crop fields throughout Europe, is now endangered due to agricultural intensification and occurs in small and isolated patches in the fragmented landscape (Albrecht & Mattheis, 1998). Our main objectives were to test potential channeling and barrier effects of linear landscape elements for pollen flow. New insights into how pollinator movement and pollen dispersal are affected by hedgerows could alter the perception of hedgerow plantings as a tool in conservation biology and pollinator management.

MATERIALS AND METHODS

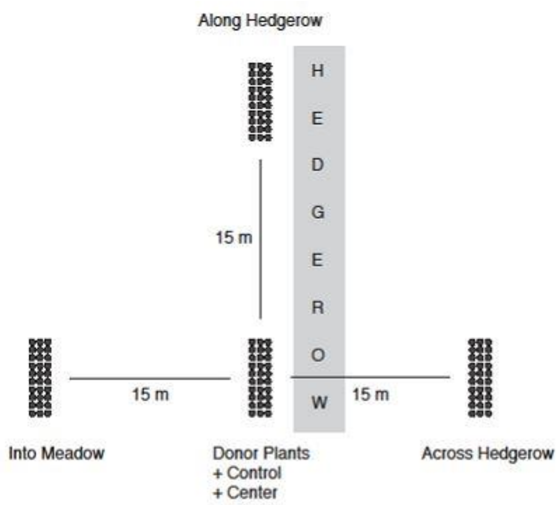
The study was conducted in Göttingen, central Germany, in July 2013. For our experiments, we selected a dense, continuous hedgerow on the experimental site of the Agroecology-institute at Göttingen University. The hedgerow had a total length of 65 meters, and an average height and width of five meters. It consisted of *Cornus sanguinea*, *Acer campestre, Prunus avium*, *P. spinosa* and *Crataegus laevigata*, none of which was flowering at the time of our experiment. The hedgerow separated two meadows, both rich in flowers (mainly *Glechoma hederacea, Crepis biennis, C. capillaris*) and nearby honey bee hives and trapnests for native bees ensured sufficient pollinator abundance. To track pollen movement, we placed six sets of potted cornflowers (*Centaurea cyanus,* Asteraceae) alongside and across the hedgerow (Fig. 1). Main pollinators of cornflowers are hymenopterans, syrphid flies (Syrphidae), as well as diurnal lepidopterans (Rhopalocera) with a peak in pollinator visits in late morning (Düll & Kutzelnigg, 2011).

A group of 30 cornflower plants was placed next to the hedgerow as the pollen donor. Yellow fluorescent dye (RadgloR, Radiant Color, Belgium) was applied to about 750 flowers in the early morning before pollinator activity (9:00 am) using a small brush. Fluorescent dye can be used as a pollen analogue to track pollen and pollinator movement. It has been shown not to change the behavior or survival of pollinators (McMullen *et al*., 1988; Nakata, 2008). Therefore, it is a useful tool to study possible effects of hedgerows and other landscape elements on the movement of pollinating insects. The variety of options using fluorescent dye in ecological research includes marking insects directly or indirectly for example by applying dye to the entrance of honeybee hives or to nests of trap nesting bees (Corbett & Rosenheim, 1996). Furthermore, flowers can be marked to track pollen flow and the use of different colors allows for a more sophisticated experimental setup. In this study, the method enabled us to directly track pollen and insect movement (Van Rossum *et al*., 2011).

Three groups of 30 unmarked (no powder applied) plants each were placed 15 meters from the plants with fluorescent dye flowers (see Fig. 1). The first group of plants was placed across the hedgerow, the second on the same side along the hedgerow, and the third into the meadow. One set of 30 unmarked plants was put next to the donor plants. Another set of 20 unmarked plants by the donor plants was acting as a control. These plants were made inaccessible to pollinators using air- and light permeable meshes.

Being of an average height of about 75 cm and in full bloom (more than 50 open flowers per plant), the cornflower plants were higher than the surrounding meadow vegetation and provided an obvious target for pollinators. They were readily visited after placement. Pollinator observations were conducted to evaluate if plants in different treatments received similar pollination intensity. Pollinators were counted three times in the morning (at 10:00 am, 10:10 am, and 10:20 am), as well as in the afternoon (4:00 pm, 4:10 pm and 4:20 pm) in each plot.

Fig. 1: Study design. Dark dots represent location of plants. Thirty plants at each location. Unmarked at 'Center', 'Along Hedgerow', 'Into Meadow', and 'Across Hedgerow'. Marked with fluorescent dye at 'Donor Plants'. Another 20 unmarked plants at 'Control' with inaccessible flowers (meshed). Distance between plots is 15m. Grey bar represents hedgerow.



One day after the fluorescent dye had been applied 20 flowers from the control site and 40 flowers from each of the other treatments were randomly collected, totaling 180 flowers. The presence of fluorescent dye particles was then determined using fluorescence microscopy (1.00 magnification). Presence or absence of fluorescent dye particles was recorded separately for each flower as an indicator of successful pollen transfer from the donor plants.

Data analysis was performed with R 0.97.173 (R Development Core Team 2011). Differences in mean numbers of contaminated flowers per patch and mean pollinator visits were compared using a Fisher's exact test and a Wilcoxon Rank Sum test respectively (Crawley, 2007).

RESULTS

Overall we observed 71 pollinators of which 56.3% were bumblebees and 33.8% were honeybees. Other pollinating insects observed were solitary bees (5.6%), as well as syrphid flies (1.4%). The numbers of pollinators did not differ significantly between sites (Fig. 2; Table 1). On average, three pollinating insects were present in the center, along the hedge and in the meadow, respectively. On the other side of the hedge, there was a mean of 2.5 pollinators abundant.

The proportion of flowers with fluorescent dye significantly differed between sites (Fig. 3; Table 2). In the center and along the hedgerow, dye was present on more than 50% of flowers. In contrast, the percentage of flowers showing dye deposition was significantly lower for into the meadow and across the hedgerow (15% and 5% respectively). Only five percent of flowers in the control treatment had fluorescent dye present indicating an unsuccessful exclusion of pollinators by the mesh or another source of error such as secondary contamination after flower collection. This indicates that dye on open flowers indeed resulted from insect-mediated dye transfer.

Fig. 2: Pollinator abundances across sites. Mean numbers of approximately three pollinators at Center, Along Hedgerow and Into Meadow. Mean of 2.5 pollinators Across Hedgerow. No significant differences. Results from Wilcoxon Rank Sum Test with pairwise comparison.

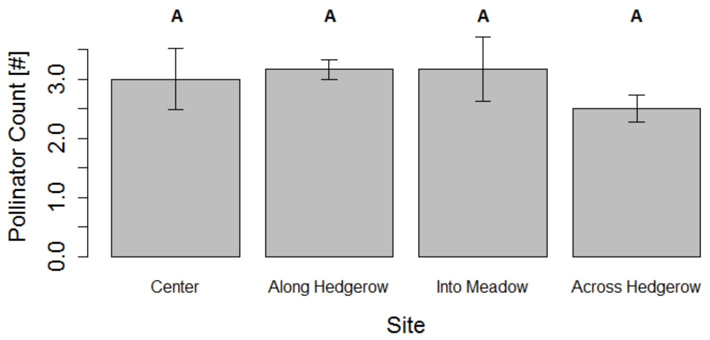


Fig. 3: Portion of flowers with fluorescent dye present across sites. Significantly higher values for Center & Along Hedgerow compared to Into Meadow, Across Hedgerow, and Control. Results from Fisher's Exact Test with pairwise comparison.

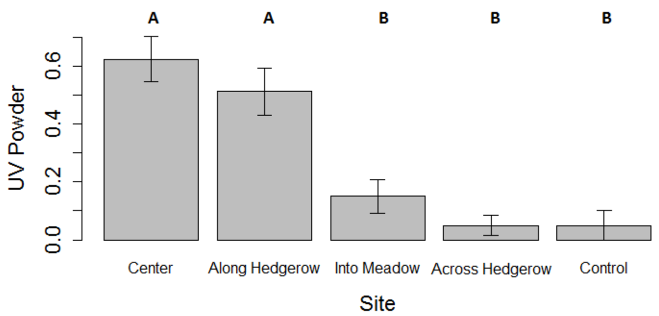


Table 1: p values from pairwise data comparison using Wilcoxon Rank Sum Test. Portion of flowers with fluorescent dye present was compared across sites. Significance for p < 0.05. No significant differences between plots.

Pair tested	*p* value	Significance
Across Hedgerow ~ Along Hedgerow	0.05429	-
Across Hedgerow ~ Center	0.3575	-
Across Hedgerow ~ Into Meadow	0.4898	-
Along Hedgerow ~ Center	0.9305	-
Along Hedgerow ~ Into Meadow	0.9328	-
Center ~ Into Meadow	0.8656	-

Table 2: p values from pairwise data comparison using Fisher's Exact Test. Portion of flowers with fluorescent dye present was compared across sites Threshold for *p* values lowered to 0.005 according to Bonferroni. Center and Along Hedgerow are significantly different from Into Meadow, Across Hedgerow, and Control.

Pair tested	*p* value	Significance
Across Hedgerow ~ Along Hedgerow	3.133e-06	***
Across Hedgerow ~ Control	1	-
Across Hedgerow ~ Center	4.204e-08	***
Across Hedgerow ~ Into Meadow	0.2633	-
Along Hedgerow ~ Control	0.0004028	***
Along Hedgerow ~ Center	0.3675	-
Along Hedgerow ~ Into Meadow	0.0007639	***
Control ~ Center	1.652e-05	***
Control ~ Into Meadow	0.4065	-
Center ~ Into Meadow	2.388e-05	***

DISCUSSION

The results of this study showed that hedgerows can affect pollinator dispersal in two different ways. First, a significantly higher pollen deposition rate along the hedgerow compared to into the meadow suggests that hedgerows channel pollinator movement. Second, hedgerows can act as barriers for pollinators and thus pollen flow, as suggested by significantly lower pollen deposition across the hedgerow compared to into the meadow. The relatively low deposition of pollen analogue in the meadow could be partly due to a loss of fluorescent powder with pollinators visiting other flowers in the meadow on their way to the target flowers.

Linear landscape elements are known to act as functional biological corridors for insects such as carabid beetles (Joyce *et al.*, 1999), dipterans (Fried *et al.*, 2005), and butterflies (Haddad *et al.*, 2003) connecting habitats in a fragmented landscape. Our results are in line with studies that found a channeling effect of hedgerows on pollinators and thus pollen movement. Cranmer *et al.* (2012) for example showed that an increased movement and activity of bumblebees along hedgerows increase the reproductive success in experimental populations of *Salvia pratensis* plants. Similarly, Van Geert *et al.* (2010) showed that linear landscape elements can enhance connectivity in agricultural landscapes by increasing pollinator movement and thus pollen transfer between otherwise isolated populations of insect-pollinated plants.

On the other hand, hedgerows have been found to slow down dispersal, for example of carabid beetles (Mauremooto *et al*., 1995), butterflies (Dover & Fry, 2001), and *Bombylius* sp. (Campagne *et al.*, 2009). Supporting these studies, our results showed that pollen flow was lower across a hedgerow compared to into a meadow suggesting that pollinator dispersal was hampered by the linear landscape element. Our abundance data were in line with data from a former study in the same region, which reported no differences in pollinator abundances between opposing sides of large hedgerows (Krewenka *et al*., 2011). Based on their findings, the authors concluded that hedgerows did not confine movement of foraging bees. Our direct quantification of pollinator movement through pollen flow however, suggests that hedgerows can impede pollinator movement. This was observed even for highly mobile species such as bees. Thus, hedgerows may generally act not just as corridors, but also channel arthropod movement. This could enhance connectivity between patches of habitat along hedgerows, as shown for wasps by Holzschuh *et al*. (2010), but also restrict movement and gene flow disconnecting populations of pollinated plants due to a barrier effect (Bhattacharya *et al.*, 2003). Such a hampering effect on arthropod movement could indeed be a common, but often ignored characteristic of hedgerows.

Experiments on butterflies revealed that different species express different behaviors in and around hedgerows (Dover & Fry, 2001). In addition, the perception of and response to landscape elements have been shown to vary across taxa of pollinators sometimes even with closely related species showing different responses (Jauker *et al.*, 2009). Future research should therefore focus on species-specific responses, especially of relevant pollinators of threatened plant species and crop plants. Extended knowledge about the effect of linear landscape elements on the dispersal of different pollinator groups could allow new management strategies to actively channel movement, for example in conservation to ensure the use of wildlife corridors, or in farming to channel pollinating insects to crop fields ensuring sufficient pollination. Furthermore, hedgerows acting as barriers and slowing down pollinator movement could be a method of reducing unwanted pollen transfer for example from experimental fields to reduce gene flow resulting in hybridization and pollen dispersal of genetically modified crops (Hayter & Cresswell, 2006; Umbeck *et al*., 1991; Walker *et al*., 2011). Vice versa deliberately leaving gaps in hedgerow plantings could ensure sufficient connectivity between pollinator and plant populations on opposite sides of the barrier. Especially tall and dense hedgerows are likely to act as a barrier confining arthropod movement (Mauremooto *et al.*, 1995). Further knowledge about how traits of hedgerows such as height, width, density, gaps, flower supply, etc. affect pollen flow and pollinator movement can make targeted hedgerow plantings an even more useful tool in pollinator management (Dover & Settele, 2009; Petit & Burel, 1998).

Our results offer new insights into the effects of hedgerows on movement and behavior of bees and other pollinators. Functional biological corridors are shown to facilitate pollen flow along the linear landscape element but also to impede dispersal across. Our findings are of importance for the conservation of endangered plants occurring in small and isolated populations across highly fragmented landscapes. Especially pollinator-dependent plants are threatened by inbreeding and rely on sufficient pollen dispersal across populations to ensure outcrossing (Osborne & Williams, 2001; Severns, 2003). Channeling, as well as barrier functions should be considered for future use of hedgerow plantings as a tool in conservation biology and pollinator management in fragmented landscapes.

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