

The influence of landscape composition and configuration on crop yield resilience

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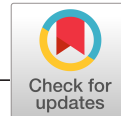
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RESEARCH ARTICLE

The influence of landscape composition and configuration on crop yield resilience

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Natural Environment Research Council, Grant/Award Number: NE/N018125/1 LTS-M ASSIST; Biotechnology and Biological Sciences Research Council, Grant/Award Number: NE/N018125/1 LTS-M ASSIST

Handling Editor: Lorenzo Marini**Abstract**

1. Sustainable agriculture aims to produce sufficient food while minimizing 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, that is, maintaining yields despite environmental perturbation.
2. We used 10 years of English wheat yield data to derive three metrics of resilience (relative yield across the time series, yield stability around a moving average and resistance to an extreme weather event) at 10 km × 10 km resolution. We used remotely sensed maps to calculate measures of landscape structure, including composition (proportions of different land cover types) and configuration (metrics of connectivity and proximity), known to affect ecosystem service delivery (e.g. control of pests by beneficial invertebrates). We then used an information-theoretic approach to identify the best-fitting combination of landscape structure predictors for each resilience metric, using a potential yield model to account for the effects of climate and soils.
3. Relative yield showed a strongly positive relationship with the area of arable land. For yield stability, this relationship was evident but alongside other landscape structure variables in the best-fitting model. No relationship with arable land was evident for resistance.
4. Yield stability showed a strongly positive effect of proximity to semi-natural habitats. For resistance, the best-fitting model included positive relationships with the cover of semi-natural habitats and proximity to semi-natural grasslands.
5. *Synthesis and applications.* Landscapes with the highest relative wheat yields did not show the highest yield stability or resistance to extreme events. As resilience metrics were derived from shorter portions of the time series, the importance of semi-natural habitats compared to arable land increased. This is probably driven by the complex interplay between landscape structure, agricultural management and ecosystem services. These results demonstrate that measuring relative yield over time may be insufficient to capture the full effect that non-arable components of the landscape, and the ecosystem services they deliver, have on other

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aspects of resilience, and that there are clear trade-offs in managing agricultural landscapes to maximize different aspects of crop yield resilience.

KEYWORDS

agriculture, climate, ecosystem services, landscape structure, resilience, resistance, stability, sustainable intensification

1 | INTRODUCTION

Global food systems are under pressure to produce sufficient food for a growing human population (Godfray et al., 2010). Agriculture has long aimed to address this challenge by maximizing crop yields (Curtis & Halford, 2014; Mitchell & Sheehy, 2018). However, intensive approaches to achieving this have driven severe declines in biodiversity (Butler, Vickery, & Norris, 2007; Green, Cornell, Scharlemann, & Balmford, 2005; Reidsma, Tekelenburg, Van den Berg, & Alkemade, 2006) and other adverse environmental impacts (Tilman, Cassman, Matson, Naylor, & Polasky, 2002; Tsiafouli et al., 2015).

Sustainable intensification aims to increase agricultural productivity, while also maintaining or bolstering biodiversity (Bommarco, Kleijn, & Potts, 2013; Garnett et al., 2013; Kleijn et al., 2019). This approach has been driven in part by increasing awareness that biodiversity provides vital ecosystem services which maintain the viability of agricultural systems (Bommarco et al., 2013), including crop pollination and natural pest control (Kremen & Chaplin-Kramer, 2007; Naylor & Ehrlich, 1997). If sustainable intensification is to succeed, we need detailed knowledge on how to manage agricultural landscapes to ensure optimal, long-term provision of these services (Gagic et al., 2017; Kleijn et al., 2019). Landscape structure has been repeatedly identified as a key driver of ecosystem service delivery. We here define landscape structure as being comprised of composition (i.e. number and proportions of different land cover types) and configuration (i.e. spatial arrangement of those land cover types), after Fahrig et al. (2011). While many studies have demonstrated relationships between landscape structure and service indicators such as beneficial invertebrate communities or crop pest populations (Bianchi, Booij, & Tscharntke, 2006; Chaplin-Kramer, O'Rourke, Blitzer, & Kremen, 2011; Haan, Zhang, & Landis, 2019; Rusch, Bommarco, Jonsson, Smith, & Ekbom, 2013), few have directly examined effects on crop yield (Holland et al., 2016, 2017; Karp et al., 2018). Those that do (e.g. Martin et al., 2019; Martin, Seo, Park, Reineking, & Steffan-Dewenter, 2016) mostly focus on average yields over time.

However, average yields are not necessarily indicative of long-term sustainability or 'resilience'. Holling (1973) defined ecological resilience as a 'measure of the persistence of systems and of their ability to absorb change and disturbance'. The guiding principle is therefore to consider not just the absolute quantity of a single function (e.g. crop yield) but also its ability to persist over time by

resisting, recovering from and adapting to perturbations (Oliver et al., 2015). In the case of crop yield, such perturbations include extreme weather events, pest outbreaks or diseases. These can have substantial impacts on livelihoods even if average yields are high (GFS, 2015). Resilience is underpinned by complex interactions between environmental factors (e.g. climate, soil health, communities of beneficial organisms) so the landscapes which deliver high average yields under normal conditions are not necessarily those which are most stable or most resistant to extreme events. The need to identify and develop resilient cropping systems has been embraced in research (Altieri, Nicholls, Henao, & Lana, 2015; Bullock et al., 2017) and policy (Defra, 2018a), but the question of how landscapes and the ecosystem services they deliver affect the resilience of agricultural systems remains a key knowledge gap preventing the widespread uptake of sustainable intensification (Kleijn et al., 2019).

In this paper we explore relationships between landscape structure and crop yield resilience. We used a 10-year time series of wheat yields from a national survey of English farms to derive metrics relating to different aspects of resilience. We analysed relationships between these metrics and aspects of landscape structure known to affect provision of biodiversity-mediated ecosystem services. We hypothesised that:

1. Area of arable land would have a positive effect on resilience, as it is indicative of the intensity of, and investment in, agricultural management.
2. Semi-natural habitats would also have a positive effect on resilience as they act as reservoirs of beneficial organisms providing ecosystem services.
3. Metrics relating to different aspects of resilience would differ in the strength of these relationships and the relative importance of landscape composition and configuration.

2 | MATERIALS AND METHODS

2.1 | Yield data from a national survey

Wheat yield data were obtained from Defra's cereals and oilseeds production survey, part of an annual survey of the English agricultural industry based on a stratified random sample of farms. Survey methods can be found in Defra (2018b). Data were available for 10 years (2008–2017), comprising average winter wheat yield per

farm and coordinates locating each to 1 km. Data were cleaned to remove anomalous yield values, giving around 22,000 individual samples (see Appendix S1).

Because a new random sample of farms is drawn each year, few had consecutive data across 10 years. To analyse yield variation over time and account for local spatial variation in farming practices, we therefore aggregated data to mean annual yield per 10 km × 10 km grid cell ('hectad'). From this dataset, hectads were identified with sufficient samples per year for analyses of resilience (Appendix S1). We ensured that our selection of well-sampled hectads did not bias our dataset towards particular landscape structures (Appendix S1, Figure S2). From 315 hectads with at least one sample per year, 137 met our criteria for sufficient sampling. All data handling and analyses were performed in R (v3.4, R Core Team, 2017).

2.2 | Constructing metrics of resilience

We here use a broad definition of crop yield resilience as 'any quantification of the agricultural system's ability to maintain consistent delivery of yields despite environmental perturbation'. There are many potential ways of quantifying resilience from temporal and spatial variability in yield. 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; Knapp & van der Heijden, 2018) but these often use only a single metric. However, resilience is conceptually complex (Donohue et al., 2016; Ingrisch & Bahn, 2018; Kéfi et al., 2019), with multiple facets derived from the capacity of a system to resist, recover from and adapt to environmental change (Béné, Headey, Haddad, & von Grebmer, 2016; Ingrisch & Bahn, 2018), so metrics vary in which aspects of resilience are examined and the time-scales over which these are measured. Single metrics may therefore be insufficient to fully understand the effects of landscape structure (Isbell et al., 2015). For every hectad with sufficient data, we calculated three metrics capturing different aspects of resilience:

1. *Relative yield across the time series.* Average difference between annual and national average annual yield (Figure 1a). This combines average magnitude and variability over the time series, accounting for surpluses (when yield exceeds the national average) 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 average yield over the years either side (Figure 1b), averaged across the time series (Iizumi & Ramankutty, 2016). This metric is sensitive to fluctuation of yield over shorter time-scales and incorporates the aspects of resistance and recovery.
3. *Resistance to a specific event.* Inverse proportional change in yield between 2012 and the pre-2012 mean (Figure 1c). Exceptionally heavy spring and summer rainfall in 2012 caused poor wheat yields (Defra, 2012; Impey, 2012), with a mean 14% decrease compared to previous years (from survey data).

All metrics were calculated such that larger values imply greater resilience (i.e. use of inverse values). We explored intercorrelations between metrics and correlations with mean yield, that is, average yield per hectad across all years in the time series (Appendix S2). Although conceptually a measure of resilience (i.e. ability to deliver yields exceeding the national average despite environmental fluctuations), the metric of relative yield was in practice strongly correlated with mean yield (Appendix S2).

2.3 | Accounting for climate and soil effects

To explore relationships between metrics of yield resilience and landscape structure, we first controlled for the effects of meteorological and soil variables. Because the way in which these interact to influence crop yields is complex, we condensed them into a single metric of potential yield. We modelled potential yield from observed, gridded data on temperature, precipitation and solar radiation (Agri4Cast JRC-MarsMet data; Biavetti, Karetsos, Ceglar, Toreti, & Panagos, 2014; Toreti et al., 2019) and soil water holding

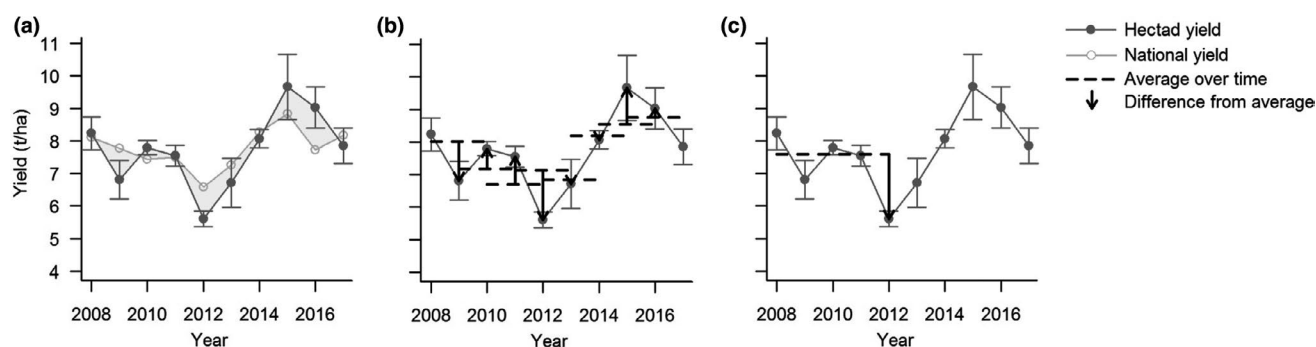


FIGURE 1 Schematic showing derivation of metrics of resilience from an example time series. (a) Relative yield, the average difference between hectad and national average yields across the time series. (b) Yield stability, the difference between any 1 year and the average over the 2 years on either side. (c) Resistance, the proportional decrease in 2012 from the pre-2012 mean. The inverse of the latter two metrics was taken such that higher values indicate higher resilience in all cases

capacity (Bell, Rudd, Kay, & Davies, 2018), based on approaches in Sylvester-Bradley and Kindred (2014) and Lynch, Fealy, Doyle, Black, and Spink (2017). The model has the following three main stages: (a) estimation of green area index from accumulated growing degree days; (b) interception of solar radiation and water-limited conversion to biomass; (c) apportioning accumulated biomass to grain yield. For a full description see Appendix S3. For each resilience metric, the equivalent metric for potential yield was included as a covariate in statistical models (Section 2.5). We also accounted for any further impacts of regional variation in soils and climate by assigning each hectad to an environmental zone, using a pre-existing classification (Bunce, Barr, Clarke, Howard, & Scott, 2007), included as a random effect in statistical models (Section 2.5).

2.4 | Landscape composition and configuration

We used a satellite-derived land cover map (LCM2015, 25 m raster; Rowland et al., 2017) to determine the composition and configuration of land cover types per hectad. We analysed three land cover classes, namely arable land, semi-natural habitats and semi-natural grasslands. Semi-natural habitats included semi-natural grassland, broadleaf woodland, heathland and wetland as these are known to affect ecosystem services relevant to crop production (Blitzer et al., 2012; Holland et al., 2017; Martin et al., 2019; Rand, Tylianakis, & Tscharntke, 2006; Rusch et al., 2013; Tscharntke, Rand, & Bianchi, 2005). We also analysed semi-natural grasslands separately as these are structurally more similar to arable land and may be especially important in providing ecosystem services (Bengtsson et al., 2019; Dufлот, Aviron, Ernoul, Fahrig, & Burel, 2015).

For each land cover class, we calculated three largely independent metrics of landscape composition and configuration. These were as follows: percentage area, mean edge:area index and mean distance to the nearest patch. These were drawn from a variety of composition and configuration metrics widely used in assessments of landscape impacts on ecological processes (Chaplin-Kramer et al., 2011; Cushman, McGarigal, & Neel, 2008; Haan et al., 2019; Martin et al., 2019) explored in preliminary analyses (Appendix S4). Mean edge:area index and distance to the nearest patch were transformed to indices of 'connectivity' and 'proximity' (Appendix S4) to aid interpretation of regression coefficients. Structure metrics were calculated in ArcGIS (v10.4, ESRI) and the LANDSCAPEMETRICS R package (Hesselbarth, Sciaini, With, Wiegand, & Nowosad, 2019).

2.5 | Statistical analysis and modelling

All statistical analyses were undertaken in R. We used an information-theoretic approach to identify the best-fitting combination of landscape structure predictors for each resilience metric (i.e.

relative yield, yield stability, resistance). For each metric, we first used the NLME package (Pinheiro, Bates, DebRoy, & Sarkar, 2017) to construct a global linear mixed effects model containing the random effect of environmental zone and all other explanatory variables as fixed effects (i.e. cover, connectivity and proximity of each of arable, semi-natural habitats and semi-natural grasslands, and potential yield). The model 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). We then ran all possible subsets of explanatory variables from the global model using the MuMIn package (Barton, 2016) and ranked models using AICc. Models were constrained to include the random effect and potential yield variable and to exclude pairs of highly intercorrelated predictors (Appendix S4, Figure S5). Where $\Delta AICc$ among top-ranked models was < 2 , the model with the smallest number of parameters was defined as the 'best' model. We then repeated the ranking procedure with all quadratic terms and pairwise interactions between variables in the 'best' model, defining a new 'best' model if $\Delta AICc > 2$. We confirmed the explanatory power of the 'best' model by calculating pseudo- R^2 values and checked for overfitting using a 200-fold cross-validation test, comparing pseudo- R^2 to the distribution from cross-validation. Because the 'best' model may exclude potentially important predictors where several models had $\Delta AICc < 2$, we calculated model averaged coefficients across all possible subsets (Harrison et al., 2018) to check that these confirmed the 'best' model. We also ran individual models (with autocorrelation and random effects as described above) for each variable in the 'best' model, to explore whether relationships were evident when analysed independently of other predictors.

3 | RESULTS

The 'best' models for all three resilience metrics contained at least one landscape structure variable and had $\Delta AICc$ of > 2 from the null model (random factor and autocorrelation structure only) and from models with the potential yield variable only (Table 1). Cross-validation of pseudo- R^2 did not suggest significant overfitting for any 'best' model. In all cases, models including interaction terms did not result in $\Delta AICc > 2$. Standardized coefficients and $\Delta AICc$ values for all candidate models with $\Delta AICc < 7$ from the 'best' models are given in Appendix S5.

3.1 | Relative yield across the time series

The 'best' model for this resilience metric included a strong positive effect of arable cover (Table 2; Figure 2a). This suggests that the highest relative yields are obtained where a higher proportion of the landscape is farmed. Results from model averaging strongly supported this predominance of arable cover, with a

TABLE 1 Properties of 'best' models as defined by minimum AICc from all possible subsets. The table shows the number of candidate models with $\Delta\text{AICc} < 2$, ΔAICc from a null model containing random effect and spatial autocorrelation structure only and ΔAICc from a model including potential resilience only. Also shown are pseudo- R^2 and p -value from cross-validation (values of $p < 0.05$ suggest significant overfitting)

Resilience metric	No. models	ΔAICc from null model	ΔAICc from potential model	Pseudo- R^2	Cross validation p -value
Relative yield	8	11.79	3.72	0.18	0.485
Yield stability	7	6.02	4.66	0.16	0.177
Resistance	4	12.99	10.80	0.39	0.245

	'Best' model			Individual models	
	Unstandardized coefficient	Standardized coefficient	p value	Coefficient	p value
Relative yield					
Intercept	672.47 (202.55)	—	0.001	—	—
Potential	-10.33 (3.53)	-7.44 (2.54)	0.004	-9.24 (3.56)	0.013
Potential ²	0.05 (0.02)	7.68 (2.54)	0.003	0.04 (0.02)	0.008
Arable cover	0.06 (0.02)	0.25 (0.10)	0.012	0.06 (0.03)	0.031
Yield stability					
Intercept	81.34 (3.29)	—	<0.001	—	—
Potential	<0.01 (<0.01)	-0.13 (0.10)	0.199	0.01 (0.01)	0.050
Arable cover	0.04 (0.02)	0.29 (0.11)	0.007	0.03 (0.01)	0.009
SNH proximity	18.59 (8.9)	0.23 (0.11)	0.039	2.79 (7.88)	0.724
Resistance					
Intercept	-25.91 (3.95)	—	<0.001	—	—
Potential	-0.11 (0.16)	-0.06 (0.08)	0.493	0.33 (0.15)	0.042
SNH cover	0.57 (0.25)	0.19 (0.09)	0.025	0.77 (0.25)	0.002
SNG proximity	52.65 (21.04)	0.25 (0.10)	0.014	69.08 (19.00)	<0.001

TABLE 2 Coefficients (± 1 SE) of landscape structure variables in the 'best' (defined by minimum AICc) mixed models for each yield resilience metric. Models were constrained to include potential yield (to account for weather and soil effects). Coefficients are given as unstandardized and standardized for comparison, alongside unstandardized coefficients from individual models including only a single predictor. SNG, semi-natural grassland; SNH, semi-natural habitats. p -values are calculated from the ratios between the estimates and their standard errors, and the associated value from a t distribution, as returned by the *summary.lme* R function

weight of 0.7 (Table 3). Other landscape variables generally had low weights and a mixture of positive and negative coefficients. Relative yield also showed a strong, positive, nonlinear relationship with modelled potential yield, suggesting a major influence of climate and soils, up to a point when yield becomes limited by other factors.

3.2 | Yield stability around a moving average

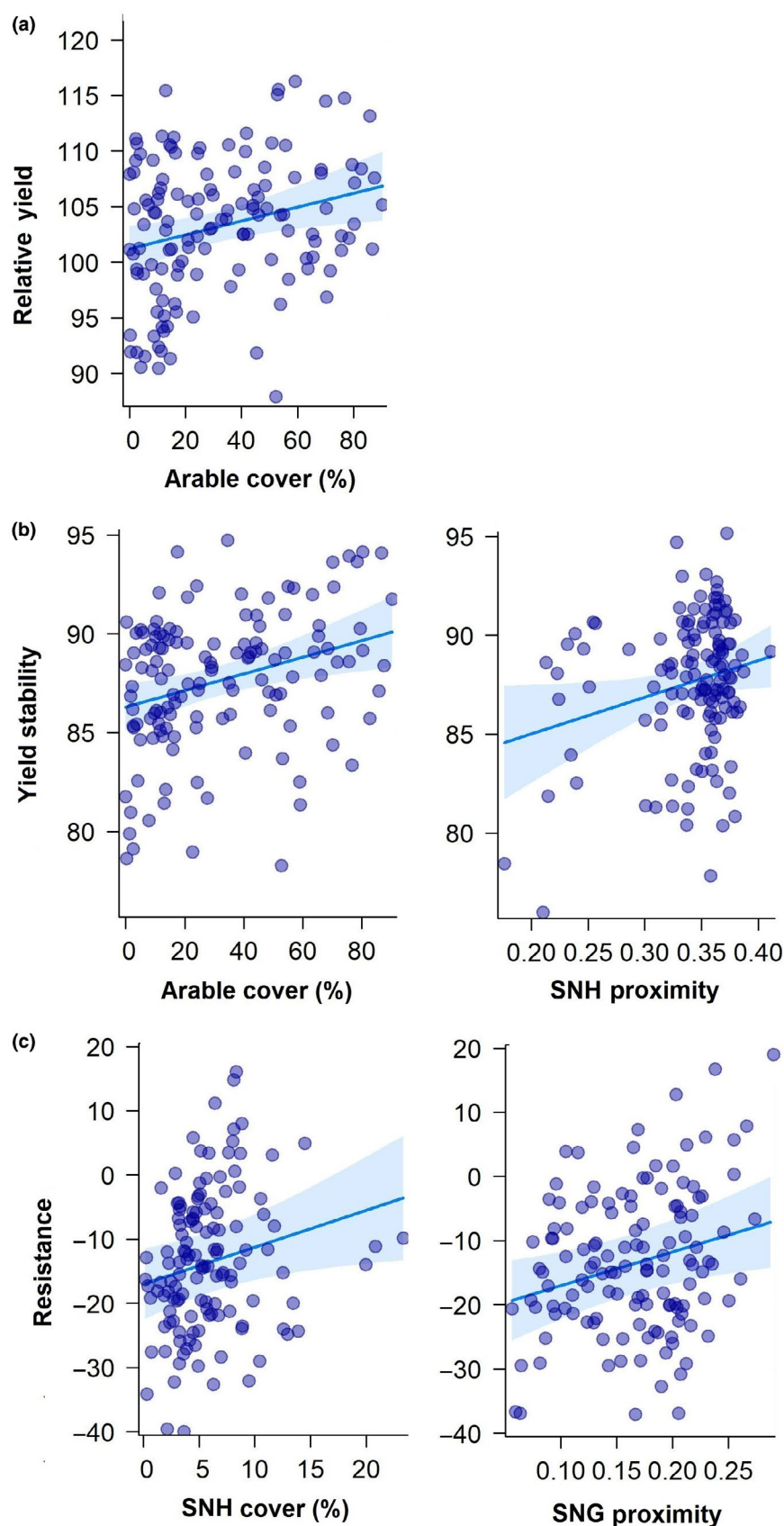
Yield stability showed a positive relationship with cover of arable land and proximity to semi-natural habitats in the 'best'-fitted model (Table 2; Figure 2b). This suggests that yields are most stable in landscapes with both a high coverage of arable land and with semi-natural habitats evenly distributed throughout the landscape (e.g. Figure 3b). The effect of proximity to semi-natural habitat was only evident in the 'best' model containing the effect of arable land, not in individual models (Table 2). The relationship with potential yield stability was weaker than

that between relative yield and potential yield, suggesting that areas with more variable climate did not necessarily experience the most variable yield, and that landscape factors potentially have a greater moderating effect. Results from model averaging (Table 3) were again supportive of those from the 'best' model, although semi-natural habitat connectivity showed a moderate weight (0.56).

3.3 | Resistance to a specific event

Resistance was the only metric not to show a positive relationship with area of arable land in the 'best' model (Table 2) and there was no support from model averaging to suggest such a relationship (Table 3). Instead, resistance showed a strong, positive relationship with cover of semi-natural habitat and proximity to semi-natural grassland (Table 1). This suggests that landscapes exhibiting the highest resistance to the poor conditions of 2012 were those with large extents of semi-natural habitat and where arable land

FIGURE 2 Partial residual plots of landscape structure variables in the 'best' models for each resilience metric: (a) relative yield, (b) yield stability, (c) resistance. Plots show the effect of a given variable after removing variance from other effects in the model. Higher values on the y-axes indicate increased resilience and are thus considered favourable for agricultural productivity. SNG, semi-natural grassland; SNH, semi-natural habitat



was generally in close proximity to grassland in particular (e.g. Figure 3c). Although resistance showed a positive relationship with potential resistance in individual models (Table 2), suggesting

that the severest decreases were in areas which experienced the most detrimental weather conditions, this relationship was not evident in the 'best' model, suggesting that the positive effects

TABLE 3 Model averaged standardized coefficients and average Aikaike weights across models containing each landscape structure variable—that is, percentage cover, connectivity index (Conn.) and proximity index (Prox.) for each of arable land, all semi-natural habitats and semi-natural grassland

	Arable land			Semi-natural habitats			Semi-natural grassland		
	Cover	Conn.	Prox.	Cover	Conn.	Prox.	Cover	Conn.	Prox.
Relative yield									
Coefficient	0.238	−0.038	0.032	−0.077	0.103	0.082	−0.043	0.028	−0.220
Weight	0.755	0.270	0.253	0.246	0.371	0.154	0.200	0.163	0.458
Yield stability									
Coefficient	0.243	0.073	−0.019	0.136	−0.177	0.199	0.006	0.022	−0.058
Weight	0.787	0.313	0.248	0.352	0.632	0.446	0.160	0.093	0.155
Resistance									
Coefficient	−0.020	−0.001	0.097	0.212	−0.126	0.228	0.101	−0.077	0.237
Weight	0.254	0.242	0.417	0.727	0.423	0.227	0.109	0.203	0.648

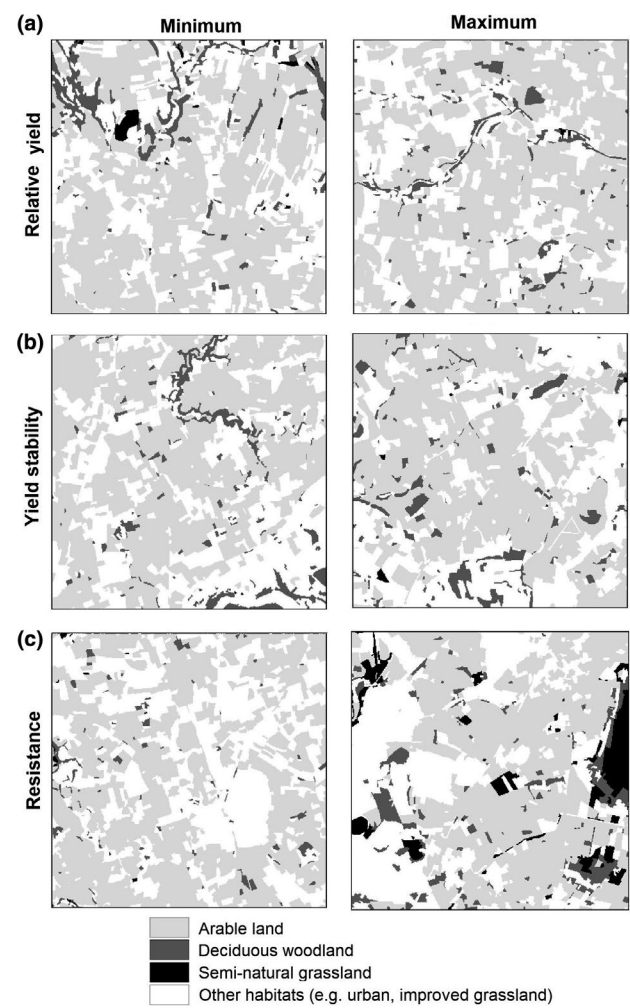


FIGURE 3 Example hectads from a single environmental zone with the maximum and minimum predicted values for each resilience metric

of semi-natural habitats can mitigate against climatic impacts. Support from model averaging for the coefficients in the ‘best’ model was high (Table 3).

4 | DISCUSSION

Our results show that wheat yield resilience, as measured by three different metrics, was influenced by landscape structure. The aspects of landscape structure which were most influential differed between resilience metrics, especially in terms of the relative importance of arable land versus semi-natural habitats, such that the landscapes which delivered the highest relative yields across the time series did not necessarily maximize yield stability or resistance to extreme events. These results suggest that there are potential trade-offs to be made in managing landscapes for resilience over shorter versus longer time-scales.

4.1 | Relationships with landscape structure

In support of our first hypothesis, two of our resilience metrics showed a positive effect of higher coverage of arable land. Higher relative yield (i.e. relative difference between local and national yield across the time series) was strongly associated with landscapes dominated by arable land. Although our metric of relative yield is conceptually indicative of resilience to wide range of perturbations over time (Oliver et al., 2015), in practice it correlates strongly with mean yield. Mean yield is in turn highly likely to correlate with coverage of arable land because farming systems in England have long developed to exploit the most productive land (Chambers & Mingay, 1966) and these areas typically receive the greatest investment in agricultural inputs. This may have a masking effect on the role of ecosystem services and the non-arable components of the landscape (Gagic et al., 2017; Martin et al., 2019; Pywell et al., 2015). A positive relationship between yield stability and cover of arable land was also evident but resistance to the poor weather of 2012 showed no evidence of such a relationship, exemplifying that average or relative yield is not necessarily indicative of the full extent to which landscape structure affects crop yield resilience.

Two metrics showed a positive effect of cover or configuration of semi-natural habitats. This supports our second hypothesis that semi-natural habitat has a role in contributing to the resilience of crop yields to environmental perturbation. The most probable mechanism underpinning the positive effect of semi-natural habitats is that they provide reservoirs of organisms providing beneficial ecosystem services (Martin et al., 2019), including those involved in natural control of pests and pathogen vectors ('natural enemies'). Although semi-natural habitats may also have other characteristics that influence yield resilience (e.g. favourable microclimates, retention of water, reduction of soil and nutrient runoff), these are likely to be influential at finer spatial scales than the hectads analysed here. Many studies have previously demonstrated positive relationships between semi-natural habitats and the abundance and richness of natural enemies (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Holland et al., 2016, 2017; Martin et al., 2016; Rusch et al., 2013; Tscharnke et al., 2005). However, natural enemies comprise a great diversity of organisms, each with their own, complex relationships with landscape structure and with one another (Chaplin-Kramer et al., 2011; Karp et al., 2018; Martin, Reineking, Seo, & Steffan-Dewenter, 2013; Martin et al., 2016; Plantegenest, Le May, & Fabre, 2007). These relationships are often highly context-dependent (Haan et al., 2019). For example, dispersing the same amount of semi-natural habitat throughout the landscape simultaneously increases the potential for movement into arable land (Blitzer et al., 2012; Rand et al., 2006; Tscharnke et al., 2005) and lessens the value of individual patches (Mitchell et al., 2015). Such trade-offs affect both natural enemies and the pests and pathogens which they help to control (Karp et al., 2018; Plantegenest et al., 2007). Effects of natural enemies can also be counter-intuitive, for example by promoting increased movement of pathogen vectors (Clark, Basu, Lee, & Crowder, 2019; Crowder et al., 2019). The complexity of these interrelationships means that positive effects of semi-natural habitat on natural enemy abundance and richness do not always translate to improved pest regulation or enhanced yields (Karp et al., 2018; Martin et al., 2013, 2019; Mitchell, Bennett, & Gonzalez, 2014; Smith et al., 2020; Tscharnke et al., 2016). By examining effects on yield of a single crop, we focus directly on the outcome of this suite of complex interactions and our results show that amount and proximity of semi-natural habitats have an overall positive effect on yield stability and resistance. Although we do not have direct evidence for the mechanisms underlying these relationships, demonstrable links between semi-natural habitat and variations in crop yield are the most directly compelling evidence for farmers of the importance of semi-natural habitat for agricultural production (Holland et al., 2017; Kleijn et al., 2019).

4.2 | Differences between resilience metrics

Given the complex interrelationships between landscape structure, ecosystem services and yield, it is unsurprising that our different metrics of resilience showed differences in their relationships with landscape structure (Haan et al., 2019). As the portions of the time

series from which resilience metrics were derived decreased, the importance of semi-natural habitat generally increased while that of arable land decreased. There are two possible explanations for this.

First, over shorter time-scales, a narrower range of environmental fluctuations are likely to be encountered. This means that the ecosystem services with greatest impact on crop yield are likely to be more limited, and thus that relationships with specific landscape structure variables are more likely to be consistent. In a single, extreme year the mechanisms governing resistance, and hence relationships with landscape structure, are likely to be even more specific. Indeed, our resistance metric showed a positive effect of not just semi-natural habitats but semi-natural grassland in particular. Grasslands are more similar to arable land, structurally and in community composition, than other semi-natural habitats (e.g. woodland). This makes them particularly important as reservoirs of beneficial species (Bengtsson et al., 2019; Duflo et al., 2015), presumably including those conferring resistance to the specific perturbation explored here.

Second, it is likely that many effects of the non-agricultural components of landscape structure are only made obvious when extreme perturbations occur. The reliance of English agriculture on intensive management such as the prophylactic use of agrochemicals (Hillocks, 2012) may, under normal circumstances, mask (or even suppress) potential benefits from ecosystem services (Gagic et al., 2017). It thus requires an extreme event where farming practices cannot fully compensate for environmental fluctuations for the value of ecosystem services to become evident.

Of course, these two explanations are not mutually exclusive. The precise mechanisms controlling the relationships between resistance and semi-natural habitat vary with spatial and temporal context (Haan et al., 2019). So a particular extreme (e.g. high rainfall, as in 2012) might increase populations of specific pests beyond the capacity of agricultural management to control them (e.g. molluscs) making resistance highly dependent on landscape factors which most affect their predators (e.g. carabids). However, another extreme year with different conditions might promote another set of pests, which are in turn controlled by different natural enemies with different responses to landscape structure (Martin et al., 2019), leading to a lack of clear response if the two extreme years were analysed in conjunction.

Overall, our results clearly demonstrate that a single metric of resilience (especially one based on average levels of function over longer time-scales) is unlikely to adequately capture the full effect of landscape structure or the benefits of ecosystem services to agriculture (Benton & Bailey, 2019). The responses of resistance and shorter term stability are indicative of where current farming practices cannot fully compensate for environmental fluctuations. Extreme weather events, as encountered in 2012, are likely to become more frequent (Rosenzweig, Iglesias, Yang, Epstein, & Chivian, 2001; Trnka et al., 2014). Other changes may have similar consequences, reducing the ability of the agricultural system to mitigate against environmental impacts, such as the regulatory loss of pesticide active ingredients (Hillocks, 2012). Such shifts may make farmers increasingly reliant on natural pest control and thus increase the importance of landscape context. For example, organic farming

systems exhibit greater fluctuations in yield than conventional ones, and show an increased dependency on landscape-mediated ecosystem services (Knapp & van der Heijden, 2018; Smith et al., 2020).

5 | CONCLUSIONS

Our results confirm that semi-natural habitats in arable landscapes have a role that extends beyond simply supporting agricultural biodiversity to enhancing the long-term viability of farming systems. At the scale we analysed, this is relevant to national or regional policy-making, including agri-environmental funding for creating, restoring and maintaining semi-natural habitats (Critchley, Burke, & Stevens, 2004). Although our sampled landscapes do not cover the full national range of possible agricultural landscape structures, they include a wide variety with moderate to high coverage of agricultural land such as dominate much of lowland England.

Our results also have a bearing on the relative merits of strategies based on land sharing versus land sparing. While land sparing is often preferable in terms of maximizing average delivery of biodiversity and crop yield (Ekroos et al., 2016; Lamb et al., 2019), our results suggest that at least some degree of land sharing (i.e. intermixtures of semi-natural habitats and arable land within hectads) is required to maximize stability and resistance. Given the increased risk of extreme events under climate change and concerns over our current reliance on agrochemicals, our finding that landscapes which most enhance relative yield are not necessarily those which confer increased stability or resistance to environmental perturbations is an important challenge to address in developing sustainable agricultural systems.

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AUTHORS' CONTRIBUTIONS

All the authors jointly conceived the ideas, contributed critically to the drafts and the design of methodology, and gave final approval for publication. J.W.R. analysed the data and led the writing of the manuscript.

DATA AVAILABILITY STATEMENT

Crop yield resilience data available from the NERC Environmental Information Data Centre (EIDC) <https://doi.org/10.5285/7dbcee0c-00ca-4fb2-93cf-90f2a5ca37ea> (Redhead, Oliver, Woodcock, & Pywell, 2020). Land cover data available from EIDC, <https://doi.org/10.5285/bb15e200-9349-403c-bda9-b430093807c7> (Rowland et al., 2017).

Soil data available from EIDC, <https://doi.org/10.5285/3b90962e-6fc8-4251-853e-b9683e37f790> (Bell et al., 2018). Environmental zones available from EIDC, <https://doi.org/10.5285/5f0605e4-aa2a-48ab-b47c-bf5510823e8f> (Bunce et al., 2007). Agri4Cast agro-meteorological data were drawn from the JRC-MarsMet (JRC MARS Meteorological Database) gridded agro-meteorological data in Europe dataset. These are third-party data developed by European Commission Joint Research Centre, Food Security Unit (Biavetti et al., 2014; Toreti et al., 2019). They are freely available for access and reuse and are currently available at <https://agri4cast.jrc.ec.europa.eu/DataPortal>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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