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Seeds in farmland food-webs: Resource importance, distribution and the impacts of farm management

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ABSTRACT

Whilst considerable research effort in Europe has linked agricultural intensification with dramatic declines of seed-feeding birds, surprisingly little is known about the wider importance of seeds in animal food-webs. Moreover, understanding the dynamics of farmland seed food resources for species of conservation concern is of considerable research interest.

We examined the distribution of berries and soil-surface seeds in the managed and unmanaged habitats of a 125 ha organic farm. We took soil suction-samples over a year, counted and identified all seeds, and compared abundances and species-richness between habitats. We constructed ecological networks from literature records and by rearing insects to investigate the importance of these seeds for insects, birds and mammals. We predicted the impacts of management on seed biomass, energy and the ecosystem service of pest control across the whole farm.

We estimated seed and berry food resources of up to 33 metric tons of biomass and 560 GJ of energy on the farm. Potentially, more than 330 species use the seeds as a food resource, the overwhelming majority of which are invertebrates (82%) relying predominantly on non-crop and weed species. Generally, uncultivated semi-natural habitats such as woodland and mature hedgerows were more species-rich and had higher seed biomass and energy than crop habitats throughout the year, but fallow land was disproportionately important for seeds during the summer. Models of increased management intensity revealed declines of up to 19% in seed biomass and energy and cascades through the network that resulted in a substantial decrease in potentially pest-controlling parasitoids.

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1. Introduction

Seed production is a fundamentally important process not only for plant population dynamics but also as a major source of food for a diverse range of animals. Seed feeding organisms typically include granivorous mammals, birds and insects (e.g. ants and beetles), but the wide taxonomic range also includes slugs, crabs, fish and earwigs (Fenner and Thompson, 2005). The proportion of seeds consumed varies greatly between species, location and years, but is often extremely high (Crawley, 1992). However, surprisingly little is known about the spatial and temporal distribution of seed resources within habitats, their importance in animal food-webs, or how environmental change might affect the structure and function of these food-webs.

Habitat modification is the leading cause of species population declines and extinctions worldwide (Foley et al., 2005), with the

conversion of natural habitats to agriculture in particular leading to substantial changes in species diversity and composition (Tilman et al., 2001). Throughout Europe, there have been significant declines in farmland birds, butterflies and arable weeds, which has been attributed to a general process of agricultural intensification in recent decades (Donald et al., 2001; Krebs et al., 1999; Marshall et al., 2003; Thomas et al., 2004). Many declining arable weed species are an important source of food for a high diversity of insects (Marshall et al., 2003) and the seeds they produce are known to underpin species of conservation concern such as farmland birds. Indeed, a lack of seed resources in winter is thought to be one of the reasons for the dramatic declines of many farmland birds, although the dynamics of seed resources in agricultural landscapes is poorly understood and has been identified as a key area for further research (Butler et al., 2010).

In the UK, 77% of the land area is in agricultural production and most biodiversity is found on farmland (Hole et al., 2005). How the land is managed therefore has considerable implications for biodiversity. The vast majority of information on biodiversity declines in agro-ecosystems is clustered around particular groups of organisms such as the groups listed above. However, studies of the distribution and abundance of these groups may not provide the

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data needed for the sustainable management of agriculture. If land managers are to manage farmland biodiversity in the long term, then agro-ecologists advising policy-makers need to understand the ways in which species interact, since these interactions can have a profound impact on a community's response to species loss, stress, ecosystem service provision and ecological restoration (Memmott, 2009; Tylianakis et al., 2010). Thus in addition to determining the identity, quantity and energy value of seeds, in this paper we also consider how other species on the farm directly or indirectly depend upon seeds.

To date, studies of the interactions between seeds and seed-feeding animals have mainly focussed on natural systems (e.g. Carvalheiro et al., 2008; Heleno et al., 2009). But information regarding non-crop and weed seed productivity in agro-ecosystems is surprisingly rare, particularly at varying temporal and spatial scales. To our knowledge, no studies have examined the importance of seeds for farmland animal communities as a whole (i.e. for seed-feeding insects, birds and mammals), nor quantified seed food resources within the different farmland habitats throughout the year. Here we present data from all of the habitats on a whole farm. Understanding which habitats provide the highest seed abundance, species richness, biomass and energy at different times of the year is crucial for finding ways of optimising and restoring seed-feeding species on degraded farmland.

We chose an intensive study on a single farm in SW England rather than an extensive study of replicate farms; this intensive approach provided detailed baseline data not possible from extensive surveys of multiple farms (cf. Macfadyen et al., 2009). In food web studies logistical and funding constraints often mean that there is a choice between constructing multiple, small networks versus a single, highly resolved network (see Hegland et al., 2010). Both approaches have advantages and disadvantages. Here, our choice of a single (but typical) study site enabled detailed, within-farm replication across multiple habitats and provided the highly resolved foodweb data necessary for predicting the impacts of land management scenarios. Our intention is that the results of this study will motivate future larger-scale comparisons across multiple farms.

We quantified the abundance and diversity of post-dispersal. soil-surface seeds, within farm habitats (both crop and non-crop) at different times of the year. We also quantified pre-dispersed berries within uncultivated habitats, such as woodlands and hedgerows, because they are known to be important sources of food for farmland animals (Snow and Snow, 1988). We used a network approach to examine the importance of seeds as a food resource for farmland birds, mammals and insects and predicted the impact of farm management directly on seeds, and indirectly on the animals that depend on them. We had five objectives: (1) to estimate the abundance and diversity of seeds in the farmland habitats; (2) to quantify the biomass and energy content of seeds within these habitats and throughout the year; (3) to assess the importance of seeds as a food resource for farmland animals using qualitative and quantitative ecological networks; (4) to predict how habitat management impacts total seed biomass and energy; and (5) to predict how habitat management can cascade through the seed network and impact on both seed-feeding insects and their associated parasitoids. This last objective was intended to provide some insight into how habitat management can potentially impact on ecosystem service provision, here the ecosystem service of pest control.

2. Methods and materials

2.1. Overview of methods

We mapped all the habitats on an organic farm in SW England, and used a suction sampler to estimate the abundance and diver-

sity of fallen, soil-surface seeds in each habitat, and visual counts to estimate the abundance of berries in woodland and hedgerows. Throughout 2007 habitats were sampled quarterly over a 10 day period, each period representing Winter, Spring, Summer or Autumn. We applied empirically-derived correction factors to account for sampling biases and estimated seed abundance, biomass and energy content in each habitat as a resource for farmland animals. To examine the cascading impacts of farm management on the food-web, we sub-sampled plant species and reared out seed-feeding insects and their parasitoids. Based on the seed species inventory for the farm, we used the literature to construct a qualitative food-web in order to investigate, more generally, the importance of seeds in agro-ecosystems for insects, birds and mammals.

2.2. The study site

Fieldwork was conducted at Norwood Farm, Somerset, England (51°18.3'N, 2°19.5'W, Fig. 1). Norwood Farm is an organic (i.e. artificial chemical fertilisers and pesticides are prohibited), mixed lowland farm (approximately 125 ha in size) comprising 23 fields of arable (mainly cereal) and grass (short-term leys in arable rotation and permanent pasture). The percentage of landscape elements at Norwood Farm is typical of other organic farms in SW England studied by Gibson et al. (2007). For example, during the study, 11.6% of the area at Norwood Farm consisted of non-crop elements (i.e. woodland, hedges, margins and rough ground) and 56.2% consisted of grass fields, compared with regional averages of $13.6\% \pm 1.3$ SE and $57.9\% \pm 3.6$ SE respectively. We identified and mapped 15 farmed and non-farmed habitat types on the farm using GIS as follows: Farmed = (1) Fallow; (2) Ley (rye grass and red clover that were sown and grown for up to 5 years as part of the organic crop rotation); (3) Lucerne (grown as a crop for silage); (4) New ley (i.e. clover-rye grass ley which had been newly sown the previous year); (5) Permanent pasture; (6) Spring-sown barley; (7) Spring-sown oats; (8) Winter-sown oats; (9) Winter-sown triticale: (10) Winter-sown wheat. Non-farmed = (11) Grass margin (i.e. grass strips around cultivated fields – often part of agri-environment schemes); (12) Mature hedgerow; (13) New hedgerow (i.e. newly planted hedgerow dominated by young trees < 1.5 m high and grass); (14) Rough Ground (i.e. uncultivated areas around farm buildings, machinery storage areas) and (15) Woodland (Fig. 1).

2.3. Objective 1: to estimate the abundance and diversity of seeds in farmland habitats

We modified a hand-held, Stihl™ model BG 85 blower-vacuum (Stihl Incorporated, 536 Viking Drive, Virginia Beach, Virginia 23452) following the methodology of Penny et al. (2006). This obtained samples of soil-surface seeds, i.e. those recently fallen and not those buried deeply in the soil. We experimentally tested the efficiency of the suction sampling device at Norwood Farm by measuring the recovery of a known number of 4 seed size classes in seven habitats between November 2007 and February 2008 (Evans et al., 2009). Vacuum sampler efficiency was dependent on seed size, habitat type and exposure of seeds to environmental conditions and we used this information to calculate suction sampler correction factors (see below).

In 2007, we collected approximately 250 suction samples per quarter (Winter: between 5/2/2007 and 15/2/2007; Spring: between 8/5/2007 and 18/5/2007; Summer: between 20/8/07 and 31/8/07 (post-cereal harvest); Autumn: between 12/11/07 and 22/11/07 (post-ploughing for autumn-sown cereals)) from the 15 farm habitat types. We used GIS to obtain sampling points that were separated by >20 m and randomly located within each of

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