The influence of landscape composition and configuration on crop yield resilience

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Abstract

A key goal of sustainable agriculture is to produce sufficient food whilst minimising environmental damage. To achieve this we need to understand the role of agricultural landscapes in providing diverse ecosystem services and how these affect crop production and resilience, i.e. maintaining crop yields despite environmental perturbation. We used ten years of English wheat yield data to derive three metrics of resilience (relative function, yield stability and resistance to an extreme event). We explored their relationships with aspects of landscape composition and configuration (10km $\times$ 10km scale) known to affect ecosystem service components (e.g. beneficial invertebrates) and delivery (e.g. pest control). We found that resilience was uniformly enhanced in landscapes with higher coverage of semi-natural habitats. However, this was most pronounced for resilience metrics derived over shorter timescales (e.g. resistance) and metrics showed contrasting responses to landscape configuration, suggesting trade-offs if managing landscapes for resilience over shorter vs. longer timescales.

Introduction

Global food systems are under increasing pressure to produce sufficient food for a growing human population (Godfray *et al.* 2010). Agriculture has long aimed to address this challenge by maximising crop yields (Curtis & Halford 2014; Mitchell & Sheehy 2018). However, the intensive approaches used to achieve this over much of the globe have been linked to severe declines in biodiversity (Green *et al.* 2005; Reidsma *et al.* 2006; Butler *et al.* 2007) and many other adverse environmental impacts (Skinner*et al.* 1997; Tilman *et al.*2002; Tsiafouli *et al.* 2015). Simultaneously, crop yields have plateaued in many systems, suggesting that new approaches are required to support future increases (Ray *et al.* 2012).

Sustainable intensification aims to increase agricultural productivity, whilst also maintaining or bolstering biodiversity (Cassman 1999; Bommarco *et al.* 2013; Garnett *et al.* 2013; Kleijn *et al.* 2019). This approach has been driven in part by increasing awareness that biodiversity provides key ecosystem services required to maintain the long-term viability of agricultural systems (Bommarco *et al.* 2013), including pollination and natural control of pests (Naylor & Ehrlich 1997; Kremen & Chaplin-Kramer 2007). If sustainable intensification is to achieve its goals we need detailed knowledge on how to manage agricultural landscapes to ensure optimal provision of these services in the long-term (Gagic *et al.* 2017; Kleijn *et al.* 2019). Landscape structure (here defined as the composition and configuration of different land cover types) has been repeatedly identified as a key driver of ecosystem service delivery. However, whilst many studies have demonstrated relationships between the amount and configuration of natural or semi-natural habitats and abundance or species richness of beneficial invertebrate communities (Chaplin-Kramer *et al.* 2011; Blitzer *et al.* 2012; Potts *et al.* 2016; Woodcock *et al.* 2016) and service indicators such as crop pest populations (Bianchi *et al.* 2006; Chaplin-Kramer *et al.* 2011; Thies *et al.* 2011; Rusch *et al.* 2013; Dainese *et al.* 2019; Haan *et al.* 2019), very few have directly examined effects on crop yield (Holland *et al.* 2016; Holland *et al.* 2017; Karp *et al.* 2018).

Of those that do (e.g. Martin *et al.* 2016; Martin *et al.* 2019), most focus on absolute measurements of crop yield averaged over short periods of time.

However, average yields are not necessarily indicative of a systems' long-term sustainability or 'resilience'. Holling (1973) defined resilience as a "measure of the persistence of systems and of their ability to absorb change and disturbance". Whilst there has been considerable debate over the use of resilience concepts in ecological systems (Carpenter *et al.* 2001; Klein *et al.* 2003; Myers-Smith *et al.* 2012; Standish *et al.* 2014; Béné *et al.* 2016), the guiding principle is to consider not just the absolute quantity of a single function (e.g. crop yield), but also to consider this function in terms of its ability to persist over time by resisting and recovering from perturbations (Oliver *et al.*2015). In the case of crop yield, such perturbations may come in the form of extreme weather events, or outbreaks of pests or diseases. These can have substantial impacts on producer livelihoods even if average yields are high (GFS 2015). Resilience is underpinned by the environmental processes supporting agricultural production, e.g. climate, soil health, abundance and diversity of beneficial organisms. The need to identify and develop resilient cropping systems as a key component of sustainable intensification has been embraced in both research (Fischer*et al.* 2006; Altieri *et al.*2015; Bullock *et al.* 2017) and policy (Defra 2011, 2018b, a), but the question of how landscapes and the ecosystem services they deliver affect the resilience of agricultural systems (particularly in terms of the stability of crop yields over time) remains as a key knowledge gap preventing the widespread uptake of sustainable intensification {Kleijn, 2019 #1}.

In this paper we explore the relationships between landscape structure and crop yield resilience. We used a ten-year time series of wheat yields from a national survey of farms in England to derive metrics relating to different aspects of resilience. We analysed relationships between these metrics and aspects of landscape structure known to affect the provision of biodiversity-mediated ecosystem services. We hypothesised that:

1. All metrics of resilience would show a positive relationship with area and connectivity of arable land, given the known higher yields in intensively arable areas of England
2. All metrics would, accounting for the above, show a positive relationship with the amount of semi-natural habitat acting as a reservoir of beneficial organisms providing ecosystem services
3. Resilience metrics would differ in the strength of these relationships given the different time-scales over which they are derived

Methods

Yield data from a national survey

Wheat yield data were obtained from Defra's cereals and oilseeds production survey, part of the annual June survey of agriculture and horticulture in England (Defra 2018c). The latter collects detailed information about the structure of the agricultural industry, as is compulsory under UK legislation (Agricultural Statistics Act 1979). The survey uses a stratified random sampling approach in which farm holdings are classified on the basis of size defined by the theoretical labour requirement to run the farm. Full details of the survey methodology can be found in Defra (2018c). Data were available for 2008 to 2017, giving 10 years of data on average winter wheat yield per farm and coordinates giving the location of each farm to 1km. Locations were mostly obtained from subsidy claims, where farms register the location of the land for which they are claiming payment. However, in a minority of cases (<1%) location was inferred from farm postcode (Defra 2018c).

Data were cleaned to remove data flagged by Defra as potentially erroneous, as well as missing and zero yield values and land used to produce whole-crop silage harvests. Zero values may be informative where they indicate crop failure pre-harvest, however, they may also arise from a lack of measurement and so cannot be used with confidence. Following cleaning, a total of around 22,000 samples were available across the ten years (mean 2204 per year).

Because a new random sample of farms is drawn each year, few locations had consecutive data across the 10 years. In order to analyse yield variation over time and to ensure anonymity of the farm returns we aggregated yield data to the 10km x 10km grid cell ('hectad'). This gives an average yield per year per hectad, accounting for local spatial variation between farms and farming practices. From this dataset, hectads were identified with sufficient samples per year across the time series for analysis of resilience (see Supplementary Material Appendix 1 for details). All data handling and analysis was performed in R (v3.4, R Core Team 2017).

Constructing metrics of resilience

Recent functional approaches have proposed that resilience of a system can be estimated by looking directly at patterns of temporal and spatial variability of the function which the system delivers and its response to known perturbations (Oliver *et al.* 2015). This approach is well-suited to cropping systems as the function (i.e. yield) is easy to measure and widely surveyed. Some studies have begun to explore links between environmental drivers and aspects of yield resilience (Di Falco & Chavas 2008; Gaudin *et al.* 2015; Iizumi & Ramankutty 2016). However, such studies often focus on only a single metric of resilience. Given the complexity of resilience as a concept (Donohue *et al.* 2016; Ingrisch & Bahn 2018; Kéfi *et al.* 2019), with multiple facets derived from the absorptive (resistance), adaptive (recovery) and transformative (reorganisation) capacities of the system (Béné *et al.* 2016; Ingrisch & Bahn 2018), reductions to a single metric may be insufficient to understand the effects of landscape structure on resilience of crop yields (Isbell *et al.* 2015). For every hectad with sufficient data, we calculated three metrics capturing different aspects of resilience:

1. **Relative function across the time series** . Average difference between per hectad annual yield and average national annual yield (Fig. 1A). This combines the average magnitude and variability of yield over the time series, taking account of surpluses (when per hectad yield exceeds national average yield) and deficits (*vice versa*), in line with the functional resilience metric proposed by Oliver *et al.* (2015).
2. **Yield stability around a moving average** . Inverse of absolute percentage difference between yield in any one year and the average yield over the years either side (Fig. 1B), averaged across the time series (Iizumi & Ramankutty 2016). This metric is sensitive to fluctuation of yield over shorter timescales and incorporates aspects of resistance and recovery.
3. **Resistance to a specific event** . Exceptionally heavy spring and summer rainfall in 2012 caused a variety of issues for UK wheat farming (Defra 2012; Impey 2012), resulting in a mean national 14% drop in yield from the previous four years (as calculated from survey data). To understand resistance to this event we quantified the inverse of the proportional drop in yield shown in 2012 from the pre-2012 mean (Fig. 1C). This metric focuses on the resistance of crop yield to specific, short-term perturbation.

All three metrics were calculated in such a way that larger values imply greater resilience (i.e. the use of inverse values). We did not use coefficient of variation, because Carnus*et al.* (2014) found it to be a potentially poor metric for exploring relationships between biodiversity and stability of ecosystem functions, despite its frequent use as such (e.g. Piepho 1998; Hautier *et al.* 2015; Ray *et al.* 2015).

Accounting for climate and soil effects

In order to explore how our metrics of yield resilience are influenced by landscape structure, we first sought to control for other potentially confounding variables. These included spatial variation in meteorological and soil variables. The way in which these influence crop yields is complex, depending on interactions between temperature, sunlight and rainfall and the growth stage of the crop. We therefore condensed these variables into a single metric of potential yield. We used a simple model to estimate potential yield from temperature, precipitation and solar radiation (Agri4Cast data, Biavetti *et al.*2014) and soil water holding capacity (Bell *et al.* 2018), based on the approaches of Sylvester-Bradley and Kindred (2014) and Lynch *et al.*(2017), and benchmark values for wheat in Sylvester-Bradley *et al.* (2015). The model has three main stages: 1) estimation of green area index as a function of accumulated growing degree days, 2) estimation of intercepted solar radiation and water-limited conversion to biomass 3) apportioning of accumulated biomass to grain yield. The model also accounts for vernalisation (Spink *et al.* 2000), drought and waterlogging (Olgun *et al.* 2008). A full description of the potential yield model is available in Supplementary Material, Appendix 2. For each of the three resilience metrics, the equivalent metric for potential yield was included as a covariate in statistical models (see section 2.5) to account for climatic and soil effects on yield. We also accounted for any further impacts of regional variation in soils and climate beyond those explicitly in the potential yield model by assigning each hectad to an environmental zone, using a pre-existing classification (Bunce *et al.* 2007), which we then included as a random effect in statistical models (see section 2.5).

Landscape composition and configuration

We used a satellite-derived UK land cover map (LCM2015, 25m raster version, Rowland *et al.* 2017) to determine the composition and configuration of land cover types within each hectad. We analysed three main land cover classes: arable land, semi-natural habitats and semi-natural grasslands. The first of these allowed us to test our first hypothesis. We refined the LCM2015 arable class by intersecting with mapped high-grade agricultural land (Natural England 2012), as the resultant class ('high-grade arable land') showed a higher correlation with mean yield over time in preliminary analyses than total area of arable land alone (Pearson's correlation; r =0.35, p <0.001; r =0.31, p =0.001, respectively, n =135 in both cases). Semi-natural habitats included broadleaf woodland, semi-natural grassland, heathland and wetland as these are known to affect sources and flows of ecosystem services which affect crop production (Tscharntke *et al.* 2005; Rand *et al.* 2006; Blitzer *et al.* 2012; Rusch *et al.* 2013; Holland *et al.* 2017; Martin *et al.* 2019). We analysed semi-natural grasslands separately as these are structurally more similar to arable land and may be especially important in the provision of ecosystem services to agricultural landscapes (Duflot *et al.* 2015; Bengtsson *et al.* 2019).

For each land cover class we calculated three metrics of landscape composition and configuration. These were: percentage area per hectad, edge:area index (a measure of fragmentation) and mean distance to the nearest patch (a metric of isolation). Calculations were made in ArcGIS (v10.4, ESRI, CA). These three metrics are widely used in studies assessing the impacts of landscape structure on ecological processes (Chaplin-Kramer *et al.* 2011; Haan *et al.* 2019; Martin *et al.* 2019) and have been demonstrated to capture much of the potential variation in landscape composition and configuration (Riitters *et al.* 1995). We did not analyse land cover diversity, as preliminary analysis showed this to be driven (at the hectad scale) largely by the presence of other land cover types (e.g. urban, coniferous woodland, improved grassland).

Statistical analysis and modelling

All statistical analyses were undertaken in R (v3.4.0 - 3.5.3, R Core Team 2017). We used linear mixed models constructed in the *nlme* package (Pinheiro *et al.* 2017). All models included a spherical spatial autocorrelation structure, which preliminary analyses found to increase model fit as determined by Akaike's Information Criterion adjusted for small sample sizes (AICc). For each resilience metric (relative function, yield stability, resistance) we constructed a global model containing the random effect of environmental zone and all other explanatory variables as fixed effects (i.e. cover, fragmentation and isolation of each of high-grade arable, semi-natural habitats and semi-natural grasslands, plus potential yield from climate and soil data). To identify the 'best' performing subset of explanatory variables from the global model we ran all possible subsets using the *MuMIn* package (Barton 2016) and ranked models using AICc. Models were constrained to contain the intercept, random effect and potential yield variable. Where ΔAICc amongst the top ranked models was <2, the model with the smallest number of parameters was selected as the 'best' model. We then tested for non-linear relationships by adding quadratic terms, and for interactions by adding all pairwise interaction terms to the model, retaining them if ΔAICc >2. We confirmed the explanatory power of the 'best' model by calculating pseudo-R^2 values and checked for potential overfitting using a 200-fold cross-validation test, comparing the pseudo-R^2 of 'best' model to the distribution of pseudo-R^2 obtained from cross validation. The 'best' model was checked for normality of residuals and homoscedasticity using diagnostic plots.

Because there is the potential for the 'best' model to exclude important predictors, where several models had ΔAICc <2, we used a multi-model inference approach (Grueber *et al.* 2011; Harrison *et al.* 2018) to check that model averaged coefficients obtained from all possible subsets of the global model confirmed those in the final model.

Results

All metrics showed relationships with at least two landscape variables, but differed in their precise relationships with landscape composition and configuration, confirming our final hypothesis (details in sections 3.1-3.3). Cross-validation of pseudo-R^2 did not suggest overfitting for any model (Table 2) and inclusion of interaction terms did not significantly increase model fit for any metric.

Relative function across the time series

The 'best' model for this resilience metric included a strong, negative effect of fragmentation (i.e. edge: area ratio) of high-grade arable land (Table 1, Fig. 2A). This suggests that resilience according to this metric is highest where land is farmed in large, spatially contiguous blocks (because edge: area ratio is lowest where patches are both large and regular in shape). Once the effect of arable land is accounted for (see Table 1), relative function showed a positive relationship with both the area and fragmentation of semi-natural habitats (Table 1, Fig. 2A), suggesting that relative function is increased by semi-natural habitat extent, especially when these habitats are dispersed throughout the landscape (i.e. showing greater 'edginess'; e.g. Fig. 3A). Relative function also showed a strong, positive, non-linear relationship with modelled potential yield, suggesting a major influence of climate and soil type, up to a point when yield becomes limited by other factors. Results from model averaging strongly supported the coefficients in the 'best' model, with weights of $>=0.68$ (Table 2).

It should be noted that relative function across the time series showed a strong, positive correlation with mean yield (Pearson's correlation, $r = 0.99$, $p < 0.001$, $n = 135$), whereas the other two metrics did not ($r = -0.29$, $p < 0.04$; $r = < 0.001$, $p = 0.95$, respectively, $n = 135$ in both cases).

Yield stability around a moving average

Yield stability showed a positive relationship with cover of high-grade arable land and a negative effect of semi-natural habitat fragmentation in the 'best' fitted model (Table 1, Fig. 2B). This suggests that yields are more stable in areas with a higher coverage of arable land but that yields are also more stable in areas where semi-natural habitats are both extensive and (unlike the previous metric of relative function) spatially contiguous (e.g. Fig. 3B). Again, this was only significant in the best-fitted model given the effect of arable land, not in individual models. The relationship with modelled potential yield stability was much weaker than between relative function and potential function, suggesting that areas with more variable climate did not necessarily experience the most variable yield, with landscape factors potentially having a greater moderating effect. Results from model averaging (Table 2) suggested a slightly weaker support for a single 'best' model, although the weights for cover of arable land and semi-natural habitat fragmentation were still high (>0.62)

Resistance to a specific event

Resistance was the only one of the three metrics not to show a positive relationship with area of high-grade arable land in the 'best' model (Table 1) and there was no support from model averaging to suggest such a relationship (Table 2). Instead, resistance showed a strong, positive relationship with cover of semi-natural grassland and a strong negative relationship with distance from semi-natural grassland (Table 1). This suggests that landscapes showing the highest resistance to the poor conditions of 2012 were those with large extents of semi-natural grassland and where a high proportion of arable land was in close proximity to this grassland (e.g. Fig. 3C), independent of the quantity of arable land. Although resistance showed a significant, positive relationship with modelled potential resistance in individual models (Table 1), suggesting that the severest drops in yield were in areas which experienced the poorest weather conditions for yield, this relationship was not significant in models which accounted for the positive effects of semi-natural grassland, suggesting that these effects can mitigate against climatic impacts. Support from model averaging for the coefficients in the 'best' model was high (Table 2).

Discussion

Relationships with semi-natural habitat area

All three metrics showed significant, positive associations with the area of semi-natural habitats, once the effects of arable land (see section 4.3), soils and climate were accounted for, supporting our hypothesis that semi-natural habitat has an important role in contributing to the resilience of cropping systems to environmental perturbation.

The most probable mechanism underpinning this relationship is that semi-natural habitats provide reservoirs of organisms providing beneficial ecosystem services (Martin*et al.* 2019). These include those involved in natural pest-control, which not only directly predate upon pests (e.g. aphids, slugs) but also on disease vectors (e.g. aphids for barley yellow dwarf virus). Reductions in pest pressure may also have further beneficial effects in terms of reducing plant stress, which in turn affects susceptibility to fungal diseases (Rosenzweig *et al.* 2001). There are many studies demonstrating positive relationships between quantity and proximity of semi-natural habitat and the abundance and richness of natural enemies (Duelli *et al.*1990; Tscharntke *et al.* 2005; Bianchi *et al.* 2006; Ricketts *et al.* 2008; Chaplin-Kramer *et al.* 2011; Thies *et al.* 2011; Rusch *et al.* 2013; Holland *et al.* 2016; Martin *et al.* 2016; Holland *et al.* 2017). However, within these broad groupings there are a great diversity of organisms, each of which may have their own, complex relationships with landscape structure and one another (Plantegenest*et al.* 2007; Chaplin-Kramer*et al.* 2011; Martin *et al.*2013; Martin *et al.* 2016; Karp *et al.* 2018). This complexity means that the generally positive effects of semi-natural habitat on natural enemy abundance and diversity frequently do not always translate to increased predation of crop pests or enhanced yields (Martin *et al.* 2013; Mitchell *et al.* 2014; Tscharntke *et al.* 2016; Karp *et al.* 2018; Martin *et al.* 2019). By examining landscape effects on yield of a single crop, over a long time period, we focussed on the outcome of this suite of complex interactions. The positive relationships with area of semi-natural habitat evident in our results should thus be more robust than those with individual natural enemy groups (Chaplin-Kramer *et al.*2011; Martin *et al.* 2016) and although we do not have direct evidence for the mechanisms underpinning these relationships, demonstrable links between semi-natural habitat and aspects of crop yield are the most directly compelling evidence for farmers of the importance of semi-natural habitat for natural pest control (Holland *et al.* 2017; Kleijn *et al.* 2019).

Relationships with semi-natural habitat configuration

The inherent complexities of the relationships between habitats, natural enemies, pests and crops are also likely to be responsible for the varied responses to semi-natural habitat configuration (Haan *et al.* 2019). The highest levels of yield over time were delivered by landscapes with a high coverage of arable land with semi-natural habitats distributed throughout the landscape, whilst yield stability and resistance were driven more strongly by the presence of unfragmented semi-natural habitats, especially grasslands. Other studies have observed that the effect of landscape configuration is highly context-dependent (Haan *et al.* 2019). For example, on the one hand, increased fragmentation maximises the boundary length over which organisms can move between semi-natural habitats and arable land (Tscharntke *et al.* 2005; Rand *et al.* 2006; Blitzer *et al.* 2012). On the other, it lessens the value of individual habitat patches by reducing area and increasing isolation (Mitchell *et al.* 2015). This trade-off occurs simultaneously for beneficial organisms and the pests and diseases which they help to control (Plantegenest *et al.* 2007; Karp *et al.* 2018). It is therefore unsurprising that by comparing metrics of resilience calculated over different timescales the balance between these factors shifts, from the more arable-dominated, fragmented landscapes which maximise a range of factors helping to stabilise yield over longer terms, to landscapes with extensive, unfragmented semi-natural grassland which best support a more specific subset of functions underpinning resistance to a particular perturbation (see section 4.4).

Relationships with high-grade arable land area

Two metrics confirmed our hypothesis that resilience would be higher in areas with a higher coverage of arable land. Higher relative function (i.e. relative difference between local and national yield across the time series) was strongly associated with landscapes characterised by large, spatially contiguous (i.e. unfragmented) areas of high-grade arable land. Because relative function correlated strongly with mean yield across the time series, it is probable that this association arises as given that farming systems in England have long developed to exploit those areas most suitable for crop production (Chambers & Mingay 1966) and these areas typically also receive the greatest investment in agricultural inputs. This result has recently been demonstrated at pan-European scales by Martin *et al.* (2019), with higher average yields in landscapes combining a high percentage of arable land with a high edge density of semi-natural habitats.

The relationship of arable land to yield stability was weaker, whilst resistance to the poor weather of 2012 showed no evidence of a positive relationship with arable land. This suggests that as timescales become shorter, and the focus of the metric shifts from maintaining high average yield to reducing temporal fluctuations, the arable component of the landscape becomes less important in comparison to other factors. This exemplifies why higher mean yield over time is not necessarily indicative of a sustainable system nor of the benefits derived by agriculture from ecosystem services (Benton & Bailey 2019).

Differences between resilience metrics

It is clear that the three resilience metrics differed in the strength and direction of their relationship with landscape structure. Most striking was the general trend for an increased importance of semi-natural habitat as metrics were derived from shorter portions of the time series. There are two (non-exclusive) explanations for this. Firstly, as alluded to in section 4.2, a smaller subset of ecosystem service components are likely to confer resistance to a specific extreme event than those which maintain yield over longer timescales encompassing a range of different environmental fluctuations. Therefore relationships with specific landscape structure variables are both stronger and more specific over shorter timescales, for example, the relative importance of semi-natural grassland rather than semi-natural habitat for the resistance metric. Grasslands are more similar to arable land than other semi-natural habitats (e.g. woodland, wetland), both structurally and in terms of community composition and may have particularly significant effects on reservoirs of beneficial species in the landscape (Duflot *et al.* 2015; Bengtsson *et al.* 2019), presumably including those which are particularly important in conferring resistance to the specific perturbation we explored here.

Secondly, it is likely that many effects of landscape structure are only made obvious when extreme events occur, given the current reliance of English agriculture on the prophylactic use of agrochemicals (Hillocks 2012) which may, under normal circumstances, mask (or even suppress) potential benefits from ecosystem services (Gagic *et al.* 2017). In our case, the poor agronomic conditions of 2012 have been attributed to a 'perfect storm' combination of factors, with a cold and wet spring which reduced plant growth and grain formation, promoted outbreaks of disease and delayed harvest (Defra 2012; Impey 2012; Met Office 2013). As mentioned in section 4.2, the precise mechanisms controlling the relationships between resistance and semi-natural habitat are likely to vary with spatial and temporal context (Haan *et al.*2019). For example, a particular extreme (e.g. high rainfall) might increase populations of specific pests (e.g. molluscs) and so resistance will be driven by the landscape factors which most affect their predators (e.g. carabids). However, another year with different conditions (e.g. drought) might promote another set of pests. These would be in turn controlled by different natural enemies which may respond to landscape structure in different ways (Martin *et al.* 2019).

Despite this complexity, reductions in resistance or short-term stability are indicative of where agricultural systems are vulnerable in terms of the failure of farming practices to fully compensate for environmental fluctuations, which might be missed by longer-term measures. Of course, this is only useful if the perturbations to which resistance is studied are representative of those predicted to occur in the future. In the case of our study, not only are extreme weather events likely to become more frequent (Rosenzweig *et al.* 2001; Trnka *et al.* 2014), but other perturbations in the agricultural system may have similar consequences, including anthropogenic factors such as the loss of pesticide active ingredients in response to regulatory changes (Hillocks 2012). Such shifts may of necessity make farmers increasingly reliant on natural pest control and thus the effects of landscape context may become increasingly important.

Conclusions and implications for landscape management

Our results confirm the current consensus that semi-natural habitats in arable landscapes have a role for society that extends beyond simply supporting agricultural biodiversity. These habitats were correlated with crop yield resilience, as measured by three different metrics, and as such have the potential to enhance the economic viability of farming systems. We also show a particular importance of semi-natural habitats in mitigating against extreme events, even if their impact on average yield over time is more limited. At the scale we analysed (10km $\times$ 10km) this is relevant to national or regional policy-making, which may include agri-environmental funding for creating, restoring and maintaining semi-natural habitats (Critchley *et al.* 2004). Whilst our results are not directly transferrable to the scale of the individual farm, there is evidence that semi-natural habitats can help increase yields (Pywell *et al.*2015; Tschumi *et al.* 2016a; Tschumi *et al.* 2016b) and reduce the impact of extreme events (Di Falco & Chavas 2008) at finer spatial scales.

Our results also have a bearing on the relative merits of strategies based on land-sharing (integrating food production and biodiversity conservation on the same land) vs. land-sparing (spatially segregating food production and biodiversity conservation). Whilst land-sparing is often determined to be preferable in terms of maximising average delivery of biodiversity and crop yield (Kamp *et al.* 2015; Ekroos *et al.* 2016; Finch *et al.* 2019; Lamb *et al.* 2019), it may not be beneficial in term of crop yield resilience, if semi-natural and agricultural landscapes become increasingly segregated beyond the scales we examined here. This highlights an essential contrast between immediate short-term agricultural production goals, and those of the long-term stability of the system, both environmentally and economically. Even within the scale of the landscapes we studied, differences in the relative strength of the responses to arable land, semi-natural habitat and its configuration suggest that there are potential trade-offs to be made in managing landscapes for resilience over shorter vs. longer timescales. Given the increased risk of extreme events under climate change and concerns over our current reliance on chemical management of pests, our finding that landscapes which most enhance average yield over time are not necessarily those which confer increased stability or resistance is an important challenge to address in developing sustainable and resilient agricultural systems.

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Figure legends

Fig.1 Schematic showing the different metrics of resilience applied to an example time series. Grey lines and filled points indicate simulated yield data for a single hectad. A) Illustrates relative function, being derived from the average difference (area between lines shaded in light grey) between the hectad (mid-grey lines and points) and national average yields (light grey lines and points) across the time series. B) Illustrates yield stability, derived from the difference (vertical black arrows) between yield in any one year and the average yield over the two years either side (horizontal, dashed black bars). C) Illustrates resistance, derived from the proportional drop in yield (vertical black arrow) in 2012 from the pre-2012 mean (horizontal, dashed black bar). Note that, for analyses, the inverse of the latter two metrics is taken, such that higher values indicate higher resilience in all cases.

Fig.2 Partial residual plots of the explanatory variables in the 'best'-fitting models for each response variable. Plots show the effect of a given landscape composition or configuration variable after removing variance from random and other fixed effects in the model (Including environmental zone and potential yield) for each of A) relative function, B) yield stability, C) resistance. Abbreviations on axis labels are SNH = semi-natural habitat, SNG = semi-natural grassland

Fig. 3 Example hectads (10km squares) from a single environmental zone predicted to have the maximum and minimum resilience values by the 'best'-fitting models for each response variable. For all plots, shading indicates land cover type, with pale grey being arable land, mid-grey being deciduous woodland and black being semi-natural grassland. White areas indicate other land cover types (e.g. urban areas, improved grassland).

Tables

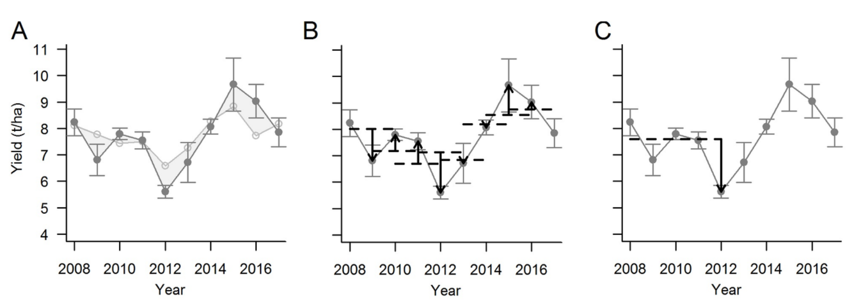
Table 1 Coefficients (+-1 S.E.) of best-fitting (defined by minimum AICc) mixed models for each yield resilience metric. Models were constrained to include the potential yield response (to account for weather and soil effects). The coefficients from individual models including only a single predictor are given for comparison, alongside the pseudo-R^2 of the model and p-value from cross-validation to detect overfitting (values of $p < 0.05$ suggest significant overfitting). SNH = semi-natural habitat, SNG = semi-natural grassland.

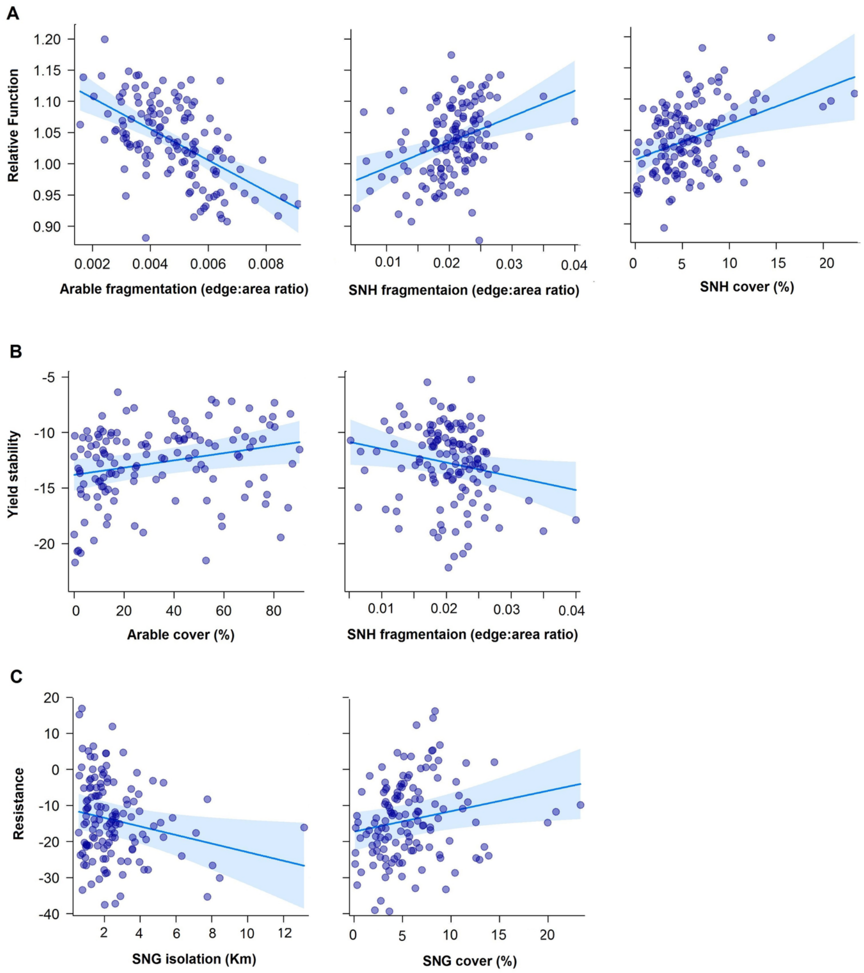
	'Best' model	**'Best' model**	**'Best' model**	**'Best' model**	**Individual models**	**Individual models**
	Coefficent (±1 S.E.)	**p-value**	**pseudo-R^2**	**Cross-validation**	**Coefficent (±1 S.E.)**	**p-value**
Relative function			0.332	0.287		
Intercept	8.21 (1.95)	<0.001			-	-
Potential	-12.76 (3.37)	<0.001			-8.97 (3.59)	0.014
Potential^2	5.66 (1.47)	<0.001			4.06 (1.56)	0.010
Arable fragmentation	-24.88 (4.46)	<0.001			-14.32 (3.9)	<0.001
SNH cover	0.57 (0.2)	0.006			-0.07 (0.15)	0.616
SNH fragmentation	4.11 (1.23)	0.001			1.72 (1.01)	0.091
Yield stability			0.211	0.138		
Intercept	-10.56 (1.72)	<0.001			-	-
Potential	0.1 (0.14)	0.496			0.23 (0.13)	0.075

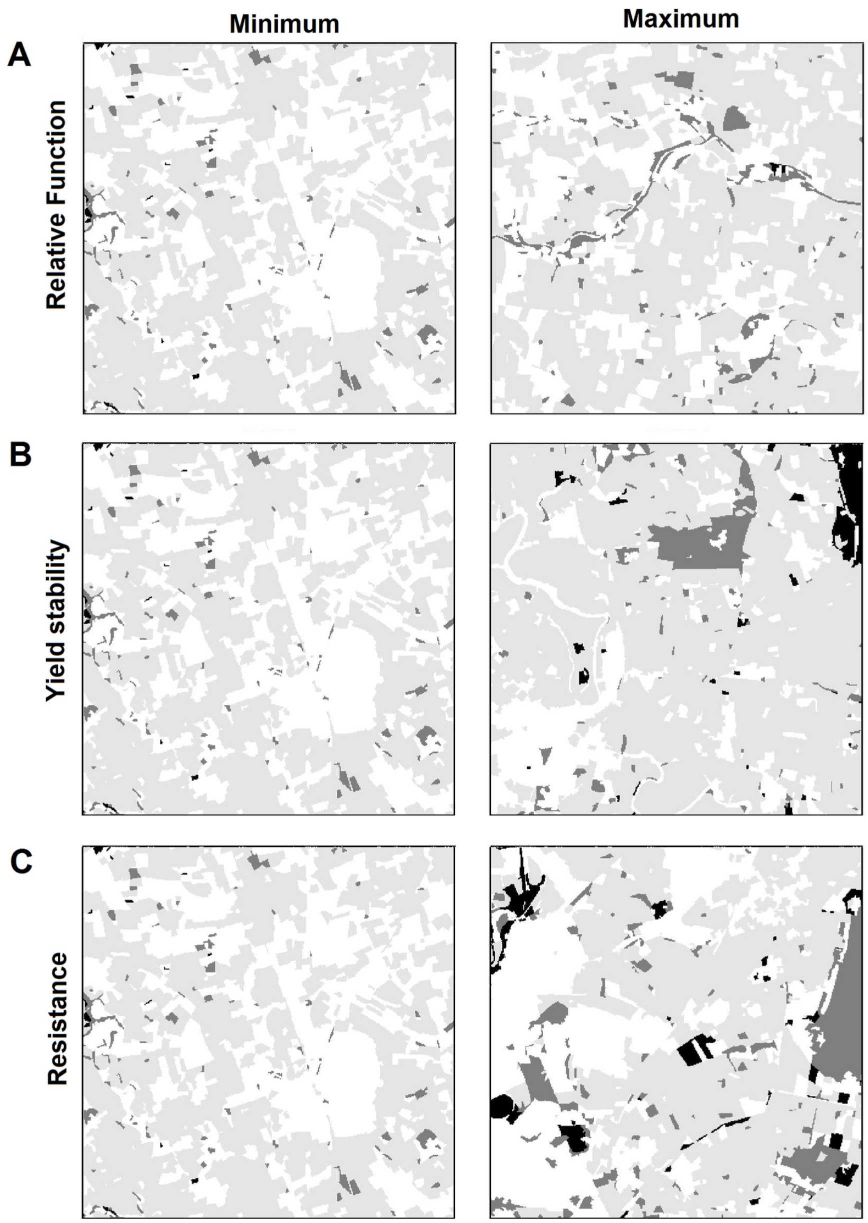
	'Best' model	'Best' model	'Best' model	'Best' model	Individual models	Individual models
Arable cover	0.03 (0.01)	0.018			0.03 (0.01)	0.008
SNH fragmentation	-123.97 (58.6)	0.036			-111.12 (59.53)	0.064
Resistance			0.394	0.188		
Intercept	-14.82 (3.31)	<0.001			-	-
Potential	-0.20 (0.16)	0.194			-0.36 (0.16)	0.024
SNG cover	56.67 (25.26)	0.027			82.25 (24)	0.001
SNG isolation	-0.01 (0.01)	0.028			-0.01 (0.01)	0.001

Table 2 Model averaged standardised coefficients and average Aikaike weights across models containing each variable of landscape composition and configuration. These are each of cover (%), isolation (Isol.) and fragmentation (Frag.) for each of high-grade arable land (Arable), semi-natural habitat (SNH) and semi-natural grassland (SNG). Also given are the number of models with ΔAICc < 2, out of the possible 382 subsets of explanatory variables from the global model.

	Arable Cover	Arable Isol.	Arable Frag.	SNH Cover	SNH Isol.	SNH Frag.	SNG Cover	SNG Isol.	SNG Frag.	N models	N models	
Relative function	**Relative function**	**Relative function**	**Relative function**	**Relative function**	**Relative function**	**Relative function**	**Relative function**	**Relative function**	**Relative function**	**Relative function**	2	2
Coefficient	0.018	0.045	-0.511	0.327	-0.181	0.289	0.097	0.175	0.038			
Weight	0.101	0.125	1.000	0.685	0.221	0.785	0.167	0.417	0.118			
Yield stability	**Yield stability**	**Yield stability**	**Yield stability**	**Yield stability**	**Yield stability**	**Yield stability**	**Yield stability**	**Yield stability**	**Yield stability**	**Yield stability**	11	1
Coefficient	0.269	0.035	0.068	0.163	-0.096	-0.194	-0.144	-0.024	0.015			
Weight	0.872	0.227	0.262	0.381	0.274	0.622	0.396	0.224	0.221			
Resistance	**Resistance**	**Resistance**	**Resistance**	**Resistance**	**Resistance**	**Resistance**	**Resistance**	**Resistance**	**Resistance**	**Resistance**	6	6
Coefficient	-0.064	-0.083	-0.051	-0.015	-0.058	0.062	0.231	-0.236	0.083			
Weight	0.255	0.313	0.258	0.246	0.252	0.272	0.754	0.823	0.310			




A
Relative Function
1.20
1.15
1.10
1.05
1.00
0.95
0.90
0.002
0.004
0.006
0.008
Arable fragmentation (edge:area ratio)
0.01
0.02
0.03
0.04
SNH fragmentaion (edge:area ratio)
0
5
10
15
20
SNH cover (%)
B
Yield stability
-5
-10
-15
-20
0
20
40
60
80
Arable cover (%)
0.01
0.02
0.03
0.04
SNH fragmentaion (edge:area ratio)
C
Resistance
20
10
0
-10
-20
-30
-40
2
4
6
8
10
12
SNG isolation (Km)
0
5
10
15
20
SNG cover (%)


Minimum
Maximum
A
Relative Function
B
Yield stability
C
Resistance