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Functional space and the population dynamics of birds in agro-ecosystems

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ABSTRACT

Managing resource availability in landscapes is a key focus of biodiversity conservation action. Continued biodiversity losses suggest that current actions are inadequate, with better targeting required to ensure resource provision offsets resource deficits. This study uses the concept of functional cover types to establish links between land-use, resource availability and population dynamics. Using UK farmland birds as a model system, the links between local population dynamics and functional space (FS) composition, and the role of landscape context in modifying these relationships, are explored. The population trends of all 19 species considered were more positive or less negative in squares with greater areas of one or more FS components. Counter-intuitively, negative relationships between population trends and FS were also common. Conspecific abundance in the surrounding landscape was also identified as being an important driver of population dynamics, both directly and through its influence on the relationship with each FS component. Targeted conservation management is needed to address the very context-specific nature of local population change.

1. Introduction

Despite increases in the scale and intensity of policy and management responses designed to halt it, the rate of biodiversity loss is not slowing (Butchart et al., 2010). This suggests that the nature, structure and scale of these mitigation measures are insufficient to counteract existing drivers of decline and are, therefore, unlikely to offset the detrimental effects of either further increases in existing pressures or the emergence of novel drivers. The governing body of the Convention on Biological Diversity (CBD) met in Japan in October 2010 to adopt a revised and updated Strategic Plan (Gordon et al., 2010). Successfully meeting the post-2010 biodiversity targets set will require a more complete understanding of the mechanistic links between drivers of biodiversity decline and population dynamics so that mitigation measures can be targeted more effectively. A major challenge for the research community is to develop the approaches and tools to support these activities.

In Europe, agriculture of one form or another occupies approximately 50% of the land surface. As a consequence, European biodiversity conservation measures are founded on policy frameworks designed to deliver environmentally beneficial land management back into agricultural systems alongside production management. This integration of production and conservation management has been termed wildlife-friendly farming (Green et al., 2005) and is perhaps best evidenced by recent reforms to the Common Agricultural Policy (CAP). The CAP is widely accepted as the main driver of agricultural changes that have resulted in biodiversity losses across Europe but is now also the main policy tool for addressing these losses through the funding of agri-environment schemes (AES). However, as with global trends, biodiversity losses in Europe continue whilst pressures on biodiversity are increasing (Butchart et al., 2010; Butler et al., 2010; Gregory et al., 2009). At the Environment Council meeting in March 2010, Ministers agreed to develop a longer-term vision for biodiversity up to 2050, and stressed the need for integration with other EU policies and strategies. Nowhere is the need to develop post-2010 conservation strategies which reflect an acknowledgement of the current failure to appropriately target conservation management more pressing than in EU agricultural policy and practice; continued biodiversity losses across Europe provide further evidence that, despite significant investment from the public purse, many AES are not delivering on biodiversity objectives (Butler et al., 2007; Kleijn et al., 2011).

To date, studies linking land-use and population dynamics have tended to focus on structural cover types, exploring the relationship between species' occurrence or abundance and particular land-uses or habitats (Rushton et al., 2004). However, such habitat association models (HAMs) are normally assumed to sacrifice generality for precision and reality and, by treating habitats independently, they can become context-specific and over-parameterised (Graf et al., 2006). Thus HAMs can be relatively successful at predicting species' occurrence or population dynamics from habitat characteristics

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when applied within the region from which the data used to parameterise them were collected but are much less successful when used to make predictions outside the area or habitat conditions for which the model has been calibrated (Schaub et al., 2011; Whittingham et al., 2007). This limits their application because they cannot be used to predict population responses to land-use change if the resultant land-use does not appear in contemporary landscapes. Thus, at a time when factors such as climate change, agricultural policy reform and the introduction of genetically-modified and bio-energy crops are all predicted to have substantial impacts on land-use patterns at local, national and global scales (Rounsevell et al., 2006; Tilman et al., 2001), new approaches to link land-use to population dynamics are required.

Ultimately, species' habitat associations are dictated by the quantity and quality of the resources they provide, rather than the habitat *per se* (Boyce and McDonald, 1999), although factors such as intra- and inter-specific competition or perceived and actual predation risks in specific habitats are also important (Brown and Kotler, 2004; Butler et al., 2005; Oliver et al., 2009). As a consequence, it has recently been proposed that, instead of using structural cover types, land use – population dynamics relationships might be better examined in the context of functional cover types, such as foraging or breeding habitat, identified on the basis of resource dependencies of species or species groups (Fahrig et al., 2011). The quantity, in terms of area, and quality, in terms of resource provision, of each functional cover type in a landscape effectively delimits the functional space (FS) available to a species. FS based models are likely to have three key advantages over structural cover based HAMs. Firstly, they provide a more mechanistic link between land use and population dynamics, whereby population change can be explained by changes in the availability of specific functional cover types. Secondly, by limiting the resolution of habitat re-categorisation to these principal functional cover types, the likelihood of over-parameterisation and context-specificity is greatly reduced (Graf et al., 2006). Thirdly, novel land uses can be readily incorporated into this framework, simply by quantifying their contribution to FS on the basis of resource provision.

Here the concept of FS is developed to examine whether it can be used to link land-use and population dynamics. Using UK farmland birds as a model system, structural land-covers (i.e. agricultural and semi-natural habitats) were re-classified into functional cover types according to the resource requirements of each species. A simple definition of a species' requirements, characterised by its diet, foraging habitat and nest site was adopted because previous research has shown that changes in the quantity or quality of these key resources can be linked to national population dynamics (Butler et al., 2007, 2009, 2010). It was predicted that local population trends would be positively associated with FS availability because resource availability should affect local demography. In wide-ranging organisms such as birds, landscape-scale population processes may also influence local population trends and alter the relationships with FS through, for example, source–sink dynamics (Pulliam, 1988) so potential interactions between local and landscape-scale dynamics were also assessed.

2. Methods

Our analyses focus on the 19 species included in the UK Farmland Bird Index (FBI) (Table 1) and were based on data collected from 601 1 km squares covered by both the Breeding Bird Survey (BBS) and Winter Farmland Bird Survey (WFBS). BBS has been the national monitoring scheme for breeding bird populations in the UK since 1994 (Risely et al., 2008) whilst WFBS documented the abundance of farmland birds in the UK in the winters of 1999/2000, 2000/2001 and 2002/2003 (Gillings et al., 2008).

During BBS, primary and secondary habitats within each 200 m section along two 1 km transects (i.e. 10 sections per square) are recorded. WFBS involved three timed visits to each 1 km square in each winter, with habitat details recorded for each patch greater than 0.3 ha in size. Details of habitat recording methodologies for each survey are provided in Appendix S1. For each species, all squares where it was recorded three or more times between 1994 and 2007 were identified. The following species-specific analyses were based on BBS summer count data and both BBS and WFBS habitat data collected from those squares. For brevity in Sections 2 and 3, species are referred to using italicised, standard BBS recording codes as defined in Table 1.

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2012.11.001.

2.1. Defining FS components

For each species, the BBS and WFBS habitat codes which defined habitats expected to contribute to the availability of three principal functional cover types – summer foraging, breeding and winter foraging space – were identified. The quality of the FS provided by each habitat type was also broadly categorised so that, in all, six components of total FS were defined: high or low quality breeding cover (hereafter BHQ and BLQ respectively), high or low quality summer foraging cover (hereafter SHQ and SLQ respectively) and high and low quality winter foraging cover (hereafter WHQ and WLQ respectively) (Tables S1, S2, S3). Habitats were assigned to each FS component on the basis of species' key resource requirements (Butler et al., 2007), vegetation structure and management and previously reported evidence of habitat preference or selection and resource availability (e.g. Chamberlain et al., 2000; Siriwardena et al., 1998; Vickery et al., 2004; Wilson et al., 1999). Sufficient data were available to confidently define the contribution of all structural cover types recorded in BBS and WFBS to the FS of all species except *WP*, for which it was not possible to determine the features which differentiate BHQ and BLQ.

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2.2. Quantifying FS component availability

The availability of the six FS components in each 1 km square was estimated from habitat data collected during each winter of WFBS and BBS in the summers of 2000, 2001, 2003. Thus FS was quantified at the mid-point of the bird count data period and it was assumed that this was indicative of FS availability over the whole time period. By quantifying FS availability at a 1 km square level and averaging values over three years, estimates of FS are effectively rotation averages; even if this period did not cover a full rotation, the relative proportion of each crop type present in a square in any one year should be broadly equivalent to the proportion of those crops in that square across the rotation. The methods of habitat data recording differed between BBS and WFBS so different approaches were used for quantifying the availability of breeding, summer foraging and winter foraging functional cover types.

2.2.1. Breeding and summer foraging cover

For each species and for each year's data, the number of 200 m transect sections expected to contribute to BHQ or BLQ given their habitat coding was recorded. The proportion of transect sections contributing to BHQ and BLQ within each square, weighted by whether it was associated with the primary and/or secondary habitat, was then calculated (Appendix S2). On the assumption that the habitat recorded along transects was representative of that available throughout the square, this was multiplied by 100 to estimate the total area (ha) of BHQ and BLQ. Finally, these areas were