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The spatial distribution of phytophagous insect larvae in grassland soils

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ABSTRACT

Most research on soil dwelling phytophagous insect larvae has arisen from their functional roles as pests in agricultural systems, but few studies have considered their spatial distribution or the possible interactions between taxa, and none have investigated the effect of scale. In this study the individual and interspecific spatial distribution of wireworms (click beetle larvae – Elateridae), leatherjackets (crane fly larvae – Tipulidae), bibionid flies (Bibionidae) and sciarid flies (Sciaridae) over three scales, and the importance of spatial, biotic and scale variables, was assessed. Soil core samples were collected from 26 sites across six grass fields on a farm in South Devon, UK. Abundance and presence-absence data were analysed over the field, site and soil core scales using variance/mean ratio and non-metric multidimensional scaling (NMDS), and deviance partitioning was used to determine the importance of spatial, biotic and scale variables for individual taxa distribution. The spatial distribution of most taxa changed from an aggregated to a random distribution from the field to the core scale. Interspecific distributions of taxa also differed between scales, though some associations held at all scales. Deviance partitioning revealed that scale was the single most important variable influencing taxa distribution, whereas spatial and biotic variables were mostly of minor importance. The results suggest that variation between taxa is likely to be due to interactions between scale-specific environmental, biotic and stochastic factors and individual taxon biology, and emphasises the need to take scale into account when interpreting data from ecological studies.

1. Introduction

Soil communities have been described as the 'poor man's tropical rainforest', due to the relatively high level of biodiversity and large proportion of undescribed species they contain, and the limited information that is known on community structure and dynamics (Giller, 1996). Ninety percent of insects spend at least some part of their lifecycle in the soil (Klein, 1988), having an influence on, for example, the diversity of plant communities, competitive interactions among plants and the yield of agricultural systems (Hunter, 2001). Despite this, information on the distribution and abundance of soil dwelling insects is lacking.

Physical, chemical and biotic factors are known to determine the presence, size and survival of invertebrate populations within the soil, causing a patchy distribution (Curry, 1987). However, spatial scale, although long recognised by ecologists as an important component influencing species distributions (Wiens, 1989; Levin, 1992), has been somewhat neglected in ecological studies. It is well recognised that spatial scale of sampling and analysis affects the observed distributions, but it has often been seen as a complicating factor rather than included as an explanatory variable in its own right, and as such multi-scale experiments are rare (Sandel and Smith, 2009). Spatial structuring, through environmental and community processes, plays a functional role in ecosystems and in order to understand this, modelling spatial patterns at multiple spatial and temporal scales is critical (Borcard and Legendre, 2002; Borcard et al., 2004). Owing to the relatively recent growth in spatial statistical techniques there are now many methods of incorporating spatial location into studies to determine how space affects species presence and/or abundance (e.g. Legendre and Fortin, 1989; Borcard et al., 1992; Coomes et al., 1999; Lichstein et al., 2002; Cocu et al., 2005). In addition, information on the relative importance of biotic, environmental and spatial factors to individual species distributions would be useful in terms of managing pests and biodiversity, and may allow better predictive models to be produced. A combination of methods that describe the spatial distribution and underlying patterns in the data, such as indices of dispersion and multivariate techniques, together with methods that use the spatial location (e.g. geographical coordinates) of samples as an indication of spatial pattern, such as deviance partitioning, might enable a better overall understanding of species distributions to be obtained.

In this study, wireworms (click beetle larvae – Coleoptera: Elateridae), leatherjackets (crane fly larvae – Diptera: Tipuli-

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dae), sciarid fly larvae (Diptera: Sciaridae) and bibionid fly larvae (Diptera: Bibionidae) were sampled from grassland soil. These taxa are commonly found in abundance in grassland, where they feed on grass roots, but when present in arable land some species can cause considerable damage to crop roots. Therefore research has mainly focused on their role as agricultural pests. Previous studies in the UK have attempted to determine the factors affecting the distribution of wireworms (Salt and Hollick, 1946; Parker and Seeny, 1997) and leatherjackets (McCracken et al., 1995), but without inclusion of either spatial, scale or biotic variables, or all three, and studies on interactions between macro-invertebrates in agricultural land and the influence of other species on the distribution of soil insect larvae are lacking. A good understanding of pest distribution, and the factors affecting this, is essential to the development of sustainable management strategies, in order that control methods can be targeted at damage causing species at the appropriate scale. For soil living pests, this is particularly important since incorporation of pesticide into the soil can be inefficient, often even with high rates of application, and many of the persistent chemicals which were effective have now been withdrawn from use (Grove et al., 2000).

With these issues in mind, the aims of our study are:

1. To assess the effect of scale of sampling, and the contribution of space, biotic interactions and scale to soil insect larvae distribution.
2. To determine whether there are any interspecific relationships between taxa, and how these relationships vary with the scale of sampling.

2. Methods

2.1. Study site and sampling

As part of a study on the use of water traps to predict the size of leatherjacket populations soil samples were collected from 26 sites over 6 grass fields from Seale Hayne Farm, South Devon, UK, between 15th January and 31st March 2008. Apart from one field which was a permanent ley, all fields were in grass for at least 3 years before sampling, previously being in an informal rotation with cereals and maize. Soils were brown earths of the Highweek and Trusham series. At each site samples were collected from the intersections of 24 radii at 15° intervals with concentric circles at 5, 10, 20 and 40 m from a central point. Soil cores were collected using a 5 cm diameter plastic pipe, which was pushed to a depth of approximately 10 cm. In total 96 soil samples were collected from each site, with the exception of four sites which were truncated due to sample points overlapping field boundaries and/or a stream, which equates to an area of 4.86 m^2 of soil sampled across the study site.

2.2. Extraction and identification of larvae

Larvae were recovered from soil cores using heat extraction (Blasdale, 1974) and placed into separate tubes containing 70% ethanol. Leatherjackets were assumed to be *Tipula paludosa* Meigen, as no other species had been captured as adults using water traps placed at the sites previously; Humphreys et al. (1993) found this assumption to be correct for the areas surveyed in their study. Bibionid larvae were identified as either *Bibio johannis* L. or *Dilophus febrilis* L. based on the posterior spiracles, using a light microscope (Brindle, 1962). Sciarid larvae could not be identified to species by their morphology and so remained unidentified and grouped as 'Sciaridae'. Wireworm DNA was extracted using a standard salt/chloroform protocol and resuspended in 0.01× TE buffer (Rico et al., 1992). A terminal restriction fragment length polymorphism (T-RFLP) technique (Ellis et al., 2009) was used to identify wireworms of the species *Agriotes obscurus* L., *Agriotes sputator* L. and *Agriotes lineatus* L. Other species were grouped together as 'non-*Agriotes*'. There were also instances in which no restriction fragment was produced, possibly due to degraded DNA. These samples have been grouped together as 'unknown wireworms'.

2.3. Data analysis

Ecological data often tend to be spatially autocorrelated, where observations from nearby locations are more similar than would be expected by chance, driven by various environmental and biotic processes (Legendre and Fortin, 1989; Lichstein et al., 2002; Kissling and Gudrun, 2008). This lack of independence violates the assumptions of most traditional statistical tests, resulting in inflation of Type I errors which can affect the interpretation of results. Moran's autocorrelation coefficient (I) was calculated using Spatial Analysis in Macroecology (SAM) software v.3.1 (Rangel et al., 2006) for each species, using geographic distances with 21 distance classes (the default) and default distance class size with equal distances. Due to the low abundance of the taxa sampled, the significance of the Moran's I values were not tested, as when applied to data with many double zeros the degree of autocorrelation may be overestimated (Legendre and Fortin, 1989). Instead, the correlograms, in which autocorrelation values are plotted against distance classes and the Moran's I values alone were checked for spatial autocorrelation. It was determined that no spatial autocorrelation was present and as a result standard statistical tests were used for the analysis.

The variance to mean ratio (VMR) was used as an index of dispersion to determine the distribution of individual taxa at each scale, using species abundance data (Taylor, 1961). This gives an idea of the spatial *distribution* and underlying patterns in the data, based on the frequency distribution of number of specimens per sample unit. However, it is not an indication of spatial *pattern*, which uses the spatial location (e.g. geographical coordinates) of samples rather than count data (Binns et al., 2000).

Non-metric multidimensional scaling (NMDS) was computed using species presence–absence data in Brodgar v.2.5.7 (Highland Statistics Ltd., 2006), to visualise the relationships between all taxa at each scale. Jaccard's coefficient, an asymmetrical binary coefficient which excludes double zeros (i.e. where the fields, sites or cores being compared both contain no taxa) was used as a measure of association between species (Legendre and Legendre, 1998). The optimal number of dimensions, or axes m, was determined by selecting the ordination with minimum STRESS, a measure of deviation from monotonicity (Kruskal, 1964); the number of axes was plotted against the STRESS values for each value of m. A clear change in stress (the elbow effect) indicates the optimal value of m (Zuur et al., 2007). For the field scale $m = 4$, STRESS = 0.0093, for the site scale $m = 3$, STRESS = 0.0247 and for the core scale $m = 4$, STRESS = 0.068.

Due to the high number of zero counts geostatistical methods were not used to assess spatial pattern as this would result in violation of the assumptions of these tests. Instead, partial linear regression, using a Generalized Linear Model (GLM) with a binomial distribution for taxa presence–absence data and logistic link function, was used to partition the deviance explained by space (latitudinal and longitudinal coordinates), biotic influences (presence–absence data for all other species) and scale for each taxon (Legendre and Legendre, 1998; Lobo et al., 2002). GLM allows for distributions other than the normal distribution and is also not constrained by the assumption of linearity between dependent and independent variables (Lobo et al., 2002). This makes it a useful technique for analysing ecological data, which is often non-normally distributed. Scale, as a nominal variable, was split further into 'field' (numbers 1–6) and 'site' (numbers 1–26) to