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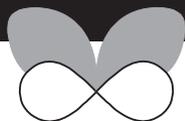
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# Susceptibility of pollinators to ongoing landscape changes depends on landscape history

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## ABSTRACT

**Aim** Pollinators play an important role in ecosystem functioning, affecting also crop production. Their decline may hence lead to serious ecological and economic impacts, making it essential to understand the processes that drive pollinator shifts in space and time. Land-use changes are thought to be one of the most important drivers of pollinators' loss, and there is increasing investment on pollinator-friendly landscape management. However, it is still unclear whether landscape history of a given region determines how pollinator communities respond to further landscape modification.

**Location** The Netherlands.

**Methods** Using geographically explicit historical landscape and pollinator data from the Netherlands, we evaluated how species richness changes of three important pollinator groups (bees, hoverflies and butterflies) are affected by landscape changes related to habitat composition, fragmentation and species spillover potential and whether such effects depend on the historical characteristics of the landscape.

**Results** The effect of landscape changes varied between different pollinator groups. While bumblebee richness benefited from increases in edges between managed and natural systems, other bees benefited from increases in landscape heterogeneity and hoverfly richness was fairly resistant to land-use changes. We found that for the majority of the pollinators past landscape characteristics conditioned, the more recent pollinator richness changes. Landscapes that historically had more suitable habitat were more susceptible to display hoverfly declines (caused by drivers not considered in this study). Landscapes that historically had greater spillover potential were more likely to suffer butterfly richness declines and the bumblebee assemblages were more susceptible to the effects of fragmentation.

**Main conclusions** The diversity of responses of the pollinator groups suggest that multispecies approaches that take group-specific responses to land-use change into account are highly valuable. These findings emphasize the limited value of a one-size-fits-all biodiversity conservation measure and highlight the importance of considering landscape history when planning biodiversity conservation actions.

## Keywords

Bees, biodiversity loss, butterflies, extinction debt, habitat composition, fragmentation and configuration, hoverflies.

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## INTRODUCTION

There is increasing concern about the status and trends of pollinators across the globe (Potts *et al.*, 2010; Winfree, 2013). Pollinators play an important role for the functioning of ecosystems and are essential for crop production (Garibaldi *et al.*, 2013; Vanbergen and The Insect Pollinators Initiative, 2013). However, they have suffered accentuated declines over the past century (Biesmeijer *et al.*, 2006; Carvalheiro *et al.*, 2013), only showing some subtle signs of recovery in some regions in recent years (Carvalheiro *et al.*, 2013). Understanding the processes that have led to shifts in pollinator diversity is essential to develop better conservation measures that stop declines and restore pollinator communities.

While there is a great diversity of potential drivers of pollinator loss (Potts *et al.*, 2010), global land-use intensification and landscape fragmentation are among the prime suspects (Winfree *et al.*, 2009). Because historical data are lacking for most regions and taxa, most studies that aim to evaluate the impacts of landscape changes compare current landscapes that vary in landscape features (Brosi *et al.*, 2008; e.g. Uehara-Prado & Freitas, 2009). Most of these studies assess shifts at small spatial scales and focus on a limited type of landscapes (Benedick *et al.*, 2006; Taki *et al.*, 2010). Studies using a space-for-time substitution approach assume that comparing recent landscapes that differ in fragmentation and composition represents the processes that have taken place in a specific location across time. However, this is unlikely to be generally true, as the landscape conditions before changes occurred (hereafter referred to as the 'original state of the landscape') could be driving the responses of the remaining biodiversity (Kuussaari *et al.*, 2009). For example, locations that have been subjected to rapid historical landscape changes may have species communities more susceptible to extinctions, presenting also an extinction debt (delayed loss of biodiversity after habitat loss and/or fragmentation events) (Tilman *et al.*, 1994), than locations that have experienced changes at slower pace through time. Therefore, the loss of a given fraction of natural habitat may have a stronger impact on locations that were already deprived of natural habitat. Moreover, (re)colonization patterns that determine in situ biodiversity may also depend on the original state of the landscape and such effects might then not be apparent in short-term studies. Evaluating whether and to what extent landscape history conditions species responses to changes in the landscape characteristics is therefore crucial for the improvement of biodiversity conservation actions.

Given that different pollinator groups (e.g. bees, hoverflies, butterflies) differ in their needs for habitat and feeding resources and also in their life history and dispersal capabilities (Fründ *et al.*, 2010), it is expected that the responses of pollinators to fragmentation and habitat loss will vary between groups. However, landscape management practices that aimed to slow biodiversity loss are usually based on the responses of single species groups (Fleishman *et al.*, 2000), suggesting a one-size-fits-all type of biodiversity conservation

measure, an approach that has been challenged by recent biodiversity conservation studies (Maes & Dyck, 2005; Gerlach *et al.*, 2013).

Different hypotheses concerning the effect of landscape modification on pollinators have been proposed (Tscharrntke *et al.*, 2012). However, these are based on evidence from space-for-time substitution studies (e.g. Hendrickx *et al.*, 2007). In this study, using historical and current landscape and pollinator information, and thus not relying on the space-for-time substitution, we analyse the impacts that changes in habitat composition and fragmentation during the last 100 years in the Netherlands have had on the species richness changes of the different pollinator groups. We further analyse whether these impacts are similar across pollinator groups and whether landscape history (i.e. landscape conditions before changes occurred) conditions the species responses to these impacts.

Landscapes with higher amount of suitable habitat and higher diversity of habitats are likely to present higher diversity of food resources and contain a more diverse pollinator assemblage (e.g.  $\beta$ -diversity hypothesis; see Tscharrntke *et al.*, 2012). Therefore, it is expected that increases in habitat heterogeneity and in the amount of suitable habitat are positively related to increases in pollinator species richness (hypothesis 1). Moreover, while landscape fragmentation is generally perceived as having negative effects on biodiversity (Potts *et al.*, 2010) (hypothesis 2), the increase in length of edges, specially between (semi) natural and managed systems, may increase the interactions between organisms and, thus, increase the functional connectivity, thus helping to maintain high local biodiversity (Bianchi *et al.*, 2006; Kuefler *et al.*, 2010). It is hence expected that the increase in edges between managed and natural land-use classes, a proxy for potential species spill-over effects (dispersal of organisms between patches of different land-use classes) (Blitzer *et al.*, 2012), favours the local species richness (hypothesis 3). Additionally high spatial heterogeneity of communities (at local and landscape scale) may reduce the negative local effects of fragmentation or loss of suitable habitat (e.g. landscape insurance hypotheses; Tscharrntke *et al.*, 2012), making it important to consider interactive effects between different landscape parameters.

## METHODS

### Species data

This study uses data from a previous study of Carvalheiro *et al.* (2013) which has applied a combination of interpolation and extrapolation techniques to species accumulation curves to deal with the unstandardized nature of historical collections and estimated richness changes of three important Dutch pollinator groups (bees, butterflies and hoverflies) for three time comparisons: 1930–1949 vs. 1950–1969 (TC1), 1950–1969 vs. 1970–1989 (TC2) and 1970–1989 vs. 1990–2009 (TC3). In the study of Carvalheiro *et al.* (2013), the bee and hoverfly data were obtained from the European Invertebrate Survey (EIS-

Nederland, <http://www.eis-nederland.nl>) and the butterfly data from the Dutch National Database of Flora and Fauna (NDDFF, [www.ndff.nl](http://www.ndff.nl)). For an in-depth explanation on how species richness changes were calculated and more details about the species richness data and methods, see Carvalheiro *et al.* (2013). The focal area of this study, the Netherlands, has been intensely sampled for biodiversity since the early 19th century and has experienced major well-documented changes in land use (Knol *et al.*, 2004; Hazeu *et al.*, 2010). Here, we used such detailed information on land use and test whether land-use change explains the patterns of pollinator richness changes detected by Carvalheiro *et al.* (2013). As in Carvalheiro *et al.* (2013) the bumblebees (Apidae, Bombini) were separated from other bees (hereafter referred to as non-bumblebees) due to their recognized high vulnerability (Williams & Osborne, 2009) and different trait characteristics (highly social, large bees with a large foraging range). A total of 40 landscapes (10 × 10 km each) for bumblebees, 144 for non-bumblebees, 432 for butterflies and 402 for hoverflies were used with more data corresponding to the most recent time periods (last two periods) (Figure S1 in Supporting Information).

### Land-use data

We obtained land-use data for the years 1900 (at 50 × 50 m resolution), 1960, 1980 and 2008 (each at 25 × 25 m resolution), with a high land-use classification accuracy ranging from 84.8% to 98% (Knol *et al.*, 2004; Hazeu *et al.*, 2010). Based on those land-use maps, for each 10 × 10 km cell ('landscapes') for which we had species richness change values, we calculated land-use changes between the following periods: 1900 vs. 1960 (LP1), 1960 vs. 1980 (LP2) and 1980 vs. 2008 (LP3). We assumed land-use data from LP1, LP2 and LP3 to be representative of the time comparisons TC1, TC2 and TC3, respectively, because most of the species' sampling period was covered by the land-use change period. These time periods are also associated with very different trends in land-use change. During LP1, the Netherlands suffered intensive and rapid habitat loss, while during LP2, there was great agriculture intensification and associated increase in pesticides use (Harms *et al.*, 1987; Geiger *et al.*, 2010). During LP3, there was an increase in investment on conservation measures and agri-environmental schemes (Kleijn & Sutherland, 2003; European Environmental Agency, 2010, 2011). For each time comparison, we calculated several metrics of landscape composition and fragmentation and their changes (explained below).

To standardize land-use type classifications between maps, the land-use classes were reclassified to match the oldest map classes (1900). This resulted in 10 final land-use classes for the four maps (Figure S2; see Table S1). The resulting land-use maps were then used for the extraction of the fragmentation and composition variables for each 10 × 10 km landscape cell as described below.

### Landscape composition and fragmentation metrics

In our study, we identified several landscape variables related to composition and fragmentation mentioned by Tscharrntke *et al.* (2012), which include the ones most commonly used in recently empirical published work (Table S2).

We selected two variables related to habitat composition: the percentage of suitable habitat (PSH) present in each 10 × 10 km cell and the number of land-use classes [patch richness (PR)]. To calculate PSH, land-use suitability values were generated by expert opinion (Vogiatzakis *et al.*, 2015) and were applied equally to all pollinator groups (Table S1). Although these values were not created for the Netherlands but for the United Kingdom, this is the best approximation currently available for the land-use classes in our study area. Following these values, we classified the land-use classes as grassland, moors/peat, deciduous/mixed forest and sandy soils as suitable habitat, and agriculture, coniferous forest, urban, water and swamps as non-suitable habitat. Due to the excessive management of Dutch grasslands (e.g. high fertilizers input), their suitability is likely lower today than it was before the 70s (Oenema *et al.*, 2012). Despite the difference in grassland suitability between periods grassland was always considered suitable as this habitat still has substantial feeding and nesting resources for pollinators in comparison with other agricultural habitats (Hegland *et al.*, 2001; Öckinger & Smith, 2007). In addition, we have at present no objective way to assess grassland suitability change. Agriculture was considered not suitable as in the Netherlands, it mostly refers to highly intensified monocultures. To calculate patch richness (PR), we used the number of land-use classes, and we consider this variable a surrogate for spatial heterogeneity of species assemblages ( $\beta$ -diversity hypothesis; Tscharrntke *et al.*, 2012).

As landscape fragmentation is a complex process, we divided the fragmentation variables into two groups. The first group included two variables representing habitat configuration per se: proximity between suitable habitat patches (proximity) and average weighted mean patch area of suitable habitat patches (PA, where a smaller value represents more fragmentation). The second group included edge density in the total landscape (ED). However, the edges between managed and natural systems may enhance functional connectivity (i.e. edges between differently managed systems) instead of acting as functional barriers (Kuefler *et al.*, 2010) and can be seen as a surrogate for landscape spillover effects. Therefore, we also calculated the edge density between managed and natural systems (ED Man-Nat) and analysed its effects separately from the total edge density. When calculating the edge density between managed and natural systems, we considered the grassland and agriculture classes as (intensively) managed and the moors, peat, the forest types, swamps and sandy soils as (semi-)natural systems. All spatial analyses were carried out in ARCGIS (v10, Esri Redlands, CA, USA). The landscape fragmentation and edge metrics were obtained using FRAGSTATS v4 (McGarigal *et al.*, 2012).

### Statistical analysis

All statistical analyses were carried out in the R platform (R Development Core Team, 2014). For each of the landscape metrics described above, we calculated the land-use changes ( $\Delta$ ) that occurred in each time period (LP1, LP2 and LP3). The land-use change data for each time period were calculated as the ratio between the post-period and the pre-period landscape value (e.g. for LP1, pre-period equals 1900 and post-period equals 1960). To normalize residuals, we log-transformed this land-use change ratio. As we also wanted to test whether the historical characteristics of the landscape conditioned the effect of such land-use changes, we also considered information of the original state of the landscape as a separate variable, hereafter referred to as T1 (i.e. for TC1, we included fragmentation and composition values in 1900; for TC2, the fragmentation and composition values in 1960; and for TC3, the values in 1980). We then analysed the impact of landscape fragmentation and composition on bumblebees, non-bumblebees, butterflies and hoverflies species' richness changes, with linear mixed effects models using the 'LME4' R package (Bates *et al.*, 2014). As we sometimes have data from the same location in more than one time period (see Figure S1), to account for the non-independence of the predictions generated based on the data from a given location and period of time we used the time comparison analysed (TC1, TC2, TC3) and landscape ID (cell location) as random effects.

For all the species groups, we created a general initial model that included all the interactions between the fragmentation and composition variables for the original state (T1) and land-use change values (Table S3). We then selected the most parsimonious model [smallest Bayesian information criterion (BIC)] by applying a model selection procedure using the R package 'MUMIN' (Barton, 2014). The species richness change data were transformed to a log ratio, and the landscape variables were centred and standardized before analyses (*z*-scores; Gelman, 2008). Given that landscapes closer to each other may present similar

species richness changes, we first tested for any spatial auto-correlation using the Moran's *I* test with the R package 'SPDEP' (Bivand, 2014), and overall no significant effects were found (Table S4). After analysis, we confirmed the applicability of our linear mixed effects model to the data as the residuals of fitted models were approximately normally distributed with no indication of over dispersion or heteroscedasticity.

## RESULTS

### Effect of changes in habitat heterogeneity and in the amount of suitable habitat

The increase in habitat diversity (i.e. diversity of land-use classes) positively impacted one pollinator group (Table 1), the non-bumblebees, where richness increased with habitat heterogeneity (Table 1a; Fig. 1a).

Although most landscapes in the Netherlands (our 10 × 10 km cells) have experienced decreases or increases over the last century between -20% and +20% (Figure S3), contrary to expectations, none of the pollinator groups were affected by changes in the amount of suitable habitat (Table 1). However, hoverfly richness changes were conditioned by the amount of suitable habitat in the original landscape (Table 1b): landscapes that contained low amounts of suitable habitat in the original state were more likely to show subsequent species richness increases than landscapes with abundant suitable habitat in the original state (Fig. 1b).

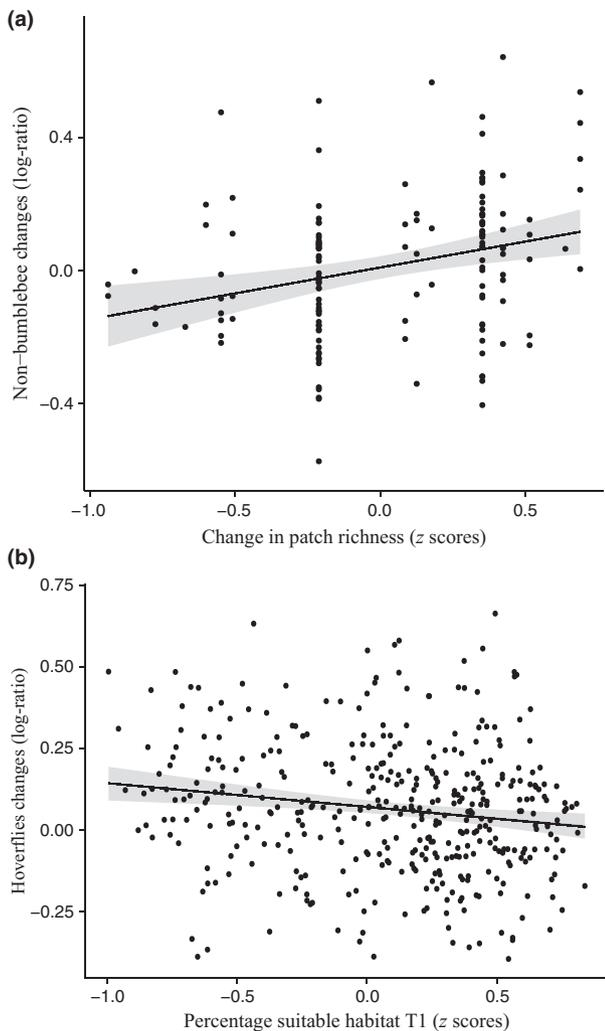
### Effect of changes in landscape fragmentation

The pollinators' responses to fragmentation differed among the different groups. In landscapes that had originally a high spillover potential (i.e. where edge density between managed and natural areas was high in T1), changes in the average patch area had an effect on bumblebees: declines in richness were more accentuated in areas where patch area increased (Table 1c; Fig. 2a). In landscapes with a high average patch

**Table 1** Results of the mixed models analysing the species richness changes as function of landscape composition and fragmentation. Details about the original starting model are presented in Table S3. The final model for each species group analysed was the best model (lowest BIC) after model selection. We also present the second best model and its BIC value for comparison purposes

|                    | Terms                       | Coefficient | SE     | BIC   | 2nd best BIC | 2nd best model                |
|--------------------|-----------------------------|-------------|--------|-------|--------------|-------------------------------|
| (a) Non-bumblebees | $\Delta$ PR                 | 0.1257      | 0.0357 | -23.2 | -22.8        | Null                          |
| (b) Hoverflies     | PSH T1                      | -0.0730     | 0.0230 | -104  | -100.7       | $\Delta$ PA + PSH T1          |
| (c) Bumblebees     | ED Man-Nat T1               | 0.1439      | 0.0914 | 22    | 25           | ED Man-Nat T1 + $\Delta$ PA   |
|                    | $\Delta$ PA                 | -0.0917     | 0.0677 |       |              | + $\Delta$ PA × ED Man-Nat T1 |
|                    | $\Delta$ ED Man-Nat         | 0.2482      | 0.0825 |       |              |                               |
|                    | $\Delta$ PA × ED Man-Nat T1 | -0.4599     | 0.2009 |       |              |                               |
| (d) Butterflies    | ED Man-Nat T1               | -0.0656     | 0.0255 | 22.5  | 22.6         | ED T1                         |

Composition and fragmentation variables descriptors = PR: number of land-use classes in the landscape; ED Man-Nat: edge density between managed and natural habitat; ED: total edge density in the landscape; PA: patch's area; PSH: percentage of suitable habitat in the landscape.  $\Delta$ : change; T1: time 1 or original landscape state. SE = standard error. All two-way combinations of terms were tested, but only the terms included in the two best models are listed.



**Figure 1** The effects of habitat composition on pollinator species richness changes. (a) Effect of habitat heterogeneity ( $\Delta$  PR) on non-bumblebees. Landscapes that increased in heterogeneity presented higher species richness than more homogeneous landscapes; (b) effect of the percentage of suitable habitat on hoverflies. Landscapes with high percentage (T1) presented significantly lower species richness changes than low percentage ones. For all plots, the values of the centred standardized explanatory variables are presented. Grey bands represent the 95% confidence interval.

area, species richness loss was more likely with increases in the density of these edges. Other groups were not significantly affected by changes in fragmentation level (i.e. changes in proximity between patches of suitable habitat or total edge density). However, responses of butterflies to other landscape characteristics (or to other drivers) were conditioned by the original state of fragmentation in the landscape (ED T1, in model 2). Landscapes with higher amount of edges in the original state were significantly more likely to suffer decreases in butterfly species richness (Table 1d; Fig. 2b).

### Effect of changes in the density of edges between managed and natural habitats, a proxy for potential species spillover effects

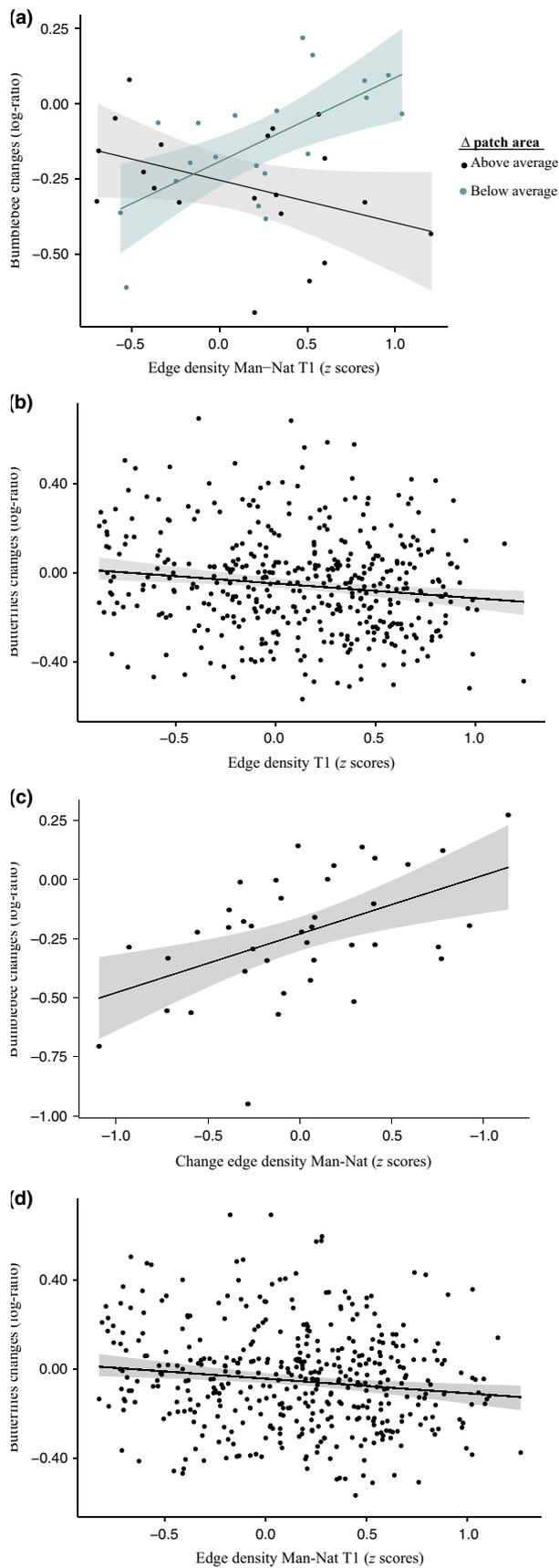
Bumblebees were the only group of pollinators affected by changes in edge density between managed and natural systems (ED Man-Nat; Fig. 2c). Increases in ED Man-Nat led to significant increases in species richness of bumblebees (Table 1c). Moreover, for bumblebees, the effects of fragmentation (i.e. patch area) described above depended on the original density ED Man-Nat (i.e. of edges which potentiate spillover effects). In landscapes with originally high spillover potential, increases in patch area led to more accentuated declines (Fig. 2a). Richness changes in butterflies were also conditioned by the original spillover potential. For this group, species richness increases were more likely to occur in landscapes with originally less edge density between managed and natural systems; conversely, landscapes with originally higher density of these edges were more likely to present species richness declines (Fig. 2d).

## DISCUSSION

Anthropogenic landscape changes are one of the main drivers of biodiversity loss (González-Varo *et al.*, 2013). Most studies evaluating the impacts of such changes focus on a limited number of species and compare current landscapes with different levels of habitat modification, mostly comparing extremes (i.e. use space-for-time substitution) (Winfree, 2013). While this approach allowed the development of important ecological approaches on the impacts of landscape changes (Tscharntke *et al.*, 2012), long-term data sets based on a large number of species are needed to better understand the role of the landscapes' history on ongoing patterns of species changes. Here, we use a long-term data sets (> 100 years) on pollinator richness change and land-use changes and show that changes in species richness were closely linked to landscape historical changes (diversity of habitats, patches' area and potential for spillover effects between managed and natural systems), but that such effects largely depended on the original state of the landscape before changes occurred (Table 2).

### Effect of changes in habitat heterogeneity and in the amount of suitable habitat

We expected that increases of the amount of suitable habitat and of the diversity of habitats would lead to increase the pollinator species richness ( $\beta$ -diversity hypothesis; Tscharntke *et al.*, 2012). Contrary to our expectations, none of the studied pollinator groups were affected by changes in the amount of suitable habitat (Table 2). This result could be related to the fact that most of the species' data come from recent time periods (last two periods; Figure S1), a time during which the available natural habitat was already very reduced in the



**Figure 2** The effects of fragmentation and edges for spillover effects on pollinator species richness changes. (a) Effect of the interaction between the edge density of managed and natural systems (T1) and the change in patch area on bumblebees. Increases in richness occurred in landscapes with originally more of these edges and smaller patches. Light colours represent negative or below average  $\Delta$  patch area. Dark colours represent positive above average  $\Delta$  patch area; (b) the effect of the total edge amount in the landscape (T1) on butterfly species richness changes. Landscapes with high densities of total edge were more likely to experience negative species richness changes of butterflies; (c) effects of changes in edge density between managed and natural systems on species richness of bumblebees. Landscapes with higher edge densities were more likely to increase their bumblebee species richness; (d) effects of edge between managed and natural systems (T1) on species richness of butterflies. Landscapes with higher densities were more likely to decrease their butterfly species richness. For bumblebees, the partial residuals (i.e. residuals after removing the effect of all other variables) are shown. For all plots, the values of the centred standardized explanatory variables are presented. Grey bands represent the 95% confidence interval.

Netherlands (e.g. by loss of natural habitat to agricultural and urban landscapes; Figure S2) and during which agricultural practices had already generated highly homogenous areas. Therefore, recent species responses might not be due to recent but to past changes in the landscape conditions, suggesting that extinction–colonization debt may be important (Bommarco *et al.*, 2014). Furthermore, in this study we defined grassland, moors/peat, deciduous/mixed forest and sandy soils as suitable habitats, and it is possible that pollinator species which resisted to the accentuated changes that occurred before 1980 are able to make use and sustain their populations in areas that we considered unsuitable (e.g. urban areas or agricultural landscapes).

Hoverflies were not affected by any of the landscape change characteristics considered by this study. This suggests that other drivers may be the most important for hoverflies (e.g. climate, other landscape characteristics). However, changes in richness of this group were conditioned by the original amount of suitable habitat in the landscape. This was expected as the majority of the Dutch syrphid species (around 2/3) present a close association with scrub and forest habitats (Reemer, 2005), and the area of such habitats used to be smaller at the beginning of the second half of the 20th century. The fact that landscapes with higher amounts of suitable habitat (included forested areas) were less likely to experience further increases in hoverfly richness suggests that such areas already contained well-established populations, and thus, great increases in species richness were not possible. Moreover, hoverflies not only benefit from forested areas but also some of them (around 20–30 common species) greatly benefit, at the larval stage, from managed areas where prey is abundant (i.e. aphids in crop fields; Reemer

**Table 2** Summary results for the composition and fragmentation hypothesis analysed. Hypothesis one analyses the effects of landscape composition on biodiversity. Hypothesis two focuses on the effects of landscape fragmentation and hypothesis three on the edges between managed and natural systems, a proxy for spillover effects. The results are group dependent. There is a predominant effect of the original state of the landscape on the pollinator species richness changes

| Group          | Landscape state | Hypothesis 1 -Composition effects          |   | Hypothesis 2 -Fragmentation effects                        |                                 | Hypothesis 1 and 2<br>3 -Fragmentation spillover effects |
|----------------|-----------------|--|---|--|---------------------------------|--|
|                |                 | > Suitable habitat →<br>> Species richness | > Habitat heterogeneity →<br>> Species richness | <Patch area,<br>Proximity; > Edges →<br>< Species richness | > Edges →<br>< Species richness | > Edges Man-Nat →<br>> Species richness                  |
| Bumblebees     | T1              | –  | –   | –  | –                               | Positive   |
|                | Δ               | –  | –   | Negative   | –                               | Positive   |
| Non-bumblebees | T1              | –  | –   | –  | –                               | –  |
|                | Δ               | –  | Positive  | –  | –                               | –  |
| Butterflies    | T1              | –  | –   | –  | Negative                        | Negative   |
|                | Δ               | –  | –   | –  | –                               | –  |
| Hoverflies     | T1              | Negative                                   | –   | –  | –                               | –  |
|                | Δ               | –  | –   | –  | –                               | –  |

T1: Original landscape state; Δ: changes; SR: species richness; >: higher; <: lower; →: then. Positive and Negative: direction of the effect. '–': lack of effect for the specific pollinator group.

*et al.*, 2009), areas that in our study were not classified as suitable habitat.

The suitability of a habitat for pollinators depends on the availability of floral and nesting/reproduction resources and hence on the characteristics of the landscape, such as habitat heterogeneity (Kremen *et al.*, 2007; Batáry *et al.*, 2011). The results of this study show that the effects of changes in habitat heterogeneity were mild, with only non-bumblebees increasing with the amount of habitat land-use classes available. However, these results show that higher diversity of habitats tend to contain a more diverse pollinator assemblage than more homogeneous areas (Table 2). It is possible that landscapes with higher habitat heterogeneity have more diverse vegetation structures providing the diversity of feeding and nesting resources required by multiple bee species (Garibaldi *et al.*, 2014). Thus, increasing the heterogeneity of land-use classes, for example by means of adding natural or semi-natural elements to more homogeneous landscapes, may improve the species richness levels of bees in these areas (Kremen *et al.*, 2007). Furthermore, this habitat improvement could especially benefit species that have different feeding preferences at different life stages and seasons of the year (Kohler *et al.*, 2008) and that without this habitat, improvement seem to be particularly threatened.

### Landscape fragmentation and spillover effects

In human-dominated areas, highly fragmented habitats (e.g. fragmented forest, urban areas) and mosaics of highly homogeneous landscapes (e.g. areas with intensive agriculture) are the rule. While fragmentation of suitable habitat may negatively affect biodiversity (Fahrig, 2003), in homogeneous landscapes, dispersal of organisms between patches of different

land-use, that is spillover effect, becomes highly important as this may increase resource availability, generate stable ecological processes and facilitate ecosystem functioning (Kremen *et al.*, 2007; Blitzer *et al.*, 2012). However, depending on the scale and on the study taxa, this may in turn reduce the overall beta diversity (e.g. Loreau, 2000; Clough *et al.*, 2007). Furthermore, these ecological processes may be reinforced in landscapes where habitat area and proximity between suitable habitats are increased (Sabatino *et al.*, 2010).

In our study, the effect of changes in landscape fragmentation (reduction in patch area) on pollinators' richness was only evident for bumblebees (Tables 1 & 2). The fact that fragmentation was associated with increased in bumblebee richness in landscapes where originally the density of edges between managed and natural systems was high was unexpected (Fig. 2a). However, this fragmentation–spillover outcome is logical if further fragmentation occurred in areas with already high amounts of managed and natural areas and thus with high species richness (given spillover potential already in place), facilitating in this manner additional potential spillover effects. The positive effect of these edges is further emphasized by the increase in species richness of bumblebees also in landscapes that experienced increases in edge density between the managed and natural systems. Thus, the edges between managed and natural systems become essential as they can potentiate the movement of species across different habitats (spillover effects; Table 2), and may facilitate the access to the diversified vegetation structures provided by a matrix of diversified patches of habitats that bumblebee communities need for feeding and nesting (Lye *et al.*, 2009). The access to these diversified resources is of primary importance for bumblebees because it has been shown that landscape resource diversity (e.g.

given by higher levels of managed natural areas) and not resource density drive bumblebee species distribution and foraging behaviour at the patch and landscape level (Jha & Kremen, 2013).

While butterflies richness changes were not associated with the patterns of fragmentation change, we found significant effects of the original landscape state (T1) of total edge density and spillover potential (Fig. 2b,d) (see also Tschamtkke *et al.*, 2008; Lucey & Hill, 2012). However, our results suggest that landscapes that were originally more fragmented (high ED T1 and ED Man-Nat T1) were more likely to suffer butterfly species losses (Table 1d, first and second models). This may be because the amount of edges in the landscape may interfere with the habitats' (micro)climatic conditions (Ries *et al.*, 2004), which are vital for the survival of many butterflies, particularly specialist species (Ries & Debinski, 2001; WallisdeVries & Van Swaay, 2006). Furthermore, these responses suggest a possible delayed effect (T1 effects) on the recent butterflies communities and imply that recent butterfly richness may still be highly determined by the past landscape characteristics. Therefore, it is possible that recent butterfly populations from more fragmented landscapes are more susceptible to local extinction (Sang *et al.*, 2010).

The lack of a significant effect of habitat fragmentation on hoverfly richness changes could be due to their high mobility and non-dependence of larvae on flower resources (Jauker *et al.*, 2009), making them less dependent on the surrounding landscape configuration and more resilient to habitat changes (Schweiger *et al.*, 2005). The lack of fragmentation effects on non-bumblebees species was unexpected as these depend on small-scale landscape characteristics (Steffan-Dewenter *et al.*, 2002; Holzschuh *et al.*, 2007). However, it is possible that weak fragmentation effects on this group had been counteracted by increases in feeding and nesting resources availability created along habitat margins (Jauker *et al.*, 2009).

### Implications for conservation and landscape management

Most studies analysing the changes in insect biodiversity in response to environmental changes focus on single species groups, for example butterflies, as insect biodiversity indicators (e.g. Fleishman *et al.*, 2000). The single-group approach has recently been challenged emphasising the need for a multigroup monitoring approach (e.g. Maes & Dyck, 2005; Gerlach *et al.*, 2013). However, butterflies tend to be the first choice because, as this group has historically caught the attention of conservationists and species are easily recognizable, data availability is greater than in other taxa. Butterflies are indeed one of the most sensitive pollinator groups (Carvalho *et al.*, 2013). However, here, we show that responses of butterflies are not always representative for responses of other insect groups (e.g. responses of butterflies to ED Man-Nat but not of hoverflies, and the fact that contrary to non-bumblebees, butterflies were not affected by changes in habitat heterogeneity; see Table 2). Consequently, conservation

measures aiming to restore pollinator populations and/or pollination functioning might be more effective when taking a broader range of pollinator responses into account.

While we analyse richness changes from three time periods from 1900 to 2009, the majority of the data originates from the most recent periods, post-1960 (Figure S1). Large-scale landscape changes in the Netherlands occurred mostly before 1980 (Figure S2), with some increases in forest area occurring in recent time periods. Therefore, it is possible that for most of the landscapes analysed and for some pollinator groups, concurrent landscape changes were not large enough to cause significant changes in species richness. Moreover, the lack of higher resolution of our historical species data (10 × 10 km) could in principle lead to lower power to detect effects of our much more accurate landscape data on species richness changes. However, despite these limitations, our study found that for all studied groups landscape history influenced the way communities responded to landscape changes. The conditions of a given landscape in the previous time period (our T1) can be seen as a snapshot of a dynamic landscape in the past and may itself represent a landscape in flux. Therefore, the results of this study alert for the potential extinction or colonization debts in studies when no effects of recent landscape changes are detected (see also Bommarco *et al.*, 2014). Results from studies that implement the space-for-time substitution approach are likely to reflect a mix of responses to the past landscape (the 'original state') and to recent change in that landscape. In these studies, strong biodiversity responses might be observed in landscapes where past and present changes occurred in the same direction (e.g. continued fragmentation or deforestation), whereas weak biodiversity responses may occur in landscapes where past and recent changes went in opposite directions (e.g. past deforestation now shifted to reforestation). The results of our study show clearly that attempts to counteract future species richness loss should consider both historical and present landscape conditions. Future monitoring schemes will be essential to determine to what extent present communities still carry signatures of past conditions and what the time window of the responses is.

Land-use variables used in this study explained a relatively small part of the variance observed in species richness changes. This suggests that other drivers might also be important, such as climatic conditions, uses of pesticides, increases in the levels of nitrogen deposition, the presence of pathogens and the competition between species (Potts *et al.*, 2010; WallisDeVries, 2014). Moreover, changes in landscape management could also have an effect on local species richness by modifying the suitability of land use for pollinators (Hudewenz *et al.*, 2012; Vogiatzakis *et al.*, 2015). For example, the intensification of agriculture that occurred in recent decades in many regions of the world, with associated increases in the use of fertilizers and pesticides and decreases in the availability of natural feeding and nesting resources, may have changed drastically the suitability of this land-use class for insect pollinators (e.g. Geiger *et al.*, 2010). More-

over, increases in anthropogenic nitrogen deposition, which were particularly after the 50s, may have drastically changed habitat suitability for the pollinator groups here analysed (Throop & Lerdau, 2004; Oenema *et al.*, 2012). Further research accounting for changes in management conditions across historical time spans is highly needed as to disentangle their effects on the distribution of biodiversity in human-dominated landscapes as agricultural areas.

Although species richness can be seen as a simple biodiversity indicator, it has been shown to be highly correlated with the functions biodiversity provides for example pollinator assemblages with higher richness were found to be associated with higher levels of pollination services delivery (Garibaldi *et al.*, 2013). Furthermore, species composition changes might have more important impacts on ecosystem functioning than species richness changes per se. Thus, further analysis incorporating changes observed in species composition, functional diversity and community homogenization across time and space would help unravelling the impact of these changes on ecosystem functioning and provide important insights for biodiversity conservation in these human-dominated landscapes.

## CONCLUDING REMARKS

Using historic data on Dutch pollinators and landscape changes covering more than 100 years, this study reveals striking differences in how pollinators responded to landscape characteristics. Among the variables investigated, some pollinators benefited from increased landscape heterogeneity (non-bumblebees), others depended mostly on landscape fragmentation levels and the potential for spillover effects (bumblebees). Strikingly, for the majority of the pollinators, the historical landscape characteristics have conditioned their pattern of species richness changes during the last century in the Netherlands. This suggests that recent species responses to landscape modification are constrained by the past landscape conditions and that future pollinator responses to further landscape changes may be dependent on the recent landscape characteristics.

It is thus evident that conservation approaches must include information about the original state of the landscape, as this might condition the effects that such conservation actions could have on biodiversity and also on the ecosystem services it provides.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Changes in richness of several important pollinator groups in the Netherlands and the changes in land-use for the same areas.

**Figure S2** The distribution of the ten land-use classes present in the study area for the three time periods analysed after the land-use classes' reclassification process.

**Figure S3** The changes in the percentage of suitable habitat in the landscape between the periods analysed.

**Table S1** Land-use classes in the Netherlands used in the study.

**Table S2** Summary of the most relevant studies for our

analysis related to the impacts of landscape composition and configuration on pollinators.

**Table S3** The General model implementation. Forward and backwards stepwise model selection was applied to the general starting model containing the below specified terms.

**Table S4** The results of the spatial autocorrelation analysis.

## BIOSKETCH

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