Small mammal responses to long-term large-scale woodland creation: the influence of local and landscape-level attributes

Elisa Fuentes-Montemayor*, [1], Mark Ferryman[2], Kevin Watts[1, 2], Nicholas A. Macgregor[3, 4], Natasha Hambly[1], Stephen Brennan[1], Ruth Coxon[1], Holly Langridge[1] & Kirsty J. Park[1]

* Corresponding author. Email: ef12@stir.ac.uk

[1] Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, FK9 4LA, UK.

[2] Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK.

[3] Former affiliation: Natural England, Nobel House, 17 Smith Square, London SW1P 3JR, UK.

[4] Current affiliation: Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury, Kent, CT2 7NR, UK.

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ABSTRACT:

Habitat loss and fragmentation greatly affect biological diversity. Actions to counteract their negative effects include increasing the quality, amount and connectivity of semi-natural habitats at the landscape scale. However, much of the scientific evidence underpinning landscape restoration comes from studies of habitat loss and fragmentation, and it is unclear whether the ecological principles derived from habitat removal investigations are applicable to habitat creation. In addition, the relative importance of local- (e.g. improving habitat quality) vs. landscape-level (e.g. increasing habitat connectivity) actions to restore species is largely unknown, partly because studying species responses over sufficiently large spatial and temporal scales is challenging. We studied small mammal responses to large scale woodland creation spanning 150 years, and assessed the influence of local- and landscape-level characteristics on three small mammal species of varying woodland affinity. Woodland specialists, generalists and grassland specialists were present in woodlands across a range of ages from 10 to 160 years, demonstrating that these species can quickly colonize newly created woodlands. However, we found evidence that woodlands become gradually better over time for some species. The responses of individual species corresponded to their habitat specificity. A grassland specialist (*Microtus agrestis*) was influenced only by landscape attributes; a woodland generalist (*Apodemus sylvaticus*) and specialist (*Myodes glareolus*) were primarily influenced by local habitat attributes, and partially by landscape characteristics. At the local scale, high structural heterogeneity, large amounts of deadwood and a relatively open understory positively influenced woodland species (both generalists and specialists); livestock grazing had strong negative effects on woodland species abundance. Actions to enhance habitat quality at the patch scale focusing on these attributes would benefit these species. Woodland creation in agricultural landscapes is also likely to benefit larger mammals and birds of prey feeding on small mammals and increase ecosystem processes such as seed dispersal.

KEYWORDS: ecological networks, forest, habitat creation, habitat restoration, landscape-scale conservation, reforestation, woodland creation, WrEN project

1. INTRODUCTION

Most ecosystems on Earth have been severely affected by habitat loss and fragmentation resulting from anthropogenic activities such as conversion to agricultural land (Haddad et al. 2015). The ecological consequences of habitat destruction and fragmentation have been extensively studied; these include long-term changes to the habitat structure of remaining fragments, disruption of ecological processes and biodiversity declines on a global scale (Haddad et al. 2015). Although the ecological impacts of habitat fragmentation *per se* on biodiversity have been debated (e.g. Fahrig 2017; Fletcher et al. 2018), there is consensus that habitat loss is one of the main causes of the current ecological crisis (IPBES 2019). Conservation efforts to counteract the negative impacts of habitat loss and fragmentation on biodiversity and ecosystem functioning are often targeted towards protecting remnant areas of natural and semi-natural habitat. In addition, large-scale restoration actions to increase the quality, amount and connectivity of semi-natural habitats across vast areas of land are increasingly implemented worldwide (e.g. *Endangered Landscapes Programme* in Europe and *Yellowstone to Yukon Conservation Initiative* in North America). However, much of the scientific evidence currently used to underpin landscape restoration strategies comes from studies of habitat loss and fragmentation, and it is unclear whether the ecological principles derived from habitat removal investigations are applicable to habitat creation and restoration processes (e.g. Munro et al. 2007; Naaf & Kolk 2015). This is because some species might persist in remnant patches for some time after fragmentation has occurred, potentially masking the effects of important factors influencing colonization and establishment events (Jackson & Sax 2010). As a result, there is much debate in the scientific and conservation communities on how to prioritize alternative restoration actions (e.g. increasing habitat quality *vs*. amount *vs*. connectivity) to re-build resilient networks of habitats (e.g. Isaac et al. 2018).

We know surprisingly little about the ecological consequences of creating and restoring habitats at large spatial and temporal scales, and about the relative value of potential actions to restore species and the functions they perform in ecosystems. The lack of empirical studies comes partly from the challenges associated with studying landscapes over sufficiently large spatial and temporal scales (e.g. to account for time lags in species colonization and capitalization of resources in new habitat patches) required to understand the ecological consequences of habitat creation and restoration activities. These challenges are more pronounced for habitats with slow development rates and of important conservation concern, such as woodlands.

Woodland is one of the most biodiverse biomes on Earth and an important habitat for many wildlife species ("woodland" is the term commonly used in the United Kingdom (UK) to describe any forested area; for convenience, we use this term hereafter in the paper). Historically, woodland cover has been drastically reduced, with worldwide deforestation resulting in a 50% decrease in woodland cover over the last three centuries (Ramankutty & Foley 1999). As well as the reduction in total cover, it has been estimated that 70% of remaining woodland is within 1 km of an edge, exposed to the impacts of an anthropogenic matrix (Haddad et al. 2015). Over recent decades, deforestation rates have slowed and woodland extent has begun to increase in some countries, particularly in temperate regions (Keenan et al. 2015). In the UK, a long history of deforestation resulted in woodland cover being reduced from a post-glacial high of 70% to a low of 5% at the beginning of the 19th century. Since then, woodland creation has increased this figure to approximately 13% of land (Forestry Commission 2019). These historical changes in land use have resulted in current landscapes containing many woodland patches that were established on former agricultural land over the last *ca.* 150 years. Increasing woodland cover further is part of environmental policy in the UK; for instance, the English Government aims to plant 180,000 ha over the next 25 years (Defra 2018), whilst the Scottish Government has a target of planting 10,000 ha of trees per year (Scottish Government 2018). Large-scale woodland creation programs have generally been successful at increasing woodland amount (and sometimes connectivity; e.g. Quine & Watts 2009); however, their effectiveness in restoring species and ecosystem processes is largely unknown. Addressing this knowledge gap is one of the aims of the Woodland Creation and Ecological Networks (WrEN) project, a large-scale natural experiment designed to study the effects of 160 years of woodland creation on biodiversity in UK landscapes (Watts et al. 2016); WrEN provides a unique opportunity to assess the long-term effects of woodland creation on biodiversity and inform landscape-scale conservation.

We have selected small mammals as one of the WrEN study taxa because they are a biologically diverse group (e.g. the Order Rodentia represents 40% of all known mammal species) inhabiting a wide variety of terrestrial habitats. They are an important component of woodland ecosystems, where they are abundant and perform important ecological roles including seed dispersal and arthropod predation (e.g. Perea et al. 2011); they are also an important food resource for birds of prey (e.g. owls; Askew et al. 2007) and mammals (e.g. foxes; Baker et al. 2006), so changes in their populations might have knock-on effects on ecosystems. Small mammals are also useful indicators of environmental change in the countryside (e.g. in arable landscapes; Coda et al. 2014; Tattersall et al. 2001) and are known to rapidly respond to changes in woodland management (e.g. browsing intensity; Bush et al. 2012).

Many small mammal species are well-adapted to live in human-modified environments (e.g. agricultural areas; Gentili et al. 2014); however, others have been affected by anthropogenic activities such as agricultural intensification, habitat loss and fragmentation (e.g. Fitzgibbon 1997; Fischer & Schröder 2014; Melo et al. 2017). Differential responses of small mammals to woodland loss and fragmentation resulting from agricultural expansion depend partly on a species' habitat breadth and its ability to move through the non-woodland matrix; in general, whilst generalist species can often easily move through agricultural land and capitalize on alternative resources (e.g. arable crops surrounding woodland fragments), woodland specialists with stricter habitat requirements usually perceive the matrix as hostile and are negatively impacted by the loss, fragmentation and degradation of woodlands (Henein et al. 1998; Nupp & Swihart 2000; Vieira et al. 2009). Similarly, generalist species are often more abundant in smaller woodland patches (and near woodland edges) than woodland specialists which require larger woodland patches and low edge-to-interior ratios (e.g. Silva et al. 2005; Pardini et al. 2005; Nupp & Swihart 2000; Telleria et al. 1991).

Small mammal population dynamics in fragmented habitats are thus influenced by a combination of local- and landscape-level characteristics. Firstly, landscape-level factors, such as the degree of connectivity and amount of woodland surrounding a woodland patch, influence small mammal abundance most likely through mediating dispersal processes (e.g. Fitzgibbon 1997; Marsh & Harris 2000; Michel et al. 2006; Nupp & Swihart 2000; Silva et al. 2005). The type of matrix surrounding woodland patches can also influence small mammal movements (e.g. with intensively cultivated fields being 'permeable' for generalist species and mostly avoided by woodland specialist which favor semi-natural habitats; Gentili et al. 2014).

Secondly, local-level attributes are important in determining the suitability of woodland patches for small mammals. For instance, small mammal abundance has been linked to vegetation characteristics, such as foliage density and stratification (Pardini et al. 2005), understory height and amount of fallen logs (Marsh & Harris 2000). Resource availability (e.g. seed crop size and food plant abundance) within a patch can also strongly influence small mammal population size (e.g. Mallorie & Flowerdew 1994; Tew et al. 2000). Furthermore, the requirements of individuals within populations are often sex-dependent and change over time such that, for example, pregnant or lactating females have particularly high energy requirements. This can lead to sex- or age-biased populations resulting from individual differences in habitat selection (e.g. females selecting larger patches or higher quality habitats than males; Diaz et al. 1999; Rosalino et al. 2011) or from displacement by more competitive animals (e.g. adults over juveniles, or those defending breeding territories over non-breeding animals; Diaz et al. 1999). In addition, intrinsic population factors such as density-dependent regulation (e.g. through reduced reproduction or increased mortality rates) can also impact population size and result in changes in population structure, for instance leading to age-biased populations dominated by older individuals if reproductive rates are low (e.g. Montgomery 1989a,b).

While small mammal ecology in relation to woodland loss and fragmentation has been extensively studied (e.g. in woodland remnants within agricultural landscapes; Silva et al. 2005; Telleria et al. 1991; Vieira et al. 2009), small mammal responses to woodland creation and restoration have received relatively little attention. In other systems (e.g. agricultural), small mammals have been shown to respond quickly to land management changes, such as the implementation of agri-environment schemes and the creation of 'set aside' fields (e.g. Macdonald et al. 2007; Tattersall et al. 2001). Small mammals have also been shown to capitalize on new resources provided by new grassland plots (< 10 years old; Churchfield et al. 1997) and young farm woodlands (< 11 years since planting; Moore et al. 2003). Small mammal communities can be influenced by natural (e.g. wildfires) and anthropogenic (e.g. clearcutting and burning) disturbances which restore forests to early successional stages, but the directionality of these effects is often species-specific (e.g. Zwolak 2009). However, these studies have investigated small mammal responses to land management changes and habitat creation over short temporal scales; this can potentially result in an under- or over-estimation of the longer-term effects of habitat creation and restoration (e.g. if a habitat becomes gradually 'better' for a species as it matures, or if species associated with young and open habitats 'lose out' as a habitat matures).

Here, we assessed the effects of a chronosequence of woodland creation spanning 150 years on small mammal communities. We surveyed 105 temperate woodland patches (which form part of the WrEN project), ranging in age from 10 to 160 years created on former agricultural land across England and Scotland, for three small mammal species with different habitat specialization (a grassland specialist, a woodland generalist and a woodland specialist; Appendix S1). We addressed the following questions:

1) Are there any time lags in small mammal responses to woodland creation (potentially associated with colonization lags driven by landscape factors, or with delayed availability of resources driven by slow woodland development)? If so, over what temporal scales?
2) What is the relative importance of a) landscape-level attributes (e.g. woodland amount and degree of connectivity; potentially important for dispersal processes), b) local woodland characteristics (e.g. patch age and vegetation structure; potentially associated with habitat quality, resource availability and species establishment) and c) intrinsic population factors for small mammals in historical woodland creation sites?

Species responses to habitat creation and development are likely to depend on life-history traits such as habitat specialization (see Appendix S1 for information on the degree of specialization of the three study species); therefore, we expected grassland specialists and woodland generalists to colonize new woodland patches and capitalize on new resources relatively quickly (e.g. higher abundance in younger, more open woodlands in early developmental stages for the grassland specialist; null to moderate positive effects of woodland age for the woodland generalist). For woodland specialists, we expected a delayed response to woodland creation (e.g. higher abundance in older woodlands which have developed an ‘old-growth’ habitat structure). We expected other population characteristics (i.e. proportion of females, juveniles, and reproductively active individuals) to follow similar trends to those described for abundance above (i.e. with increases in these metrics seen as a favorable sign and an indication of higher habitat quality). Furthermore, we expected the importance of local- and landscape-level attributes to vary according to species habitat specialization (e.g. with woodland specialists being more strongly influenced by local woodland habitat quality, amount and connectivity than generalist species).

2. MATERIAL AND METHODS

2.1 Study area and site selection

Our study sites (part of the WrEN project) were located in two regions of the United Kingdom (central Scotland and central England) dominated (>70%) by agricultural land and representing fairly typical lowland landscapes in these countries. We used a systematic site-selection protocol to identify 105 secondary, broadleaved woodland patches created over the past 160 years on former agricultural land (see Watts et al. 2016 for further details on site selection and Fig. 1 in Watts et al. 2016 for a map of sites). Sites ranged in age (10–160 years old), size (0.5–30 ha), amount of surrounding broadleaved woodland (0–22% of area within 1 km) and proximity to nearest broadleaved woodland (10–1570 m). Study sites were > 1 km from each other (in most cases > 3 km). We surveyed woodlands of different character evenly throughout the duration of the field seasons and across the study areas, avoiding any seasonal or spatial bias.

2.2 Landscape attributes

We used digital maps and GIS software (ArcGIS 10.2; ESRI, Redlands, California, USA) to quantify the proportion of different land cover types within 1 km of each study site. We measured broadleaved woodland using National Forest Inventory (NFI) data (Forestry Commission 2012) and other semi-natural habitats (e.g. rough grassland and scrub) using Land Cover Map 2007 data (Morton et al. 2011). We also quantified the Euclidean distance to the nearest broadleaved woodland (using NFI data) and the density of hedgerows (manually mapped using satellite imagery from Google Earth Pro; Google Inc. 2017) within 1 km of each study site. This spatial scale of 1 km was selected because it encompasses average home range sizes of small mammal species present in the study areas (e.g. Tattersall et al. 2001).

2.3 Local attributes

We conducted field surveys to characterize the vegetation structure of all woodland patches using the point-centered quarter method along an edge-to-interior transect to collect data on tree density, tree diameter at breast height (DBH; only trees ≥7 cm DBH were measured), understory cover (%) and amount of woody debris (see Table 1 for further details). We also recorded livestock presence/absence within each woodland. We determined woodland age (i.e. the time-period when each woodland patch ‘appeared’ in maps) using the OS Historic Digimap collection (EDINA 2013). We quantified woodland patch size using NFI data (Forestry Commission 2012) and GIS software (ArcGIS 10.2; ESRI, Redlands, California, USA).

2.4 Small mammal surveys

Small mammals were live-trapped between 24th June and 26th August 2013 (Scotland) and 23rd June and 1st September 2014 (Scotland and England) using Ugglan traps #2 (multi-catch wire mesh traps with roof covers; Grahnab, Sweden). Traps were arranged in a 9x4 grid (i.e. 36 traps per night per woodland) with traps spaced 10 m apart in the interior of each woodland (as far from the edges as possible), operated for four continuous nights at each site and checked/reset every morning. Traps were baited with grain and fresh carrot (to prevent dehydration) and bedding material was provided. Traps were fitted with escape holes (12 mm in diameter) to prevent mortality in the eventuality of catching shrews (Gurnell & Flowerdew 2006). Individuals captured were identified to species and temporarily marked by fur clipping to identify recaptures; we also took morphometric measures (total length, tail length and weight) and determined sex, age class (juvenile, adult) and reproductive condition (active, inactive) based on characteristics described by Gurnell & Flowerdew (2006); animals were released at the site of capture immediately afterwards.

2.5 Small mammal population metrics (response variables)

We evaluated the effects of landscape-level attributes and local woodland characteristics (see sections 2.2 and 2.3) on small mammal abundance and population structure (i.e. proportion of juveniles, females and reproductively active individuals). 'Abundance' was estimated as the total number of individuals captured in each woodland patch (excluding recaptures and juveniles, as the latter presumably do not yet have established territories). We also estimated population size using the Lincoln-Petersen method; however, given that the two metrics were strongly correlated (Appendix S2), and that we were interested in small mammal *relative* abundance (i.e. differences between sites, and how these relate to site characteristics) rather than in total population size, we used the simpler metric of 'abundance' for statistical analyses. 'Juvenile ratio' was the number of juveniles divided by the total number of individuals in a woodland (excluding recaptures). 'Female ratio' was the number of females divided by the total number of individuals in a woodland (excluding recaptures and juveniles). 'Female reproductive ratio' was the number of reproductively active females divided by the total number of females in a woodland (excluding recaptures and juveniles); we chose to focus on females because they contribute to reproductive productivity more than males. 'Body condition' (used as an index of food resource availability) was calculated by running linear regressions of body weight and total length of all individuals (excluding recaptures, juveniles which have not yet reached their full size/weight, and pregnant females which carry additional weight), and then using regression residuals as an index of body condition of each individual (Schulte-Hostedde et al. 2001); we then calculated average body condition values for each woodland site and used this as an interim variable to test for resource-dependency effects on small mammals. We conducted separate analyses for each small mammal species.

Preliminary analyses indicated that there were no significant differences in the abundance of small mammals (of any species) between 2013 and 2014 (Appendix S3), so data for the two survey seasons were pooled for subsequent analyses and the effect of 'year' was ignored. Preliminary analyses also showed that small mammal abundance differed between England and Scotland, so 'region' was incorporated as a factor in subsequent analyses.

2.6 Statistical analyses, model specification and rationale

We used piecewise Structural Equation Models (piecewiseSEMs; Lefcheck 2016) to quantify the relative importance of landscape-level attributes and local woodland characteristics on small mammal population metrics. SEMs are a multivariate technique that can be used to test whether a priori hypothesized direct and indirect causal relationships between variables are supported by observed data, and to compare relative effect sizes of predictor variables (e.g. to assess the relative importance of local- *vs.* landscape-level attributes). SEMs also identify relationships between variables that were not initially predicted (i.e. 'missing paths'); these can then be incorporated into the models, or otherwise allowed to freely covary if they are not considered causative but are strongly correlated.

We used ecological theory and evidence to guide the construction of a global conceptual model (Fig. 1) of hypothesized direct and indirect causal relationships (presented as a series of GLMs) between predictor variables described in Table 1 and response variables described in section 2.5. Our conceptual model incorporated: 1) landscape-level attributes likely to influence dispersal processes (e.g. can small mammals *reach* woodland patches?); 2) local-level attributes likely to determine habitat suitability (i.e. can small mammals *use* woodland patches?); and 3) 'biological' variables (i.e. abundance and body condition) likely to indicate density- and resource-dependency effects (Fig. 1). Specifically, we made the following predictions:

At the landscape level, we accounted for the fact that land-use intensity differs between the two study areas (e.g. higher proportion of farmland and lower proportion of woodland cover in England than in Scotland; Watts et al. 2016). We therefore tested for direct effects of 'region' on small mammals (e.g. due to differences in the relative abundance of different small mammal species between England and Scotland) and indirect effects mediated through changes in the proportion of different land cover types, specifically woodland and other semi-natural habitats (e.g. scrub and rough grassland) which were expected to positively influence small mammal populations. Preliminary data analyses indicated higher hedgerow densities in England than in Scotland, and this was incorporated into the conceptual models. Additionally, woodland isolation was expected to be negatively related to proportion of woodland in the landscape, and we tested for direct effects of woodland % on small mammals and indirect effects mediated through decreased distance to nearest woodland patch in landscapes with a higher proportion of surrounding woodland.

At the local level, we expected patch age to influence woodland vegetation structure; specifically, that older woodlands have lower tree densities, higher structural complexity (quantified as standard deviation of tree diameter), larger amounts of woody debris and a denser understory cover (the latter was also hypothesized to be negatively influenced by presence of grazing stock). We tested for direct effects of patch age on small mammals (e.g. older woodlands having been wooded long enough to allow several colonization events leading to higher population abundance) and also for indirect effects of patch age mediated through changes in woodland vegetation structure (e.g. older woodlands having higher structural complexity and potentially providing more resources for small mammal populations). We predicted the presence of grazing stock to have a direct negative effect on small mammal populations (through disturbance) and an indirect effect by reducing the amount of understory cover (potentially used as shelter). We expected larger woodlands to provide more resources and sustain larger small mammal populations.

We also expected density- and resource-dependency effects, for example negative associations between abundance and reproductive female ratio, and positive associations between female body condition (as an index of food availability) and reproductive female ratio. ‘Abundance’ and ‘body condition’ were therefore included as interim variables in models for age, sex and reproductive condition ratio.

In addition, ‘Date’ (days since first small mammal survey of the season) was included as a covariate to account for potential seasonal variations. Models using counts as response variables (e.g. abundance) were fitted using a Negative Binomial error distribution to account for overdispersion (function glm.nb in the MASS v7.3-50 package). A Binomial error distribution was used for response variables expressed as proportions (e.g. female ratio), which were weighted by the value used as the denominator to calculate any given proportion (e.g. female ratio = female adults / total adults; weights = total adults). All vegetation and landscape metrics used as response variables (most of these log10 or square root transformed to fit a normal distribution), were modelled with Gaussian error distributions. All models were validated by visual examination of residuals (e.g. plotting residuals *vs*. fitted values to check for constant variance; Crawley 2013). In the Results we present standardized parameter estimates (centered and scaled) to compare relative effect sizes of predictor variables and R^2 values as a measure of model fit; statistical details are presented in Appendix S4. All statistical analyses were conducted in R v3.5 within Rstudio v1.1.456 (R Core Team 2018; RStudio Team 2018).

3. RESULTS

3.1 Effects of patch age, management and regional context on the attributes of woodland creation sites

Woodland age had a significant effect on some vegetation attributes; specifically, structural heterogeneity (quantified as standard deviation in tree diameter) and amount of woody debris were higher in older woodlands, whilst tree density was lower (Figs. 2-4; Appendix S5). Understory cover was not influenced by woodland age, but it was significantly lower in sites where grazing stock was present (Figs. 2, 3a & 4a; Appendix S5). At the landscape scale, the amount of surrounding broadleaved woodland and other semi-natural habitats was significantly higher in Scotland than in England, while hedgerow density was lower. Distance to nearest broadleaved woodland was lower in landscapes with a higher proportion of broadleaved woodland (Figs. 2-4).

3.2 Small mammal populations in woodland creation sites

We surveyed a total of 38 sites in England and 67 in Scotland for a total of 15,120 trap nights (i.e. 105 sites x 36 traps x 4 survey nights). We captured small mammals in 93% of sites (i.e. 98 out of 105) and recorded 1,676 individuals of four species; the most common were Bank voles (*Myodes glareolus*; a woodland specialist) followed by Wood mice (*Apodemus sylvaticus*; a woodland generalist), Field voles (*Microtus agrestis*; a grassland specialist) and Yellow-necked mice

(*Apodemus flavicollis*; another woodland specialist) (Table 2). Due to small sample size, we restricted data analyses for *M. agrestis* to adult abundance; *A. flavicollis* was excluded from any further analysis. Overall sex ratios (male:female) for *M. glareolus* and *A. sylvaticus* were 0.47:0.53 (n=760 adults) and 0.69:0.31 (n=456 adults) respectively. Fifty-nine percent of *M. glareolus* and 73% of *A. sylvaticus* adult females were reproductively active at the time of trapping. Juveniles comprised 24% of *M. glareolus* and 20% of *A. sylvaticus* individuals.

3.2.1 Effects of landscape-level attributes, local woodland characteristics and intrinsic population factors on small mammals

Small mammal populations were influenced by both local- and landscape-level woodland attributes, but associations with specific variables were species-specific (see Appendix S6 for plots of key associations). After accounting for seasonal (positive effect of date) and regional (higher abundance in Scotland than England) effects, the abundance of the grassland specialist *M. agrestis* was significantly higher in woodlands surrounded by larger amounts of semi-natural habitat within 1 km. No other factors significantly influenced the abundance of this species (Fig. 2).

After accounting for seasonal effects (positive effect of date), the abundance of the woodland generalist *A. sylvaticus* was negatively impacted by the presence of grazing stock (direct effect) and was higher in woodlands with larger amounts of woody debris and higher structural heterogeneity (i.e. older woodlands), located in close proximity to their nearest broadleaved woodland and with relatively low proportion of semi-natural habitat within 1 km (marginal effect; Fig. 3a). There were proportionally more *A. sylvaticus* females in smaller woodlands and in woodlands where adults were in better body condition (marginal effect); in turn, *A. sylvaticus*'s body condition was higher in Scotland than in England, and marginally higher in woodlands with higher tree densities (i.e. younger woodlands), indicating an indirect negative effect of woodland age on female ratio (Fig. 3b). After accounting for regional differences (10% more reproductive females in England than Scotland), the proportion of reproductively active females was higher in woodlands with relatively little understory cover (i.e. where grazing stock was present), and where adult females were in better body condition (Fig. 3c). After accounting for regional differences (13% more juveniles in Scotland than in England), there were proportionally more *A. sylvaticus* juveniles in woodland patches surrounded by lower amounts of broadleaved woodland (marginal effect) and other semi-natural habitats; the proportion of juveniles was also higher in woodlands where adults were in better body condition, indicating an indirect negative effect of woodland age on juvenile ratio (i.e. younger woodlands with higher tree densities result in marginally better adult body condition and higher proportions of juveniles; Fig. 3d).

For the woodland specialist *M. glareolus*, abundance was negatively impacted by the presence of grazing stock, and this was a direct effect (i.e. not mediated through changes in the vegetation structure; Fig. 4a). There were proportionally more *M. glareolus* females in woodland patches with relatively little understory cover and with higher hedgerow densities in the surrounding landscape (marginal effect; Fig. 4b). After accounting for regional differences (8% more reproductive females in England than Scotland), the proportion of *M. glareolus* reproductively active females was higher in woodlands with relatively little understory cover and of smaller sizes (marginal effect). The proportion of reproductive females was also positively associated with female body condition and negatively with adult abundance (Fig. 4c). After accounting for regional differences (8% more juveniles in Scotland than England) there were proportionally more *M. glareolus* juveniles in older woodlands (direct effect not mediated through changes in vegetation structure) and located in landscapes with lower hedgerow densities within 1 km (Fig. 4d). Additionally, the proportion of *M. glareolus* juveniles was negatively associated with adult body condition, which was in turn positively influenced by tree density, indirectly reinforcing the positive effect of woodland age on *M. glareolus* juvenile ratio (i.e. older woodlands with lower tree densities resulting in lower adult body condition and higher juvenile ratio; Fig. 4d).

4. DISCUSSION

We used an array of historically created woodland sites to examine small mammal responses to woodland creation over long temporal (up to 160 years) and large spatial (over 15,000 km square) scales. Specifically, we assessed the relative influence of local- and landscape-level attributes of secondary woodland sites, and of density- and resource-dependency effects, on three small mammal species of varying woodland affinity. In accordance with our expectations, we found species-specific responses which correspond to some degree with species' habitat specificity. For example, we detected differences in the relative importance of local- and landscape-level attributes for grassland *vs.* woodland species, and also observed differential responses to woodland age and habitat structure.

4.1 Time lags in small mammal responses to woodland creation

Woodland age can influence species occurrence and abundance in two ways; firstly, older woodlands have been wooded long enough to allow more colonization events by woodland species which are often poor dispersers; secondly, older woodlands are often characterized by an old-growth habitat structure, such as high structural heterogeneity and large amounts of deadwood. Such characteristics influence habitat quality and are often important in determining the abundance and diversity of many species groups (Humphrey et al. 2014).

All small mammal species in this study were detected in woodlands across a range of ages, even in relatively young sites (*ca*. 10 years since planting); their presence in these sites demonstrates that small mammals are quickly colonizing and capitalizing on new resources in secondary woodlands.

Although we did not detect any significant effects of woodland age on the grassland specialist *M. agrestis*, we observed the highest abundance in younger sites < 60 years old. This species was present in less than a third of our study sites, and when they occurred it was in relatively low abundance (average 3 and maximum 14 individuals per site). In comparison, a previous study conducted in young (< 11 years old) farm woodlands reported this species was present in the majority of their sites being ‘quite numerous’ (Moore et al. 2003). This suggests that, according to our expectations, *M. agrestis* prefer to use relatively young woodlands; however, this grassland specialist can continue to use older woodlands particularly if these are in landscapes with high proportions of semi-natural habitats (e.g. unimproved grasslands).

We did not detect any direct effects of woodland age on the woodland generalist *A. sylvaticus*, suggesting that this species is able to reach secondary woodlands regardless of time since planting. This woodland generalist was however more abundant in woodlands with larger amounts of woody debris and higher structural heterogeneity (i.e. older woodlands), indicating that woodlands become more suitable for *A. sylvaticus* as they mature and develop an ‘old-growth’ habitat structure. Previous studies have also found higher overall abundance and number of breeding animals in more mature woodlands with larger trees and higher amounts of fallen logs (Fitzgibbon et al. 1997; Marsh & Harris 2000). Contrastingly, we detected weaker indirect effects of woodland age indicating that adult body condition is marginally better in younger woodlands with relatively high tree densities; this in turn resulted in slightly higher proportions of females and juveniles in younger woodlands.

In contrast to our expectations, the abundance of the woodland specialist *M. glareolus* did not increase with woodland age, indicating that this species can colonize woodlands soon after tree establishment (i.e. within 10 years), and that habitat quality does not markedly increase over time for this species. However, the proportion of juveniles of this species was higher in older woodlands, suggesting that these are higher quality habitats for *M. glareolus*; this effect was only partially mediated through habitat structure and resource availability (older woodlands with lower tree densities resulting in lower adult body condition and higher juvenile ratios). The weaker (positive) direct effect of woodland age on juvenile ratio could potentially be explained by habitat characteristics unaccounted for in our analysis.

4.2 Relative effects of landscape-level attributes and local woodland characteristics on small mammal populations in historical woodland creation sites

Animals interact with their environment at multiple spatial scales. For example, whilst landscape-level attributes are likely to influence dispersal processes, local-level attributes determine the suitability of such patches to sustain populations. Understanding the relative and combined effects of local habitat and landscape characteristics is crucial for prioritizing alternative actions to restore woodland ecosystems (e.g. is improving local habitat quality more important than increasing landscape connectivity?).

We found species-specific responses to local- and landscape-level attributes which correspond to some degree with species' habitat specificity. The grassland specialist *M. agrestis* was influenced only by landscape attributes; the woodland generalist *A. sylvaticus* and the woodland specialist *M. glareolus* were influenced by both local habitat and landscape characteristics. We expected the woodland specialist *M. glareolus* to be more strongly influenced by local woodland habitat quality, amount and connectivity than *A. sylvaticus*, usually regarded as a generalist species. However, local habitat attributes appeared more important than the landscape for both species. In addition, and contrary to our expectations, the woodland generalist *A. sylvaticus* was influenced by a larger set of attributes (at both local and landscape scales) than the woodland specialist *M. glareolus*.

The abundance of *M. agrestis* was only influenced (positively) by the proportion of semi-natural habitats within 1 km of focal woodland patches. The lack of association with local-level woodland characteristics matches our original hypothesis and is in accordance with this species' ranging behavior and habitat preferences (particularly for ungrazed and set-aside areas; Tattersall et al. 2002). However, the relatively low capture rate of this species in our study sites only allowed for analysis of adult abundance; therefore, changes in age, sex and reproductive condition ratio in relation to local- and landscape-level woodland characteristics might have gone unnoticed.

The woodland generalist *A. sylvaticus* was influenced by both local- and landscape-level attributes; at the local scale, they were more abundant in woodlands with larger amounts of woody debris and higher structural heterogeneity (i.e. older woodlands; see section 4.1). We also found contrasting effects of the presence of grazing stock on *A. sylvaticus*. Firstly, adult abundance was markedly lower where livestock were present, possibly due to direct disturbance; similar negative impacts of deer grazing have been reported for this species before (Putman et al. 1989; Bush et al. 2012). Secondly, the presence of grazing stock marginally reduced the amount of understory vegetation; woodlands with more open understories were in turn associated with a higher proportion of reproductively active females. In addition, proportionally more females were present in smaller woodlands; even though patch size does not generally influence *A. sylvaticus* abundance (Fitzgibbon 1997; Marsh & Harris 2000; this study; but see Telleria et al. 1991), previous work has reported more male-biased sex-ratios, a larger proportion of sexually active adults and fewer juveniles of this species in small (<10 ha) than in large (>100 ha) woodland remnants (Diaz et al. 1999).

Landscape attributes influencing *A. sylvaticus* populations had, in general, smaller effect sizes than local-level factors. Wood mice were more abundant in woodlands closer to other woodlands (negative association with 'distance to nearest woodland') and surrounded by lower amounts of semi-natural habitats; there were also proportionally more juveniles in woodlands with lower amounts of surrounding semi-natural habitat, including woodland. Previous studies have reported negative effects of woodland isolation on the proportion of reproductively active *A. sylvaticus* (Marsh & Harris 2000), whilst others have reported higher proportion of juveniles in more isolated woodlands, possibly as a result of limited dispersal opportunities (Fitzgibbon 1997). The observed associations with amount of semi-natural and woodland cover could be a result of a 'dilution effect' where instead of being confined to a focal woodland patch, animals disperse towards other suitable habitats in the landscape (Ouin et al. 2000; Fitzgibbon 1997). Alternatively, it is also possible that these patterns are driven by the proportion of surrounding agricultural land (negatively correlated with proportion of woodland and other semi-natural habitats in our study areas), particularly of arable areas which might provide food and shelter and are frequently used by generalist species such as *A. sylvaticus* (Tattersall et al. 2001; Michel et al. 2006; Gentili et al. 2014).

Myodes glareolus (a woodland specialist) was also influenced by both local- and landscape-level habitat characteristics. Of these, the most important factors influencing this species were local-level factors; specifically, the presence of grazing stock (reducing *M. glareolus* abundance) and amount of understory cover (negatively associated with the proportion of females and reproductively active females present at each site). Strong negative impacts of grazing (by deer) have previously been reported for this species (Putman et al. 1989; Bush et al. 2012), however, the observed effect of understory cover was unexpected. There were also more juveniles in older woodlands (see section 4.1) and marginally fewer reproductively active females in larger woodland patches. The only landscape attribute influencing *M. glareolus* was hedgerow density; we found proportionally fewer juveniles and marginally more females in woodlands surrounded by a higher density of hedgerows. Bank voles often make use of hedgerows (Tattersall et al. 2002; Moore et al. 2003) and previous studies have reported higher abundances of this species in woodlands well connected with hedges (Fitzgibbon 1997), although we did not detect this effect. It has also been suggested that isolated woods limit juvenile dispersal (Fitzgibbon 1997), which could explain the higher proportion of juveniles we observed in woodlands surrounded by lower hedgerow densities.

4.3 Effects of population density and resource availability on small mammals in historical woodland creation sites

In addition to local habitat quality and landscape characteristics, small mammals can be influenced by intrapopulation dynamics (e.g. density dependence) and resource availability (Mallorie & Flowerdew 1994; Montgomery 1989a,b), factors which might in turn potentially be driven by local- and landscape-level habitat attributes.

Resource availability (e.g. seed crop size and food plant abundance) has been identified as an important factor influencing population size of *A. sylvaticus* and *M. glareolus* in woodlands (e.g. Montgomery & Dowie 1993; Mallorie & Flowerdew 1994; Tew et al. 2000). We detected resource-dependency effects on population structure parameters of *A. sylvaticus* and *M. glareolus*. Resource availability was determined by local habitat attributes; specifically, younger woodlands with higher tree densities resulted in individuals of both species in better body condition (indicating higher resource availability); this led to slight increases in female and juvenile proportions for *A. sylvaticus* and decreases in juvenile ratios for *M. glareolus*. The proportion of reproductive females of both species was also positively influenced by resource availability; however, this was not affected by any of the habitat characteristics included in our analyses. Females, particularly when reproductively active, have high energy requirements and are likely to select higher quality habitats (e.g. with higher resource availability) than non-reproductive females and males (e.g. Coda et al. 2014; Diaz et al. 1999; Rosalino et al. 2011). For example, *A. sylvaticus* show sex-based selectivity for areas with high abundances of certain food plants, potentially due to differing nutritional and energetic requirements of male and female reproduction (Jensen 1993; Tew et al. 2000).

We detected density-dependency effects on the population structure of *M. glareolus*; specifically, woodlands with higher *M. glareolus* abundance had proportionally fewer reproductively active females. Bank voles have been shown to display some density dependence (Mallorie & Flowerdew 1994), and curtailment of the breeding season at high population densities has been suggested as a possible mechanism (Alibhai & Gipps 1985). Whilst *A. sylvaticus* usually display strong density-dependent population regulation (Montgomery 1989a; Mallorie & Flowerdew 1994), we did not detect any such effects here. It is possible that density effects are overridden when food resources are abundant (Mallorie & Flowerdew 1994; Macdonald et al. 2007), or that they only occur at very high population densities, whereas other factors (e.g. habitat quality) are more important in controlling abundance and population structure at relatively low densities. Additionally, we may have underestimated density/resource dependency effects because our analyses used relative abundance rather than overall population sizes (although these two metrics were strongly correlated; Appendix S2) and because our measure of resource availability (i.e. body condition) was indirect.

4.4 Conservation and management implications

Historical woodland creation sites are quickly colonized by small mammals (both generalists and specialists); even young woodlands are valuable habitats for these animals. However, there is some evidence that woodlands become gradually better over time for some species (e.g. higher *A. sylvaticus* abundance in sites characterized by an old-growth habitat structure).

In general, local habitat characteristics are more important than landscape attributes, suggesting that small mammals are not strongly limited by dispersal (but see below), and that enhancing habitat quality at the patch scale would benefit these species. Specifically, management to reduce grazing pressure, promote an old-growth habitat structure (large amounts of dead wood and high structural heterogeneity) and maintain a relatively open understory is likely to be beneficial for both woodland generalists and specialists. Local habitat attributes also influence resource availability; specifically, younger woodlands with higher tree densities provide more food resources for small mammals, which can lead to changes in small mammal population structure (e.g. higher proportions of females and juveniles for *A. sylvaticus*). Maintaining a mosaic of woodland patches in the landscape which includes a mixture of relatively young stands and older woodlands is likely to benefit small mammal communities, including woodland generalists, specialists and non-woodland species.

Landscape characteristics are of lower importance for small mammals in secondary woodlands; however, increasing the amount of woodland and other semi-natural habitats in the landscape and improving woodland connectivity (e.g. through reducing distance between woodland patches and increasing hedgerow densities in the landscape) are likely to increase habitat availability, facilitate dispersal and benefit small mammal communities in secondary woodlands.

5. CONCLUSIONS

Restoring woodland patches in agricultural landscapes benefits small mammal communities and other wildlife (e.g. birds and invertebrates; Whytock et al. 2018; Fuller et al 2018). It is also likely to benefit higher trophic levels (e.g. larger mammals and birds of prey) feeding on small mammals and increase ecosystem processes such as seed dispersal (further work is needed to explore these processes). However, other species groups might require different conservation strategies (e.g. at larger spatial scales) depending on their mobility and habitat specialization (e.g. Fuentes-Montemayor et al. 2017). In addition, the value of secondary woodlands for biodiversity in unlikely to match that of older, larger, undisturbed woodlands (ongoing work by the authors); new woodland plantings should therefore not be regarded as an immediate replacement for higher quality habitats such as ancient woodlands.

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SUPPORTING INFORMATION

Additional supporting information may be found online.

DATA AVAILABILITY

Data associated with this paper have been deposited in the University of Stirling's Online Repository for Research Data (DataSTORRE): http://hdl.handle.net/11667/136.

TABLES

Table 1. Local and landscape-level attributes measured for all woodland sites.

Variable type	Variable	Description	Obtained from
Local – vegetation structure	Patch age	Years since woodland patch appeared on historical maps.	Historical maps
	Tree density	Number of trees per hectare.	Field surveys
	Tree DBH (SD)	Tree diameter at breast height (standard deviation; used as indicator of structural heterogeneity).	Field surveys
	Woody debris	Index of woody debris on ground. Ranges from 1–3 where 1 = leaf litter & small twigs (about 1 cm in diameter), 2 = larger branches (<10 cm) and 3 = coarse woody debris >10 cm diameter (including fallen trees).	Field surveys
	Understory cover	Proportion of understory cover in 10x10 m quadrats (average value). Uses Domin scale.	Field surveys
Local – management	In-site grazing	Livestock presence (or indication of, e.g. prints, dung, wool).	Field surveys
Local – patch geometry	Patch size	Area of woodland patch (ha).	Digital maps / GIS
Landscape	Woodland spatial isolation	Distance (m) to nearest broadleaved woodland.	Digital maps / GIS
	Woodland % [a]	Proportion of landscape covered by broadleaved woodland.	Digital maps / GIS
	Semi-natural % [a]	Proportion of landscape covered by semi-natural habitats.	Digital maps / GIS

Hedgerow density [a]	Total length of hedgerows within 1 km of each study site.	Google Earth Pro / GIS

[a] Calculated within 1 km buffers.

Table 2. Small mammal species detected during field surveys in WrEN woodland sites.

Species	Number of sites detected [a]	Total number of individuals (% of total)	Average number of individuals per site (range)
Bank vole (*Myodes glareolus*)	80	1006 (60.0 %)	9.58 (0–67)
Wood mouse (*Apodemus sylvaticus*)	72	571 (34.1 %)	5.44 (0–54)
Field vole (*Microtus agrestis*)	33	98 (5.8 %)	0.93 (0–14)
Yellow-necked mouse (*Apodemus flavicollis*) [b]	1	1 (<0.1 %)	0.03 (0–1)

[a] Out of 105 sites.

[b] Species absent from Scotland; average calculated with n = 38 sites in England.

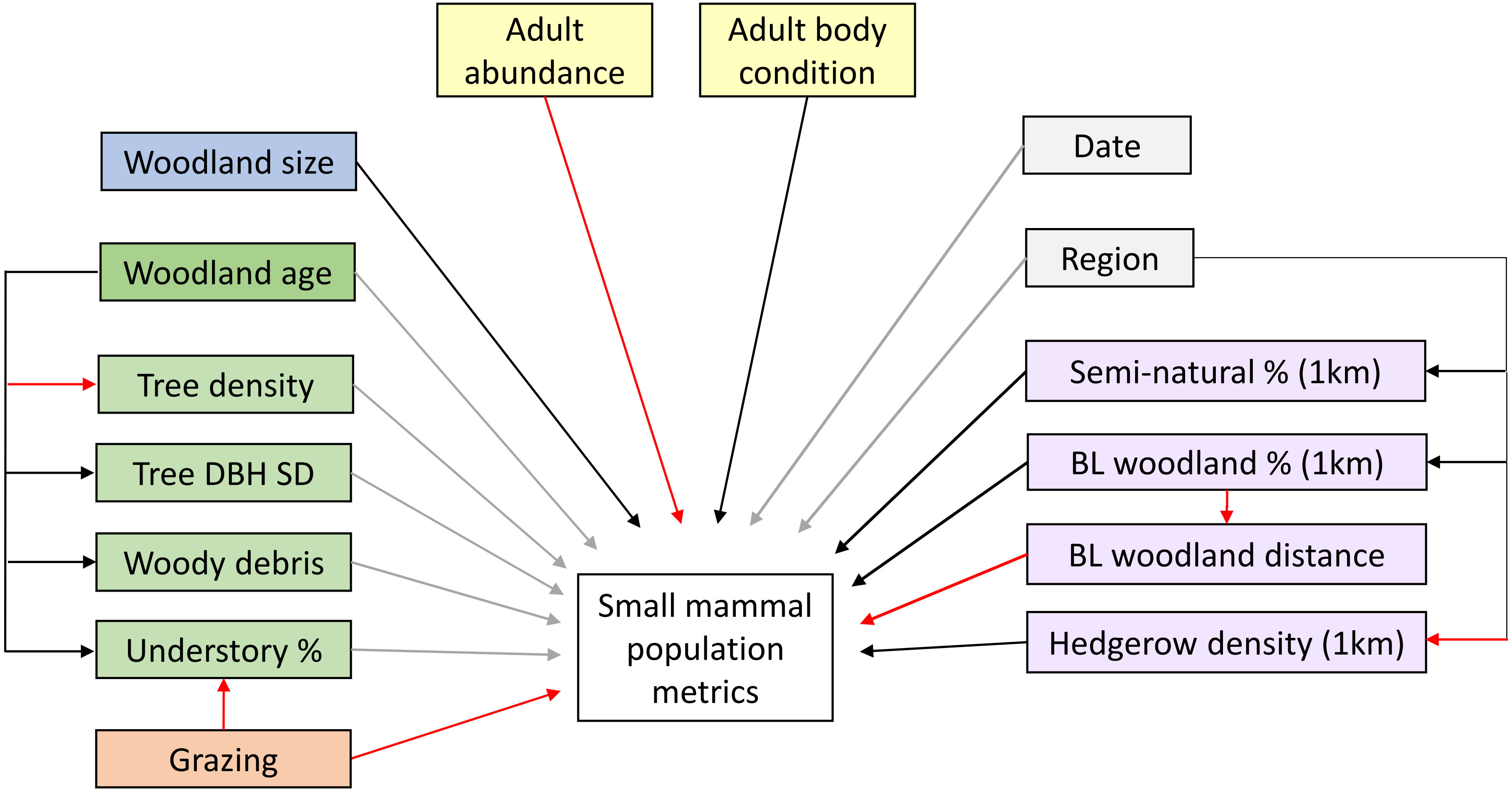
FIGURE LEGENDS

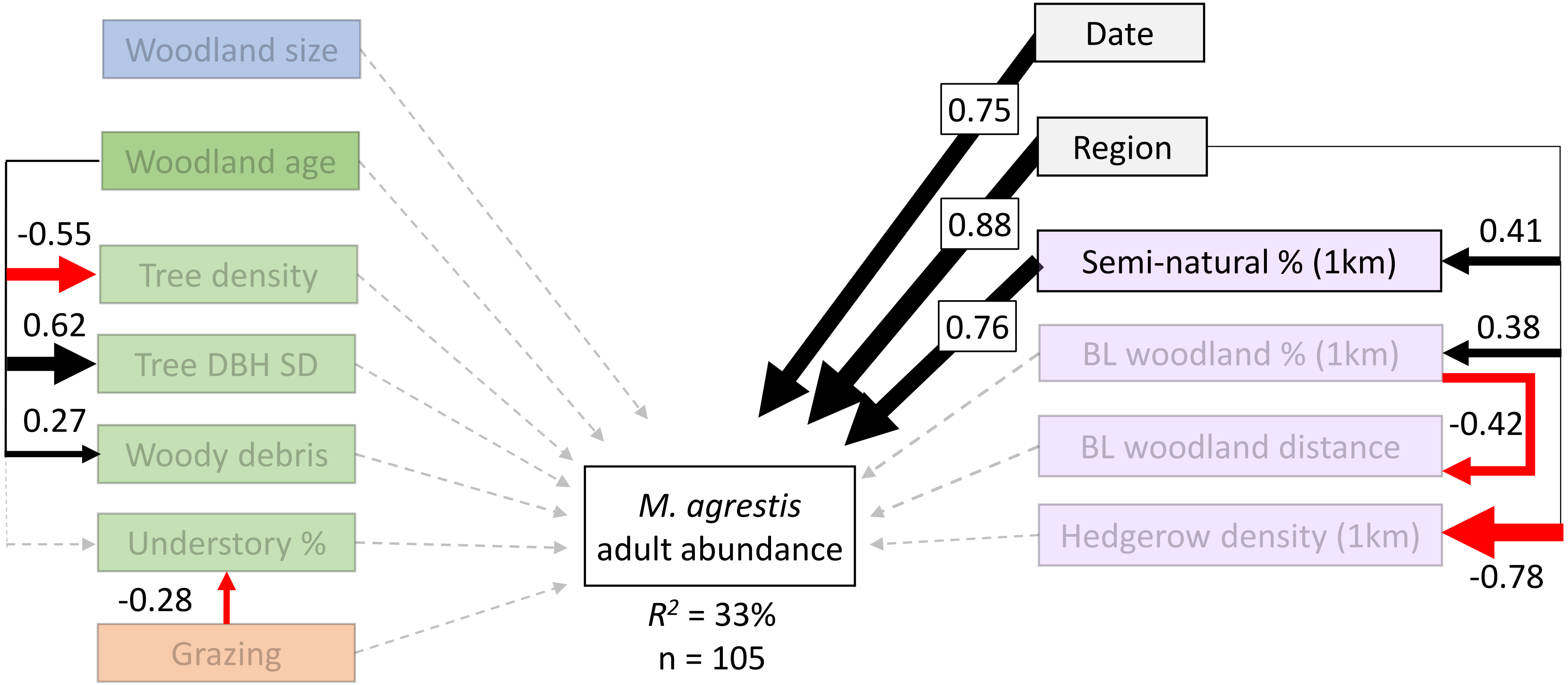
Figure 1. Conceptual model of hypothesized direct and indirect causal relationships between small mammal response variables and predictor variables: 1) landscape-level attributes likely to influence colonization and dispersal processes (purple boxes), 2) local-level attributes related to habitat quality (green boxes), patch size (blue box) and management (orange box), 3) 'biological' variables (i.e. abundance and body condition) likely to indicate density- and resource-dependency effects (yellow boxes) and environmental variables (i.e. date and region; grey boxes). Arrow color indicates directionality of hypothesized associations (black = positive; red = negative; grey = variable e.g. species-dependent).

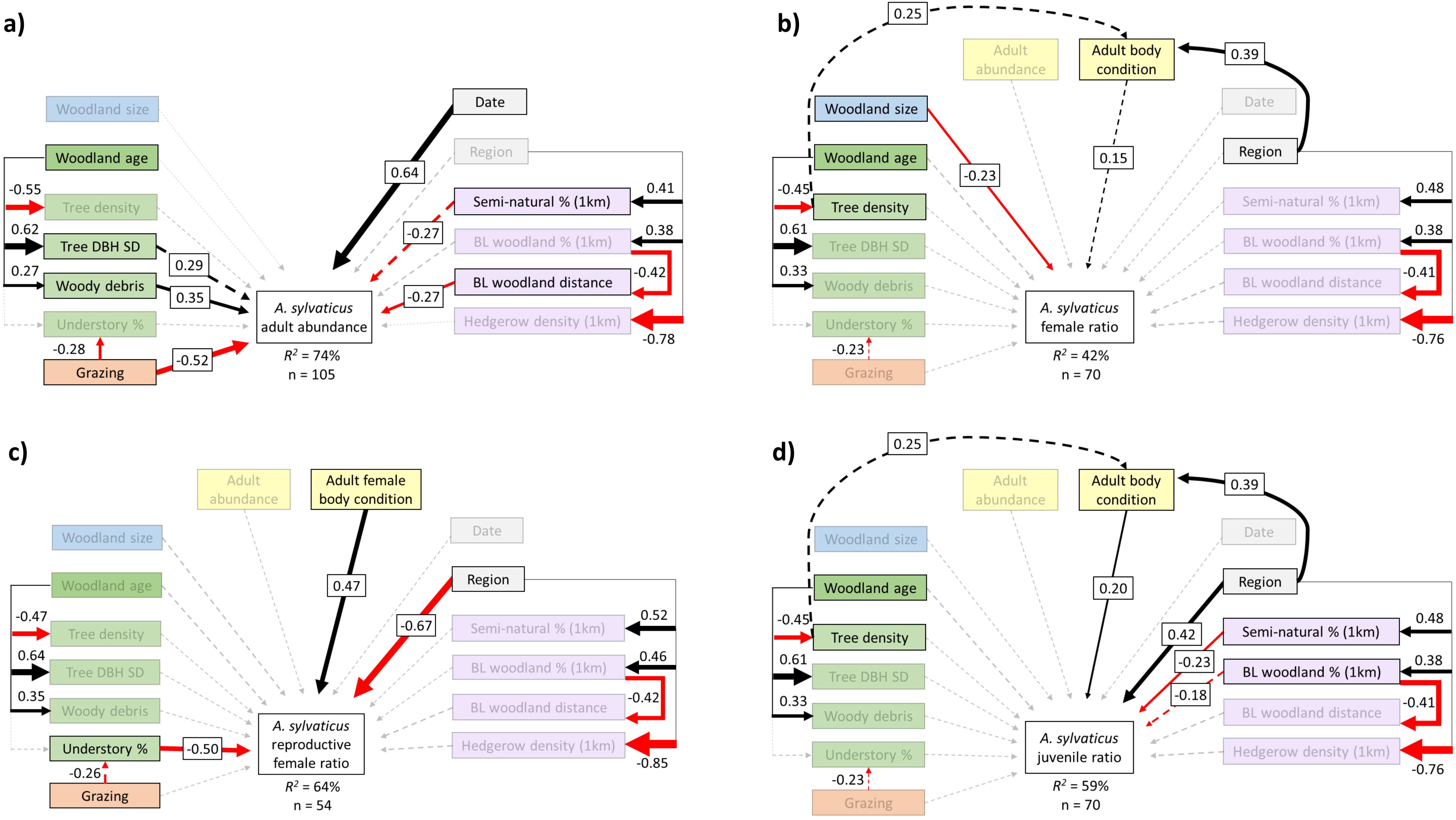
Figure 2. SEM of relationships between Field vole (*M. agrestis*) abundance and predictor variables. Colored boxes indicate variable types: purple = landscape; green = vegetation structure; blue = patch geometry; orange = management; yellow = biological; grey = environmental/seasonal. Arrow type and color indicate statistical significance (solid black/red = significant association, i.e. $P<0.05$; dashed black/red = marginally significant association; i.e. $P<0.1$; dashed grey = non-significant association, i.e. $P>0.1$) and directionality of associations (black = positive; red = negative). Arrow thickness represents relative effect sizes (thicker arrows = larger effect sizes). Effect sizes are shown for all significant associations.

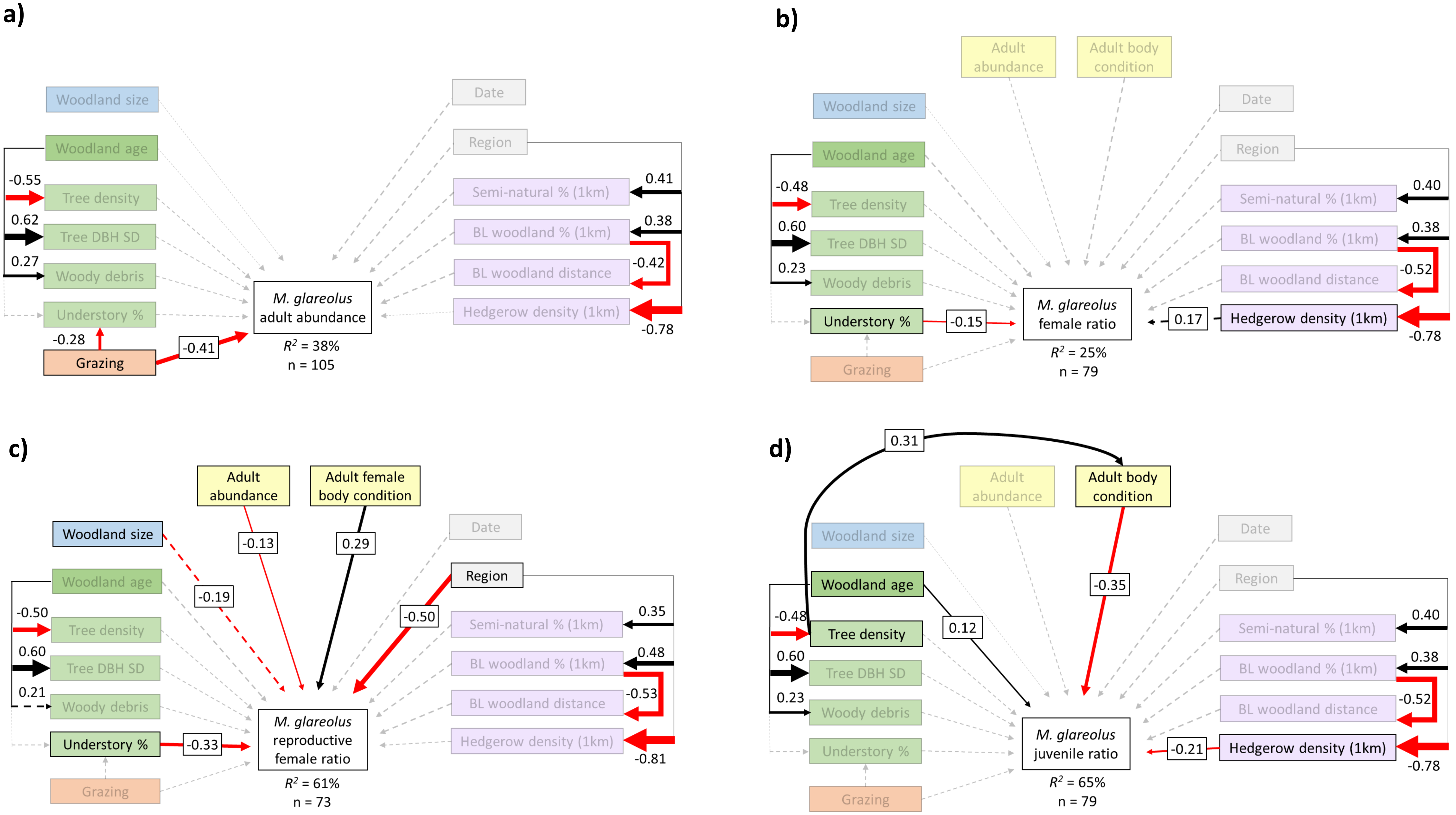
Figure 3. SEM of relationships between Wood mouse (*A. sylvaticus*) abundance (a), female ratio (b), reproductive female ratio (c), juvenile ratio (d) and predictor variables. Colored boxes indicate variable types: purple = landscape; green = vegetation structure; blue = patch geometry; orange = management; yellow = biological; grey = environmental/seasonal. Arrow type and color indicate statistical significance (solid black/red = significant association, i.e. $P<0.05$; dashed black/red = marginally significant association; i.e. $P<0.1$; dashed grey = non-significant association, i.e. $P>0.1$) and directionality of associations (black = positive; red = negative). Arrow thickness represents relative effect sizes (thicker arrows = larger effect sizes). Effect sizes are shown for all significant associations.

Figure 4. SEM of relationships between Bank vole (*M. glareolus*) abundance (a), female ratio (b), reproductive female ratio (c), juvenile ratio (d) and predictor variables. Colored boxes indicate variable types: purple = landscape; green = vegetation structure; blue = patch geometry; orange = management; yellow = biological; grey = environmental/seasonal. Arrow type and color indicate statistical significance (solid black/red = significant association, i.e. $P<0.05$; dashed black/red = marginally significant association; i.e. $P<0.1$; dashed grey = non-significant association, i.e. $P>0.1$) and directionality of associations (black = positive; red = negative). Arrow thickness represents relative effect sizes (thicker arrows = larger effect sizes). Effect sizes are shown for all significant associations.


Adult abundance
Adult body condition
Woodland size
Date
Region
Woodland age
Tree density
Semi-natural % (1km)
Tree DBH SD
BL woodland % (1km)
Woody debris
BL woodland distance
Small mammal population metrics
Understory %
Hedgerow density (1km)
Grazing


Woodland size
Woodland age
-0.55
Tree density
0.62
Tree DBH SD
0.27
Woody debris
Understory %
-0.28
Grazing
M. agrestis
adult abundance
R^2 = 33%
n = 105
Date
0.75
Region
0.88
Semi-natural % (1km)
0.41
0.76
BL woodland % (1km)
0.38
-0.42
BL woodland distance
Hedgerow density (1km)
-0.78


a)
Woodland size
Woodland age
Tree density
Tree DBH SD
Woody debris
Understory %
Grazing
-0.55
0.62
0.27
-0.28
0.29
0.35
-0.52
Date
0.64
Region
Semi-natural % (1km)
BL woodland % (1km)
BL woodland distance
Hedgerow density (1km)
0.41
0.38
-0.42
-0.78
-0.27
-0.27
A. sylvaticus adult abundance
R^2 = 74%
n = 105
b)
0.25
Adult abundance
Adult body condition
0.39
0.15
Date
Region
Woodland size
Woodland age
Tree density
Tree DBH SD
Woody debris
Understory %
Grazing
-0.23
-0.45
0.61
0.33
-0.23
Semi-natural % (1km)
BL woodland % (1km)
BL woodland distance
Hedgerow density (1km)
0.48
0.38
-0.41
-0.76
A. sylvaticus female ratio
R^2 = 42%
n = 70
c)
Adult abundance
Adult female body condition
0.47
Date
Region
-0.67
Woodland size
Woodland age
Tree density
Tree DBH SD
Woody debris
Understory %
Grazing
-0.47
0.64
0.35
-0.26
-0.50
Semi-natural % (1km)
BL woodland % (1km)
BL woodland distance
Hedgerow density (1km)
0.52
0.46
-0.42
-0.85
A. sylvaticus reproductive female ratio
R^2 = 64%
n = 54
d)
0.25
Adult abundance
Adult body condition
0.39
0.20
Date
Region
0.42
-0.23
-0.18
Woodland size
Woodland age
Tree density
Tree DBH SD
Woody debris
Understory %
Grazing
-0.45
0.61
0.33
-0.23
Semi-natural % (1km)
BL woodland % (1km)
BL woodland distance
Hedgerow density (1km)
0.48
0.38
-0.41
-0.76
A. sylvaticus juvenile ratio
R^2 = 59%
n = 70


a)
Woodland size
Woodland age
-0.55
Tree density
0.62
Tree DBH SD
0.27
Woody debris
Understory %
-0.28
Grazing
-0.41
Date
Region
Semi-natural % (1km)
0.41
BL woodland % (1km)
0.38
BL woodland distance
-0.42
Hedgerow density (1km)
-0.78
M. glareolus adult abundance
R² = 38%
n = 105
b)
Adult abundance
Adult body condition
Woodland size
Woodland age
-0.48
Tree density
0.60
Tree DBH SD
0.23
Woody debris
Understory %
-0.15
Grazing
Date
Region
Semi-natural % (1km)
0.40
BL woodland % (1km)
0.38
BL woodland distance
-0.52
Hedgerow density (1km)
0.17
-0.78
M. glareolus female ratio
R² = 25%
n = 79
c)
Adult abundance
Adult female body condition
-0.13
0.29
Woodland size
-0.19
Woodland age
-0.50
Tree density
0.60
Tree DBH SD
0.21
Woody debris
Understory %
-0.33
Grazing
Date
Region
-0.50
Semi-natural % (1km)
0.35
BL woodland % (1km)
0.48
BL woodland distance
-0.53
Hedgerow density (1km)
-0.81
M. glareolus reproductive female ratio
R² = 61%
n = 73
d)
0.31
Adult abundance
Adult body condition
-0.35
Woodland size
Woodland age
0.12
-0.48
Tree density
0.60
Tree DBH SD
0.23
Woody debris
Understory %
Grazing
Date
Region
Semi-natural % (1km)
0.40
BL woodland % (1km)
0.38
BL woodland distance
-0.52
Hedgerow density (1km)
-0.21
-0.78
M. glareolus juvenile ratio
R² = 65%
n = 79