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Research Article

Green veining: landscape determinants of biodiversity in European agricultural landscapes

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Abstract

Many semi-natural landscape elements, the so-called green veining, are disappearing from the intensively used agricultural landscapes of Europe. In order to develop or restore biodiversity in these networks, it is necessary to quantify the relation between biodiversity and amount, spatial arrangement and management intensity of green veining elements. In this review, we investigate whether biodiversity increases with the amount of green veining in an agricultural landscape following the species–area relationship, and whether a certain level of biodiversity can be reached at lower densities of green veining if green veining elements are better connected (higher spatial connectivity) or if they are managed less intensively (lower management intensity). We reviewed studies on aboveground biodiversity in green veining structures in 39 scientific papers on field and experimental studies within Europe. More of these studies focussed on management intensity than on amount or spatial configuration of green veining. Also more studies focussed on the spatial scale of individual landscape elements than on the farm or landscape scale, which may be caused by the large number of studies focussing on plant or invertebrate species. Species living at larger spatial scales, e.g. mammals and birds were not often studied at the level of green veining elements as they also use agricultural fields as part of their habitat. We could not verify the species–area relation for green veining, nor the effect of amount, spatial configuration or management intensity on this relation, because only few studies quantified the found effects and no studies were found on the effect of management intensity or spatial configuration on the species–area curve in green veining. We addressed the most important challenges for future field and model research in order to fill the identified gaps in knowledge.

Introduction

It is widely recognised that biodiversity in many parts of the world is rapidly decreasing (Pimm and Raven 2000; Woodruff 2001; Hubbell 2001). Therefore, much attention has been paid to conservation and restoration of biodiversity in protected nature reserves (Margules and Pressey 2000). Besides natural areas, also agricultural landscapes have a high potential for biodiversity, due to their diversity in habitat types (Waide et al. 1999). In nutrient poor regions, the increased productivity of agricultural activities may also enhance biodiversity. However, in many European landscapes land use intensity has increased to the extent where agricultural fields are being exposed to high inputs of fertilisers, pesticides, herbicides and to frequent crop rotation. Consequently, these fields have been converted into hostile habitat for many species, resulting in a drastic decline in biodiversity (Vandermeer et al. 1998; Donald et al. 2001; Wagner and Edwards 2001; Benton et al. 2003).

In these intensively used agricultural areas, most of the remaining biodiversity is found in semi-natural features (Baudry et al. 2000a; Kleijn et al. 2001). These features comprise several types of landscape elements that are not being used primarily for agricultural production. They include many linear elements like field margins, road verges, ditch banks, hedgerows, and wooded banks. Also patch elements like woodlots and ponds are part of these non-cropped elements. The term 'green veining' has been adopted for these elements, because, being arranged around the agricultural fields, they form a fine-meshed network of 'veins' embedded in the agricultural landscape (Opdam et al. 2000). In the green veining, the linear elements connect the different parts of the network, while the patch elements can be seen as nodes within the network or as patches beneath the network that support the biodiversity found in it.

How does this network function for biodiversity in agricultural landscapes? First of all, many species find their reproduction habitat in these elements. Some species depend on one habitat type for their entire life cycle. For sessile species like plants this is quite obvious. Most plant species are restricted to one or a few habitat types. Wood anemone (*Anemone nemorosa*) for instance, grows in woody fringes and wooded banks, but can sometimes colonise adjacent grassy fields (Falinski and Canullo 1985). Also some animal species depend on one specific habitat type, like the ringlet butterfly (*Aphantopus hyperantus*) that finds its host plants and nectar plants in grassy habitats and brushwood (Bink 1992). Other species are also restricted to green veining, but use different parts of the network during their life span. The tree frog (*Hyla arborea*) for instance reproduces in ponds, but its land habitat comprises shrub and woody vegetation (Vos 1999). Other species reproduce in the green veining, but forage in the adjacent agricultural fields, like farmland birds (Henderson et al. 2000). Some species reproduce outside the green veining, but use the non-cropped elements for shelter or as dispersal corridor like the pine marten (*Martes martes*, Müskens et al. 2002), for orientation while moving through the landscape like butterflies or bats (Verboom 1998), or for foraging like the barn owl (*Tyto alba*, de Bruijn 1979). Finally, green veining is used for instance by invertebrates and bank voles for wintering or as refuge habitat (Kozakiewicz and Gortat 1994; Lys et al. 1994; Dabrowska 1995).

Many green veining elements, however, are disappearing from agricultural landscapes, because they have lost their economical values like providing fuel and partitioning fields (Jongman 1996). Therefore the remaining biodiversity in these green veining elements is also threatened, including species that serve agricultural purposes, e.g. some invertebrates assisting in pest control and pollination (Duelli 1997; Altieri 1999; Paoletti 1999).

Although the relationship between the decrease in farmland biodiversity, agricultural intensification and loss of heterogeneity of habitat has been demonstrated (Benton et al. 2003), the question remains how important green veining is for the restoration of biodiversity in agricultural landscapes. Could these non-cropped elements contribute to the increase of farmland biodiversity and, if so, what are then the requirements for these elements? Benton et al. (2003) suggest that heterogeneity at multiple spatial and temporal scales is the key factor to farmland biodiversity. In this paper we argue, however, that also spatial structure (amount and spatial configuration) of green veining is an important property for biodiversity found in green veining networks. Aiming at maximizing habitat heterogeneity could lead to insufficient area of specific habitat types at the element or landscape level. Namely, green veining patches are mostly quite small and linear elements narrow. Therefore, green veining can only support biodiversity if it functions as a compilation of habitat networks (Baudry et al. 2000a) supporting patchy populations or metapopulations of species at corresponding spatial and temporal scales (Levins 1970; Hanski and Gilpin 1991; Verboom et al. 1993; Freckleton and Watkinson 2002). Consequently, the diversity of species inhabiting a specific habitat type is expected to increase with increasing coherence of those landscape elements that provide their habitat. As different species use different habitat types, overall biodiversity will increase with the increase of the spatial structure of all corresponding habitat types of the species groups under consideration.

Besides by spatial structure, biodiversity is also affected by the habitat quality and disturbance regime of green veining elements. In agricultural landscapes, habitat quality and disturbance are largely determined by management intensity of the elements themselves, but also by management intensity of (adjacent) agricultural fields (Kleijn et al. 2001). For instance, frequent addition of manure in these fields can lower the habitat quality of field margins, while for some species it can even turn field margins into unsuitable habitat. As management intensity has many aspects at the level of individual landscape elements (fertilisation, mowing, grazing, pest and herb control) as well as on the farm or landscape level (type of land use), insight in all these aspects is required to determine management restrictions that are needed to restore biodiversity.

In this paper, our main goal is to quantify the relation between biodiversity and the amount of green veining. Furthermore, we want to assess how this relation is affected by spatial arrangement of green veining, and by management intensity of green veining and of adjacent agricultural fields. We will focus on the diversity of specific species groups at the level of individual landscape elements as well as on overall biodiversity on the landscape scale. We expect to find that biodiversity increases with the density of green veining (amount of green veining in the studied agricultural landscape) following the species–area relationship (Barnaszak 1992; Hubbell 2001; Olff and Ritchie 2002). Such relationship is illustrated in Figure 1, and has been observed for many species of larger natural areas. We assume that the same relation between species richness and habitat area is valid for species living in (semi)natural habitat that is embedded in an agricultural landscape. At low densities of green veining, only few species will find the minimum amount of habitat needed for their survival. Increasing the amount of habitat at this point will increase the number of species rapidly, as the minimum area requirements for many species will then be met. This results in a steep increase of the species–area curve. However,

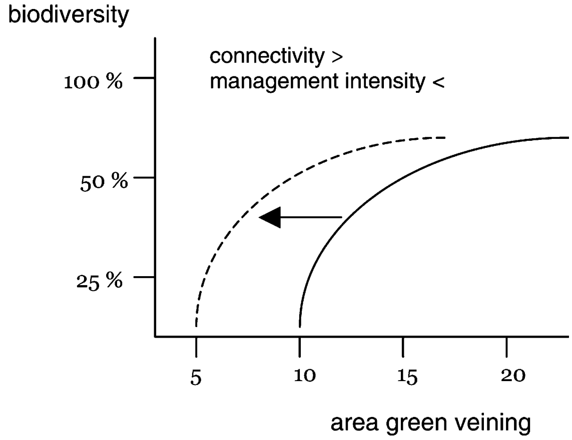

Figure 1. Hypothetical relation between biodiversity and amount of green veining on a local to regional scale conform the species–area relationship. Amount of green veining is presented as density: percentage of the total area of the studied landscape (solid line). This curve will shift to the left if connectivity of green veining is increased or if management intensity of green veining is decreased (dashed line). This indicates that at higher connectivity or at lower management intensity, less green veining is needed to reach the same level of biodiversity in these semi-natural elements.

at relatively high amount of green veining habitat, further increase of green veining area will only add a few species with high area requirements, resulting in flattening of the curve. Secondly, we expect that increasing the spatial connectivity and lowering the intensity of management will lower the amount of green veining needed to reach a specific level of biodiversity. As improving management or spatial structure can improve the occupation frequency and/or occupation density of habitat (Burel et al. 2004), it can be expected that the same species can survive at lower densities of green veining habitat if management intensity is lower or if spatial coherence is higher.

The relation between biodiversity and amount of green veining will be studied by literature research, in which we focus on the quantification of this relation and on a possible shift in this relation by changing the spatial structure and management intensity of green veining. Furthermore, we will identify the most pressing gaps in knowledge in the reviewed literature that should be assessed in future research in order to improve the insight in the mentioned relations. Filling in these gaps would make it possible to predict biodiversity at a specific amount of green veining at specific management or spatial conditions in an agricultural landscape. Also, we would be able to determine the needed amount of green veining habitat at certain levels of management intensity and spatial configuration to reach a desired biodiversity level.

Methods

We tried to answer the above mentioned questions by collecting information from scientific papers on field and experimental studies that have addressed the effects of amount and spatial configuration of green veining and/or have analysed the effect of management intensity of green veining elements or agricultural fields on biodiversity. Whereas Benton et al. (2003) focuses mainly on the biodiversity of the agricultural fields, we have limited the focus of this paper to studies concerning diversity of aboveground species groups that depend largely on the green veining for living and reproducing. This means that we did not include species, for example meadow birds, that reproduce mainly on agricultural fields or that otherwise depend strongly on agricultural fields. Neither did we include studies on individual species. We have further limited our study to agricultural landscapes that are characterised by conventional agricultural practice in the European temperate climate zone. We systematically searched literature databases from 1994 to 2003, but incidentally other literature sources have been used. The literature we found on this topic is represented in Table 1, and the numbering followed in this table will be used to refer to these literature sources in the results and in the synthesis. We distinguished effects on biodiversity of area or density, spatial configuration and management intensity of green veining, while for each of these effects we distinguished between effects at the scale of the individual element and effects at a farm and landscape scale (Table 2). Management intensity was defined as management intensity of green veining itself, as well as management intensity of (adjacent) fields. If reviewed studies quantified the found relations, we presented the type of relation in Table 3. We categorised the results by the species group(s) under study, the used biodiversity indices and by the used parameters of area, spatial configuration or management intensity at different spatial scales in Table 4.

In the results section, we will give an overview of the found effects of area, spatial configuration and management intensity of green veining on biodiversity, on a local scale as well as on the farm and landscape level. In the synthesis, evidence for the species–area relation in green veining will be discussed, as well as the influence of spatial configuration and management intensity of green veining on this relation. Also the appropriate spatial and temporal scales of species and measurements will be discussed. Finally, important challenges for further experimental and model research will be presented.

Results

Area of green veining

At a local level, five studies assessed and found positive effects of area of single green veining elements or patches on plant and butterfly diversity (see Tables 2 and 4). In study 31 the area effect is larger for butterfly species that are specialised on certain food resources, as the effective habitat of food specialists comprises only specific parts of the total habitat patch. Study 17 studied the species–area relation within single buffer zone elements for plants, and this relation was only significant plants if area was separated in length and width, as width contributed much more to the species–area relation than length.

At the landscape level, the area of green veining elements has been studied in nine studies, and seven of them found significant effects on spider, bird, plant and butterfly diversity. Both study 10 and 25 studied butterflies, but only the latter found effects of area on diversity. This study took the amount of all semi-natural habitats into account while study 10 only focussed on woody green veining. This indicates that butterflies depend on all types of uncultivated area, especially on linear types. Study 14 shows the importance of small woods for migrant woodland birds, but study 2 and 11 both show that woody green veining is also important for farmland birds. Study 2 found effects of tree lines on farmland birds as well on the site (5 ha) as on quadrate level (25 ha). One study focussed on mammal species (23), but no effect was found of the amount of woodlots or hedges in the studied area.

Table 1. Studied species, used biodiversity indices, measurements of amount, spatial configuration and management intensity, spatial scale and study area of reviewed empirical studies on aboveground biodiversity of non-cropped landscape elements (green veining) in Europe.

Study No.	Author(s)	Species	Biodiversity measure	Green veining area	Spatial config (local)	Spatial config (landscape)	Management intensity (local)	Management intensity (landscape)	Scale	Study area
1	Anderlik-Wesinger et al. (1996)	Foliage-dwelling spiders of field margins	Species number	Margin density	Margin width		Disturbance frequency	–	Local	96 1 × 50 m plots in field margins in 7 agricultural landscapes, Southern Germany
2	Arnold (1983)	Farmland birds	Species number in winter and summer	Amount of tree lines, hedges and ditches within site, amount of wood, hedgerow and tree lines around quadrate			–	–	Landscape	47 sites of 5 ha in 25 ha quadrates of agricultural area in East Anglia, UK
3	Aude et al. (2003)	Vascular plants and bryophytes of hedges	Plant diversity	–	–	–	Nitrogen and phosphate content of soil	Farm type (organic vs. conventional)	Local, farm	6 plots of 10 m^2 in 213 hedges on organic and conventional farms in Jutland, Denmark
4	Bäckman and Tiainen (2002)	Bumblebees of field margins	Species number, Shannon diversity index	–	–	Mean margin width	–	–	Landscape	Field boundaries in 20 patches of farmland in Lammi, Finland
5	Baines et al. (1998)	Spiders of field margins	Species number	–	–	–	Cutting, spraying and leaving cuttings	–	Local	Field margins expanded to 2 m × 50 m by fallowing and sowing

Table 1. Continued.

Study No.	Author(s)	Species	Biodiversity measure	Green veining area	Spatial config (local)	Spatial config (landscape)	Management intensity (local)	Management intensity (landscape)	Scale	Study area
6	Burel et al. (1998)	Diptera, Carabidae, small mammals and birds in hedgerows	Species number, Sorensons community index; Squires overlapping index	–	–	–	–	Three areas of different agricultural intensity	Landscape	Blocks of 100 × 100, 500 × 500 and 750 × 750 m in 3 bocage areas of 5000–1000 ha in Brittany, France
7	Chamberlain et al. (2000)	Farmland birds	Species number	–	–	–	–	Crop type	Landscape	10 km square grids of agricultural areas in England and Wales
8	Le Coeur et al. (1997)	Vascular plant species of field margins and hedgerows	Species composition	–	Length of margin	Grain size of three study areas (fine, intermediate, coarse)	Grazing, mowing, crushing, herbicide use adjacent land use	–	Local landscape	338 plant relevés in 3 bocage areas in Brittany, France
9	Delettre and Morvan (2000)	Chironomidae in hedges	Species number, Shannon's diversity index, Sorensen's similarity index, Bray–Curtis distance	Hedgerow density	Distance to stream	Field mosaic	–	–	Local, landscape	128 pan traps in hedges of 3 bocage areas in Brittany, France
10	Feber et al. (1997)	Non-pest butterflies of field margins	Species number	Amount of farm wood, hedgerow density within plot	–	–	–	Farm type (organic vs. conventional)	Farm	8 pairs of farms across England, UK

11	Fuller et al. (2001)	Farmland birds	Species number, similarity index	farm wood cover hedgerow density	–	–	–	–	Farm	33 farmland plots (29–185 ha) in England and Wales, UK.
12	Hald (2002)	Plant species of stream borders	Species number	–	–	–	Adjacent land use, distance to crop rotation	–	Local	1135 fields along streams in 18 study areas in Denmark
13	Hegarty et al. (1994)	Plant species of hedges and neighbouring boundary strips and ditches along grasslands	Species number	–	Hedge width	–	Management intensity, adjacent land use	–	Local	10 × 1 m plots in 418 hedges in six study areas in Northern Ireland
14	Hinsley et al. (1998)	Resident and migrant birds of small woods	Species number	Woodlot density	–	–	–	–	Landscape	5 agricultural areas in The Netherlands, UK., Denmark and Norway
15	Kleijn and Verbeek (2000)	Herbal plant species of grassy field margins	Species number	–	–	–	Management type, herbicide, nitrogen and phosphate input on adjacent crop, rotation of adjacent crop	–	Local	4 m quadrates at 0–33, 34–66 and 67–100 cm from crop in 105 field boundaries in Central and Eastern regions of the Netherlands
16	Kleijn et al. (2001)	Vascular plants, hover flies and bees of field margins	Species number	–	–	–	Field margins with and without management agreements	–	Local	78 fields in nine different agricultural areas throughout the Netherlands

Table 1. Continued.

Study No.	Author(s)	Species	Biodiversity measure	Green veining area	Spatial config (local)	Spatial config (landscape)	Management intensity (local)	Management intensity (landscape)	Scale	Study area
17	Ma et al. (2002)	Plants of buffer zones	Species number	Area of buffer zone elements	–	–	–	–	Local	59 buffer zones along stream banks in Lepsämänjoki, Finland
18	McAdam et al. (1994)	Plant and carabid beetles of hedges along grasslands	Species diversity	–	–	–	Ploughing and/or crop sowing in adjacent strip of 2 m. fertilising and rotationally grazing of adjacent grassland	–	Local	4 treatments in 30 m. blocks in three hedges in Northern Ireland
19	Moonen and Marshall (2001)	Herbal plant species of hedges	Species number	–	–	–	Management type, adjacent land use, width of uncultivated zone, presence of sown flower strips	–	Local	117 releveés of 25 m long on two neighbouring farms of 200 ha each in Yatesbury, Wilthshire, UK.
20	Moser et al. (2002)	Plant and bryophyte species	Species number	Patch area, number of patches	Shape complexity	–	–	–	Local, landscape	Plots of 10 m radius in 10 cells of 120 m^2in each of 30 landscape grids of 600 m^2 Viennese basin, Austria

21	Mountford et al. (1994)	Plants of hedges, verges and field margins	Species number of 17 selected species	Element area	Margin width, length	–	Adjacent land use (Grass, arable land or semi)	–	Local	131 transects of 200 m. in Mare and Middle Fen, Overcote and Cow Fen, Swavesey, Cambridgeshire, UK.
22	Oostenbrink et al. (1994)	Birds of wooded banks	Species number	–	Presence of nodes, T and X-crossings or parallel banks	–	–	–	Local	Sites of 25 ha in Twente, The Netherlands
23	De la Peña et al. (2003)	Small mammals	Species number, diversity and composition (Shannon, equitability, Simpson's index)	Woodlot density, length hedges/ha		Intensification gradient (open to high hedge connectivity)	–	–	Local, landscape	12 bocage study sites of 1 km^2 of different agricultural intensification in Brittanny, France
24	Petit and Usher (1998)	Ground beetles (Carabidae, Coleoptera) of wooded banks	Species number, species diversity and species composition	–	–	–	Grazing intensity	–	Local	700 ha: transects with 43 woody habitats in West Lothian district, Scotland, UK.
25	Ouin and Burel (2002)	Butterflies of herbaceous elements	Shannon–Wiever index, evenness index, Simpson index	Linear uncultivated area, non-linear uncultivated area within landscapes	–	Grain size, mean distance to nearest neighbour	–	–	Landscape	Five hedge row network (bocage) landscapes (0.09 to 0.42 km^2) in Brittany, France

Table 1. Continued.

Study No.	Author(s)	Species	Biodiversity measure	Green veining area	Spatial config (local)	Spatial config (landscape)	Management intensity (local)	Management intensity (landscape)	Scale	Study area
26	Saarinen (2002)	Butterflies of field margins	Species number, relative species abundance, species diversity	–	–	–	Traditional or intensive management on adjacent fields	–	Local	Field margins (430–490-m along 17 meadow, hey and cereal fields in 2 study areas in Finland
27	Schaffers (2002)	(vascular) plants of road verges	Species number	–	Perimeter–area ratio	–	Mowing frequency, hay removal	–	Local	74 plots of 25 m^2 in roadside verges across the Netherlands
28	Siriwardena et al. (2000)	Farmland birds	Species number	–	–	–	–	Crop type	Landscape	10 km square grids of agricultural land in the UK.
29	Snoo and van der Poll (1999)	Monocotyledonous and dicotyledonous plants of ditch banks	Species number	–	–	–	Spraying on adjacent crop	–	Local	Strips of 75×1 m ditch banks along three crops in the Haarlemmer-meer-polder, the Netherlands
30	Sparks and Parish (1995)	Butterflies of field margins	Species number	–	Boundary width	–	Adjacent land use (arable land, grassland or intermediate), number of pesticide and herbicide applications	–	Local	131 transects of 200 m surveyed in verges, margins and along ditches in Swavesey fens, Cambridgeshire, UK.

31	Steffan-Dewenter and Tscharntke (2000)	Butterflies of calcareous grassland margins	Species number of functional groups	<u>Margin area</u>	Habitat isolation	–	–	–	Local	33 calcareous grassland (300–76000 m^2) in Southern Lower Saxony, Germany
32	van Strien (1991)	Plant species of ditch banks	Species number	–	–	–	<u>Ditch cleaning frequency</u> and method, amount of mud dressing, nitrogen supply and adj. land use (meadow / pasture)	–	Local	300 plots in ditch banks on 100 dairy farms in the Netherlands
33	van Strien et al. (1989)	Plant species of ditch banks	Species number and number of quality index species, nature-value index	–	–	–	<u>Adjacent land use, nitrogen supply</u>	–	Local	220 ditch banks on 100 farms of constant management of adjacent fields in the Netherlands
34	Tscharntke et al. (1998)	Predators/ parasitoids of bees and wasps of field margins	Species number	–	<u>Distance to nearest grassland habitat</u>	–	–	–	Local	42 island of four plant pots in cleared agricultural landscape Göttingen, Germany
35	Twisk et al. (2003)	Submersed, floating and emergent plants in ditches	Species number and nature values index	–	<u>Ditch width</u>	–	<u>Management type, nitrogen and phosphate supply (on adj. field)</u>	–	Local	123 sections of 2 × 15 m in 240 ditches in 84 dairy farms in peat areas in the Netherlands

Table 1. Continued.

Study No.	Author(s)	Species	Biodiversity measure	Green veining area	Spatial config (local)	Spatial config (landscape)	Management intensity (local)	Management intensity (landscape)	Scale	Study area
36	Wagner and Edwards (2001)	Plants of different habitat types	Specificity of each taxon	<u>Patch area</u>	<u>Circularity</u>	–	–	–	Local	0.23 km^2, 20 quadrates of 1 m^2 in each of 42 landscape elements in Luzerne canton, Switzerland
37	Weibull et al. (2001)	Butterflies	Species diversity (Shannon–Wiener, Simpson's and evenness index)	–	–		–	Farm type (organic vs. conventional)	Farm landscape	Small scale 400 m grids, large scale 5 km grids in central Sweden
38	Wickramasinghe et al. (2003)	Bat species	Species number	–	–	–	–	<u>Farm type (organic vs. conventional)</u>	Farm	Observations in woodland, water, pastures and arable land on 24 pairs of farms in Southern England and Wales, UK.
39	Zechmeister and Moser (2001)	Bryophytes	Number of threatened species	–	–	–	–	<u>Hemerobic states</u>	Local, landscape	Substrate – (1–4 m^2), habitat – (10 m radius circle) and landscape grids (600 m^2) in the Viennese basin and in the Alp region, Austria

Underlined parameters had a significant effect on the diversity of the studied species group(s).
config = configuration.

Table 2. Number of reviewed studies that analysed and that found effects of amount, spatial configuration and management intensity of green veining at a local scale and at a farm or landscape level.

Parameter analysed	Scale	Analysed in literature studies	Count	Significant effects found	Count
Area	Local	17, 20, 21, 31, 36	5	17, 20, 21, 31, 36	5
	Farm/landscape	1, 2, 9, 10, 11, 14, 20, 23, 25	9	1, 2, 9, 11, 14, 20, 25	7
Spatial configuration	Local	1, 8, 9, 13, 20, 21, 22, 27, 30, 31, 34,35, 36	13	1, 8, 9, 13, 20, 21, 22, 27, 30, 34, 35, 36	12
	Farm/landscape	4, 8, 9, 23, 25	5	8, 9, 25	3
Management intensity	Local	1, 3, 5, 8, 12, 13, 15, 16, 18, 19, 21, 24, 26, 27, 29, 30, 32, 33, 35	19	1, 3, 5, 8, 12, 13, 15, 18, 19, 24, 26, 27, 29, 32, 33, 35	16
	Farm/landscape	3, 6, 7, 10, 28, 37, 38, 39	8	3, 6, 7, 10, 28, 38, 39	7

The numbers refer to the studies listed in Table 1.

Table 3. Overview of reviewed studies that quantified the relation between biodiversity and amount, spatial configuration or management intensity of green veining.

Study	Species	Effects	Type of effect
Spatial configuration			
17	Plants	Area (width) of patch	Saturating
31	Butterflies	Area of patch	Saturating
1	Spiders	Width of patch	Saturating
34	Invertebrates	Isolation of patch	Linear
11	Farmland birds	Percentage of farm wood	Linear
11	Farmland birds	Hedgerow density	Optimum
14	Woodland birds	Percentage of woodland	Saturating
Management intensity			
39	Bryophytes	Hemerobic states	Exponential

The numbers refer to the studies listed in Table 1.

Table 4. Overview of number of reviewed literature that studied the effect of amount, spatial configuration and management intensity of green veining on biodiversity at a local or farm/landscape scale: For each of these parameter types the number of studies focussing on these parameters and (between brackets) the number of studies that found significant effects of these parameters are given, categorised by (a) studied species group and (b) by used diversity measure.

		Area local	Area farm/ landscape	Spatial configuration local	Spatial configuration landscape	Management local	Management landscape	Total no. studies
A	Plants	4 (4)	1 (1)	7 (7)	1 (1)	14 (12)	2 (2)	17
	Invertebrates	1 (1)	4 (3)	5 (4)	3 (2)	7 (5)	3 (2)	15
	Mammals	0 (0)	1 (0)	0 (0)	1 (0)	0 (0)	2 (2)	2
	Birds	0 (0)	3 (3)	1 (1)	0 (0)	0 (0)	3 (3)	6
B	Species number	4 (4)	8 (5)	12 (10)	3 (1)	17 (14)	6 (6)	33
	Diversity	0 (0)	3 (2)	1 (0)	4 (2)	4 (4)	3 (2)	10
	Composition	0 (0)	1 (1)	1 (1)	2 (1)	2 (2)	0 (0)	4
	Nature value	1 (1)	0 (0)	2 (2)	0 (0)	2 (2)	0 (0)	3
	Total no. studies	5	9	13	5	19	8	39

The numbers refer to the studies listed in Table 1.

Spatial configuration of single landscape elements

Twelve out of thirteen studies found effects of spatial configuration of single elements on biodiversity (Table 2). Despite the relative higher importance for plants of width compared to length for plants within a buffer zone found in study 17, two studies (8, 21) found effects of the length of linear elements on plants. Five studies supported the importance of width of linear elements on the number of spiders, plants and butterflies (study 1, 13, 21, 30 and 35). More qualitative results were only found in literature from the USA, where Spackman and Hughes (1995) concluded that 90% of streamside plant species were present if streamside width was at least 10–30 m wide. These results indicate that length is a substitute for area in green veining networks while width adds a new component to area, referring to shape. Indeed, the complexity of the shape or perimeter–area ratio increases biodiversity of green veining (study 20, 27). In study 36, plant diversity was reduced by increasing circularity of patches, but here agricultural patches were also included, so that most species were found in the linear elements. More complex shapes and linear elements could lead to higher diversity because more ecotone habitat is then available, fulfilling habitat demands of species of several vegetation types (Dabrowska 1995). On the other hand, interior species might be lost in linear elements and population density of any species is likely to be lower in elements if their linearity increases (van Langevelde and Grashof-Bokdam in preparation). This could explain why study 22 found higher bird species numbers in wooded banks with nodes, or with X or T-crossings. Forman and Baudry (1984) have unpublished evidence of higher species number of forest herbs in intersections of hedgerows in New Jersey, while Constant et al. (1976) showed this effect for bird species. Also in the USA, Riffell and Gutzwiller (1996) found higher plant species richness in X-shaped intersections of fencerows compared to T or L-shaped ones.

Diversity in green veining can also be affected by isolation of a specific landscape element in relation to other elements or in relation to nature areas that can act as population sources, but isolation is only studied in three studies. Study 9 revealed that less benthic Chiromidae in hedges are found at larger distances from the nearest stream, while more predatory species of bees and wasps were found in field margins closer to the nearest chalk grasslands (study 34). Study 31 could not find an affect of distance to nearest grasslands on butterfly diversity in herbaceous linear elements, however, if studied together with area. In this case, patch area seems to affect butterflies more than isolation.

Spatial configuration of green veining at the landscape scale

Three out of five studies found effects of the spatial configuration of green veining or of the spatial structure of the landscape on species diversity (Table 2). Study 4 and 25 focussed on mean margin width and on mean distance to the nearest element, which in fact are local isolation indices averaged for the whole landscape. Study 8 and 25 took grain size into account, which refers to the mean field size in the area. Study 9 used three landscapes differing in 'field mosaic', also referring to increasing field size leading to a lower landscape complexity and higher degradation of the network of woodland, hedges and streams. Smaller field sizes indicate, indirectly, a higher density and connectivity of green veining elements, but in these studies no direct indices of green veining connectivity were used in the analysis. Study 23 found no effect of the intensification gradient of several landscapes on small mammal diversity or composition, although in this gradient low intensification was, among other landscape parameters, measured by parameters directly referring to landscape structure like openness and hedge connectivity. Openness was computed as the average distance between the different landscape elements, while hedge connectivity was measured as the total number of connections between hedges per km^2. Unfortunately, species number or diversity was not directly tested against these parameters.

Management intensity of single landscape elements

Effects of management intensity of green veining elements have been studied in 19 of the reviewed studies, while 16 of them found significant effects (Table 2). Management intensity in these studies comprises both management intensity of the elements themselves as well as adjacent land use. Management intensity of the elements themselves concerns for instance mowing, which appears to have different effects on different species groups. For example, mowing of field margins and leaving the cut material on the surface enhanced spider richness (study 5), while mowing frequency and hay removal was beneficial for plant diversity in study 27, whereas study 8 found no effects of mowing on plant composition. Crushing and ditch cleaning however, decreased plant diversity in field and ditch margins (study 8 and 32). Intensive grazing has been found to decrease diversity of plants and invertebrates in woody elements and field margins (study 8 and 24). In general, more intense management seems to decrease plant biodiversity in green veining elements (study 13 and 26). However, some management (coppicing, gapping up) can be beneficial for plant biodiversity because of increased light conditions (study 19).

In addition to mechanical management, biodiversity can also be affected by addition of nutrients, pesticides or herbicides. Fertilisation will mostly be applied on adjacent agricultural fields, but pesticides and herbicides are often applied locally on field margins. Negative effects of nitrogen or phosphate input have been found in 5 out of 6 studies, on plant species number or on nature value in field margins, ditch banks and hedges and on carabid diversity in hedges (3, 15, 18, 33 and 35). Study 32 did not find effects of nitrogen on plant number in ditch banks. Study 32 indicated that species richness increases significantly if total nitrogen input is reduced to less than 200 kg/ha/yr. Experiments on grasslands indicated that plant diversity was only increased if no fertiliser was added at all. Reducing the level of the commonly used 110 N kg/ha/yr had no effect (Kleijn and Snoeijing 1997).

Negative effects of herbicide or pesticide applications have been shown on plant richness (study 29), but other studies did not find effects on spiders, butterflies or plants (study 5, 15, 30). Herbicides may enhance annual weed species and in this way reduce plant diversity (Le Coeur et al. 2002). The different results could be caused by the spot-wise application of herbicides. Another possible explanation is the influence of exposure to drift of such compounds in the past (Kleijn and Snoeijing 1997). An indirect way to reduce drift of fertiliser, herbicides or pesticides into green veining is to create an uncultivated zone along the crop, but this has not proven to increase diversity of plants or insects (study 12, 18, 19), while in study 19 sowing a strip of flowers along the crop did increase plant species richness in field margins.

An indirect index of the total pressure of mechanical management, fertilisers, herbicides or pesticides is to compare conventionally managed field margins with margins that are under nature management regimes. Study 16 found that species diversity of hover flies and bees was slightly higher on field margins with management agreements compared with diversity of fields without agreements, but plant diversity was not enhanced by these agreements. For a review of management agreements, mostly on agricultural fields and grasslands, see Kleijn and Sutherland (2003).

Effects of management intensity or management type have been found for plants and butterflies in three studies (13, 26, 35). Another indirect measurement of management intensity on a local level is the type of adjacent field use, which was found to affect species diversity of plants and invertebrates in four studies (12, 13, 18, 33). The results of these studies imply that the intensity of land use (mechanical pressure and high application of nitrogen) is reflected by the type of adjacent land use, and that land use intensity is related to disturbance frequency of adjacent land. According to Le Coeur et al. (2002), margins adjacent to cropped fields are e.g. more likely to receive fertiliser or pesticide misplacement or mechanical disturbance by machinery than those along permanent grassland. This was supported by the found effects of disturbance frequency on spider diversity in study 1.

Management intensity at the landscape scale

Seven out of eight studies found effects of management intensity on species diversity at the landscape level. In four studies land use intensity has been indicated by farming system (conventional or organic). Organic farming is often related to less intensive management, which in three cases increased biodiversity of plants, butterflies and bats of green veining elements. It is remarkable that study 10 found higher butterfly diversity in field margins on organic farms, while study 37 could not find effects of farm type on butterfly diversity. Weibull et al. (2001) explained this by the fact that in study 10 differences were explained by higher frequency of clover leys on organic farms. The study of Weibull et al. corrected for this factor in paring the farms. Study 3 and 38 found effects of farm type on plant and bat diversity, respectively. These results are in agreement with the higher diversity of birds, invertebrates and mammals found in less intensively used agricultural areas in study 6. Also study 39 found increased bryophyte diversity with less intensive management, indicated by hemerobic state. Study 7 and 28 indicate that farmland birds prefer certain crop types.

Synthesis

In this study, we reviewed empirical literature on effects of spatial structure and/or management intensity of green veining elements on the biodiversity in these elements in European agricultural landscapes. Although we systematically searched digital databases from 1994 to 2003, some specific literature may have been missed. Many studies were omitted, mostly because they were not focussing on species diversity, not on green veining or on landscapes outside our selected region. In the selected papers, spatial structure was studied by area or configuration (width, length, shape) of single elements on a local scale, and by the amount of green veining (density) and spatial configuration of elements on a landscape scale. Management intensity was studied by various aspects of management intensity of the green veining elements themselves or by adjacent land use on a local scale and by land use intensity on a landscape scale. First, we will revisit our research questions mentioned in the introduction. Next, we will try to quantify spatial and management demands of green veining biodiversity. Finally, we will discuss consequences for future research.

Does biodiversity of green veining follow the species–area relation?

Our main question was whether biodiversity would increase with amount of green veining following a species–area curve. Five studies found area effects of individual green veining elements, while seven out of nine studies found effects of amount of green veining on species diversity on a landscape scale (Table 2). However, only two of these studies tested the shape of this curve (Table 3). Study 11 found a linear relation between farm bird diversity and percentage of farm wood on a landscape level, but still showed a tendency to plateau at higher levels of farm wood coverage. This diversion from the species–area curve could be explained by the fact that area of farm wood does not comprise all habitat types of the studied bird species. In the same study, farm bird diversity showed an optimum relation with hegerow density. This was explained by the fact that some farmland species might prefer open landscapes while others prefer a more closed landscape (Fuller et al. 2001). Study 14 indeed found a species–area curve for the relation between number of woodland birds and percentage of woodland area. Here it is plausible that woodland area comprises the complete habitat of woodland birds. But in general we found too few studies quantifying the species–area relation in green veining to answer our research question or to define thresholds for green veining area for diversity of specific species groups.

Can increased connectivity or decreasing management intensity lower the needed amount of green veining?

Our second question was whether the needed amount of green veining to derive a certain level of biodiversity was less if the spatial connectivity was increased or if management of the green veining was less intensive. Focussing on spatial effects, study 17 reveals that, for plant species, width of linear elements is the most important factor in the species–area relation. Indeed, spider diversity appeared to follow a saturating curve against habitat width, following the species–area curve (Table 3). Five other studies also successfully found a positive effect of the width of linear elements. Together with the found effects of perimeter–area ratio, nodes, T, L and X crossings and parallel hedges on species diversity (study 22, 27), the found effects of element width may indicate that species number or diversity is limited in linear elements by the lack of core habitat, or by high edge effects from adjacent land use. They may also indicate that in more complex linearly shaped elements more habitat within home-range is available than in habitat arranged in a straight line (van Langevelde and Grashof-Bokdam, unpublished model results). Besides the shape of the green veining element itself, also isolation affected bioversity of these elements in two out of three studies (9, 34), showing a linear decrease in study 34 (Table 3). In this study, isolation has been measured as the distance to possible source populations. Populations in green veining elements may function as sink populations that are depending on recolonisation from source populations in larger and more stable populations in nature reserves (Foppen et al. 2000). Only few studies focussed on spatial effects on the landscape scale, while two used mean values of width or isolation of green veining elements. Three other studies (8, 9 and 25) compared several landscapes differing in grain size, which probably is correlated heavily to green veining density and also to spatial structure of elements that do not belong to the green veining. Therefore it is not clear in these studies whether, or to what extent, connectivity of landscape elements affects species diversity in green veining. Neither have spatial effects on a landscape scale been quantified in one of these studies.

When we focus on effects of management intensity in individual green veining elements, it becomes clear that some management may increase species diversity, if it removes biomass or increases light availability, but intensive management reduces diversity. This implies that biodiversity forms an optimum curve against management intensity, but no evidence was found for this. Nitrogen and phosphate supply reduce species diversity in green veining in all studied cases, while herbicide application does not reduce diversity in all studies. The found effects of adjacent land use could be related to nitrogen supply, but also to herbicide or pesticide use or to mechanical management intensity. This lack of causal relations argues against the use of these indirect management indices. On a landscape level, land use intensity was measured by farm type, crop type and hemerobic stages or landscapes of different management intensity. The effects of hemerobic states on bryophytes (study 39) showed an exponential curve (Table 3). However, all these indices are indirect indices and difficult to translate to direct indices of management intensity.

These results make clear that, although many studies assessed the effect of spatial configuration or management intensity on biodiversity, the found relations are hardly quantified. Also, definition of land use intensity varies considerably among studies, which makes it difficult to make unequivocal conclusions. Furthermore, none of the reviewed studies assessed how spatial configuration or management intensity changes the relation between biodiversity and amount of green veining, which makes it impossible to assess our second question.

Relative importance of management intensity and spatial configuration

In the reviewed studies, effects of management intensity were studied more often (27 studies) compared to effects of spatial configuration of habitat (19 studies), but significant effects were only slightly more often found for management intensity (86%) compared to spatial configuration (79%). Only seven out of 39 reviewed studies (studies 1, 8, 9, 13, 21, 27, 30 and 35) have compared the effect of both management intensity and spatial structure of green veining elements on biodiversity, all on the local scale. On a landscape scale, often landscapes have been compared that differ in management intensity as well as in landscape complexity, which makes it difficult to distinguish whether differences in biodiversity can be attributed to management intensity or to spatial structure. For instance, studies 6, 8, 9 and 25 all studied bocage landscapes in Brittany. Study 8 attributed changes in biodiversity on a landscape scale to grain size, while the studies 9 and 25 explained these changes by differences in field mosaic and/or to mean isolation of these elements within the landscape and study 6 attributed them to changes in land use intensity. The same problem arises when comparing conventional and organic farms (study 3, 10, 37, 38) or when classifying landscapes into hemerobic states (study 39).

Therefore, both spatial structure of green veining as well as management intensity of the green veining seem to be important to biodiversity, but there is no strong evidence that one of the parameters is most important.

Matching the temporal and spatial scale of species and diversity indices

According to Baudry et al. (2000b), habitat quality and physical parameters are variable at the spatial scale of the agricultural field, whereas spatial parameters are defined at the landscape level. However, some other abiotic factors like hydrology and atmospheric deposition, are also defined at the landscape level. The species composition at the local scale can be viewed as a subset of the species pool at a regional scale (Olff and Ritchie 2002). Processes and parameters at a regional scale can therefore affect species richness at a local level, but it is less likely that processes at the local level affect species at a regional level. In the reviewed studies, management intensity as well as area and spatial configuration were mostly studied at the level of individual landscape elements (Table 2).

The reason for this focus on the local scale could be explained by the species under study: a large part of the studies concentrated on plant and invertebrate species (Table 4). Although some insects, butterflies or spiders are quite mobile and mobility differs considerably between different species, these species are smaller and in general less mobile than larger species like birds or mammals. For smaller species management intensity and spatial structure of green veining at the local scale could be more relevant, while the same parameters at the farm or landscape scale could be more relevant for larger species. However, plants and invertebrates are not more often affected at the local level than at the landscape level (Table 4). For these species, indeed processes at the landscape level are evenly important than those at the local level. On the other hand, mammals and birds were studied in so few cases, mostly at the landscape level (Table 4), that we cannot conclude that these species are mainly affected by parameters at the landscape level. Study 6 was the only study that compared several species groups at the landscape level, but it showed no clear relation between the mobility of studied species groups and the scale at which they are affected by management intensity or spatial structure of green veining. Several studies do not only take spatial structure of green veining into account, but also that of agricultural fields. For species that are limited to green veining structures, other habitats should not be taken into account. On the other hand, some species like farmland birds are not restricted to green veining areas, but also use agricultural fields for e.g. foraging. These species experience the landscape as a habitat mosaic instead of patches of habitat and non-habitat. Especially for larger, mobile species as mammals or birds this may be the case, and this could be the reason why we did not find many studies on the relation between diversity of these species and green veining features. For these species, heterogeneity of landscapes is probably a more often used parameter (Benton et al. 2003). Indeed, Atauri and de Lucio (2001) found in Mediterranean landscapes that richness of amphibians and reptiles was more related to abundance of certain land-use types, whilst landscape heterogeneity explained the richness of birds and butterflies better. Another problem with larger species is that there are, for instance, much less bat species than invertebrate species. This limits the possibilities of finding effects on species number of larger species in advance.

Considering time scales, some insect species having several generations per year may respond much more quickly to changing landscapes than for instance long-lived plant species (Ruremonde and Kalkhoven 1991; Grashof-Bokdam 1997; Chamberlain et al. 2000; di Giulio et al. 2001). For the latter species, the green veining in the past may affect species diversity more than the current network (Le Coeur et al. 2002).

Besides the spatial or time scale, the used measurement of biodiversity in the reviewed studies also influences the possibility of finding effects of green veining management intensity and spatial structure. First, most studies concern only one species group, while conclusions of this type of research should be translated into effects on overall biodiversity. As it is impossible to consider all species of green veining structures, it is important to select indicative species that are representative to different habitat types, spatial and time scales. Also it could be important to select species that are indicative for certain landscape types like those of hedges in the French bocage or species of ditches in the Dutch polder landscapes. The identity of these regions depends greatly on the presence of specific green veining structures and the accompanying regionally distinctive species. Indicator species of specific regions should be more or less limited to these regions, preferably show a downward trend there and should be relatively rare in these regions (Wamelink 2002). Furthermore, the way in which biodiversity is measured can influence the results of the reviewed studies. The most often used (Table 4), and easy to interpret measurement is species number, also referred to as species richness. Species diversity (e.g. Shannon and Simpson diversity index) is composed of the number of species, which is highly affected by rare species, and by the abundance of each species (evenness), which is highly affected by dominant species (Hill 1973; Peet 1974; Magurran 1988). However, a community of many common species can result in an evenly high score as a community of a few rare species (Harper and Hawksworth 1995). Sorensen community and Squires' overlapping index take into account whether species are being replaced by other species, while species quality scores or nature value indices value certain species more than others

(Painter 1999). Specificity is a measurement that values sessile species more if they are restricted to a specific habitat type. This characteristic may be important, as nature policy may aim to preserve green veining for species that cannot survive elsewhere. In general, however, we can state the importance of the use the same simple and comparable indices in biodiversity studies, because the great variety of indices makes it quite hard to translate results of different studies into recurring patterns and rules of thumb.

Consequences for future research

The reviewed studies were carried out to demonstrate significant effects of amount, management intensity or spatial structure of green veining on biodiversity. However, effects of spatial arrangement are underexposed and found effects have not been quantified into minimum amount demands needed to achieve a given level of biodiversity, neither has been shown how these minimum demands are affected by management intensity or spatial configuration of green veining. The data used in the reviewed studies might however provide the relevant information to answer these questions, but this is not possible to conclude from the papers. Also large-scale monitoring surveys like the Countryside Survey carried out in the UK (Haines-Young et al. 2000) and the Small Biotope project of Denmark (Brandt et al. 2002) probably contain many appropriate data base to relate species richness to amount, connectivity and management intensity of elements. In the GREENVEINS project (Bugter 2003), data in seven European countries on effects of land use intensity and green veining structure are being collected and analysed in a quantitative way in order to identify ‘vulnerability zones’; ranges in land use intensity and green veining structure where a small deterioration of conditions would cause a large collapse of biodiversity.

We suggest revisiting existing data or collecting new empirical data by which presence or abundance of individual indicator species as well as overall number of species can be plotted against amount of specific habitat elements and against total amount of green veining. For this, several landscapes should be surveyed that vary in amount, say 5, 10 and 20% of the green veining type under focus. Several duplicate landscapes should be surveyed which represent the equal percentages of green veining, but with higher habitat quality, higher spatial configuration or with lower disturbance regime. This is needed to study the interaction between needed amount of green veining for certain biodiversity levels on the one hand and spatial configuration, habitat quality and disturbance regime on the other hand.

When focussing on the management intensity of green veining elements themselves, direct indices should be used, such as nitrogen or herbicide/pesticide supply on adjacent fields, in stead of indirect ones, such as less or more intensively used landscapes, or organic versus common farms. Direct indices appeared to correlate stronger to biodiversity and they lead to better insight in causal processes. When focussing on effects of disturbance regime, the relation between different crop types on adjacent fields and their accompanying rotation frequency should be determined. Few European studies focussed on the role of amount of spatial structure of green veining on biodiversity. We identify a gap in studies focussing on effects of spatial arrangement of green veining structure on a local and especially on a landscape scale, using direct indices that can be distinguished from management intensity or area effects.

In future empirical studies, we stress the priority of species indicator groups representing the identity of a landscape, using simple species number measurements that are easy to compare as well as indices that consider the composition of a group of species representing this identity. Furthermore, in addition to small and relatively immobile species such as plants and invertebrates living on a local scale, larger and more mobile species such as small mammals and birds should be taken into account for conclusions relevant at the landscape level. Many of these species are not restricted to green veining elements but use a mosaic of habitat types (see Benton et al. 2003). Also, the selected species should be sensitive to the spatial and management parameters under focus. This implies that the selected species should represent species groups of different mobility (dispersal distance, ability to bridge gaps) in order to study spatial effects, groups of different nutrient demands to define the effect of nitrogen application, and groups with different abilities related to disturbance regime (seed banks, generation time, longevity).

In field situations, it is very hard to find a set of landscapes that match the criteria mentioned above for spatial and management parameters, especially since landscapes with higher spatial connectivity appeared to be mostly combined with landscapes having lower management intensity. It is also very time consuming to survey all these landscapes during several years and it is very hard to get information on the management intensity of green veining elements of (private) owners. Modelling exercises will therefore be needed to investigate the effect of changing conditions of amount, management intensity and spatial arrangement of green veining, represented by one or a few parameters and their interactions, on green veining biodiversity. Moreover, such exercises can extrapolate the results of fieldwork to all possible combinations of green veining area, management intensity and spatial configuration and can provide hypotheses that can be tested with small-scale experiments. Such an approach is valid for either simple relations between overall biodiversity and general landscape indices, as well as for complex relations between diversity of indicator species and indices of specific landscape features. Especially the interaction between spatial structure and management intensity is very hard to study in the field and will have to be hypothesised for a large part by modelling. A good example of such an approach is the model study of plant species of ditch banks of Geertsema (2002) that revealed the relative importance of spatial clustering of ditch banks under management agreement for population survival probability of plant species, compared to habitat quality and disturbance frequency of the ditch banks. To get insight in causal relations, such models should be supported by field data, should use spatially explicit configurations of green veining and should translate management intensity into changes in habitat quality and disturbance. Also the spatial and temporal scales of the simulations should fit to the mobility and life history traits of the studied species.

In this review, we limited or scope to species that are restricted to green veining structures. To evaluate the overall biodiversity of agricultural landscapes, also species will have to be considered that depend on agricultural fields or use several types of landscape elements and experience the landscape as a mosaic of habitat types. Basically, the same line of research as described above will be needed to predict biodiversity of landscape mosaics. However, spatial parameters like isolation will have to be redefined as habitat is often not clearly separated by non-habitat in such landscape mosaics. The combination of future field, experimental and modelling research, concentrating on the posed hypotheses and gaps in knowledge may enable us to search for optimal combinations of type, amount, spatial configuration and management intensity of green veining needed to reach desired biodiversity levels in the agricultural landscapes of Europe.

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