Original Articles

The simpler the better: When decreasing landscape complexity increases community stability

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ABSTRACT

Herbivores and their predators are affected by changes in land-use and habitat fragmentation. Past studies of tri-trophic herbivore communities have found that increasing land-use intensity leads to declines in community stability. The majority of these studies analysed community stability in highly fragmented ecosystems characterised by intensive agriculture. In this study we considered how landscape configuration and composition affected habitat networks and parasitoid food webs under moderate but increasing land use. We used gall wasp communities as models to test the effects of landscape change on multi-species hierarchical communities of plants and animals. We investigated characteristics of networks formed by rose bushes and quantitative webs of rose gall parasitoids along a gradient of land-use intensity. We found that link density and compartmentalisation of rose bush networks, and local extinction within parasitoid webs increased with increasing landscape homogenization. Because these network and web characteristics are linked with resilience, our results suggest that stability of these communities can increase as landscapes become less complex. This is an intriguing aspect of landscape homogenisation effects on biological communities that contrasts with most expectations and the majority of the relevant literature, where decreasing community stability is usually associated with landscape homogenization.

1. Introduction

Increasing land use intensity and habitat fragmentation are primary threats to global biodiversity, especially in agricultural landscapes where changes in land use can occur rapidly due to shifting economic and political pressure (Fischer and Lindenmayer, 2007; Munteanu et al., 2014). Landscape composition (Gagic et al., 2011) and configuration (Kaartinen and Roslin, 2011) have important implications for population and community-level processes, including community composition and structure (Tylianakis et al., 2007; Tscharntke et al., 2012). Community structure and composition affect ecosystem functioning (Massol et al., 2011), and maintaining ecosystem services is generally thought to require heterogeneous landscapes with diverse communities (Pasari et al., 2013). Landscape composition and configuration also contribute to changes in spatial and trophic aspects of communities. Structural changes of landscapes due to agricultural land use and other human activities also alters habitat patch networks through habitat patch isolation (Fischer and Lindenmayer, 2007).

In the last decades network theory was also implemented in the analyses of landscape change effects of different animal communities

(Bascompte, 2007). The effect of landscape change may be not evident on habitat patch network structure at a small scale, i.e. a host plant (León-Cortés et al., 2003) or roost tree networks (Rhodes et al., 2006). However, a major gap in network theory regarding community and landscape structures is the link between individuals and their spatial distribution (Blick et al., 2012).

Food web structure is crucially related to community stability and function. A parasitoid web is a relatively constrained and specialised food web that contains host plants, insect hosts, parasitoids, and hyperparasitoids (Memmott et al., 1994). Although they contain prey and predator species, parasitoid webs are relatively easier to construct than many other food webs, because of the number of consumer and host associations (Lewis et al., 2002). Parasitoid webs can also be relatively easily quantified, incorporating information about the relative densities of all species (Memmott et al., 1994).

Many interactions between insects and their host plants are described by island biogeography (Whittaker and Fernández-Palacios, 2007) and metapopulation ecology (Hanski, 1999). An individual plant may be thought of as an island, or as a patch in space and time for the individual insects that feed on it (Gripenberg and Roslin, 2005; Kuris

et al., 1980; Looney and Eigenbrode, 2011). A habitat network is a set of separate but connected patches, within which individuals of mobile species can freely move (Rayfield et al., 2011). Habitat networks incorporate the spatial arrangement of habitat patches through connectivity determined largely based on distances between these patches (Bodin and Norberg, 2006). Treating host-plants as individual habitats in habitat networks (especially in the case of monophagous or oligophagous plant "parasites", such as gall inducers) provides an opportunity to consider spatial dimensions of food-webs, adding nuance to the patterns of simpler prevalence or incidence measures.

Parasitoid food web structure also responds to changes in landscape composition and configuration (Gagic et al., 2012). The impacts of landscape changes on community structure are frequently idiosyncratic, with both readily observable effects (Chisholm et al., 2011) and relatively subtle responses (Gripenberg and Roslin, 2005) documented in the literature. Effects are frequently scale-dependent, with measurable local impacts obscured at larger scales (Schnitzler et al., 2011). Spatial arrangement of habitats, the species pool and community differences across habitats have all been found to determine how food webs respond to landscape structure (Gagic et al., 2011). Land-use intensification, and corresponding homogenization, tends to produce webs with low complexity and uneven interaction strengths, and those in the most severely modified habitats, like anthropogenic pastures, show consistent and characteristic differences relative to other habitats (Tylianakis et al., 2007). However, due perhaps to the complexity of scale-dependent factors, clear effects of landscape structure on many food webs remain elusive.

To further explore the relationship between food webs and landscape change we used gall wasps and their component communities as a model. Our data set was collected from a temperate agroecosystem along a gradient of changing land-use intensity, and reports species abundances and interaction frequencies between a host plant, a gall-inducing wasp, and its parasitoid community. We constructed host plant networks and gall-parasitoid food webs with quantitative trophic links and measured landscape characteristics to address the following questions:

(1) What is the relative importance of landscape composition and configuration to the structure of wild rose spatial arrangement and rose gall communities?
(2) To what extent are host plant networks and gall-parasitoid food web structure influenced by landscape characteristics?
(3) Do landscape level changes affect the stability of the rose gall community?
(4) Are local or landscape-level variables more influential on food web structure?

2. Methods

2.1. Study area and studied species

Data were collected over three years from seven study sites along a South-East/North-West axis of 328 km through the Transylvanian Plateau (Romania) and the Great Hungarian Lowland (Eastern Hungary) (Fig. 1.). The landscape in this region is traditionally a small-scale mosaic of diverse agricultural and natural land-covers, and is recognized in the EU for its contribution to regional biodiversity (Loos et al., 2014). However, this landscape has undergone several changes in land use intensity over the past several decades. Notable among the landscape-level changes was abandonment of farmland following the end of the communist era in Romania, resulting in the creation of large patches of shrubby grasslands. More recently, the region has seen an increase in high-intensity agriculture subsequent to Romania joining the European Union, although this type of landscape change did not occur in our sites during the study period. Wild roses are a common component of this landscape, encroaching and dominating much of the

abandoned farmland. Wild roses support complex gall wasp communities, including those of the rose bedeguar, *Diplolepis rosae* (Hymenoptera: Cynipidae). The shrubby landscapes are becoming increasingly homogenized, as they are being replaced by agriculture. Our study sites included local landscapes with both large and small proportions of agricultural cover type. We considered homogenous landscapes to be those with a high proportion of agricultural cover type and a low shrubby cover type. Thus, the fine scale heterogeneity can be high, but when agricultural cover increases heterogeneity on the landscape scale is small.

Diplolepis rosae is widespread in Europe and North America (where it is introduced), and is one of the most abundant cynipid galls in the Carpathian Basin and Eastern Europe. Gall wasp females produce multi-chambered galls on many wild rose species, without a demonstrable host preference (Kohnen et al., 2011). The gall wasps in turn form the base of a complex community of inquilines, parasitoids, and hyperparasitoids (Fig. 2). The most abundant parasitoid species reported for the galls of *D. rosae* are *Orthopelma mediator* (Ichneumonidae), *Torymus bedeguaris* (Torymidae), *Glyphomerus stigma* (Torymidae), and *Pteromalus bedeguaris* (Pteromalidae) (Fig. 2). *Periclistus brandtii* (Cynipidae), an inquiline of the gall inducer, is a gall forming species that is unable to initiate its own galls, instead commandeering and modifying parts of *D. rosae* galls.

A distinct community of parasitoid wasps attacks *P. brandtii*, primarily *Caenacis inflexa* (Pteromalidae) and *Eurytoma rosae* (Eurytomidae); the latter behaves more like a predator, feeding on multiple *Periclistus* larvae during its life cycle (Claridge and Askew, 1960; Nordlander, 1973). Although generally confined to feeding only on parasitoids, some research suggests they may also attack *D. rosae* at low rates (Todorov et al., 2012). Other parasitoids and hyperparasitoids include *Torymus rubi* (Torymidae), *Eupelmus urozonus* (Eupelmidae), *E. vesicularis* (Eupelmidae), and *Stepanovia eurytomae* (Eulophidae); all are less common in rose bedeguar gall communities (Nordlander, 1973; Redfern, 2011) The boundaries between parasitoids and hyperparastioids in these communities are somewhat plastic for many of these species. *Torymus bedeguarensis* and *P. bedeguaris* are facultative hyperparasitoids, attacking *O. mediator* as well as the gall inducer (Blair, 1943; Nordlander, 1973), while both *Eupelmus* species are likely to attack many of the species in the community based on their broad host range (Nordlander, 1973).

The data set was collected over three consecutive years (2004–2006) and consisted of 65 50 × 50 m plots of rose shrubs. Galls were collected from randomly chosen 50 × 50 m plots where wild roses were present (as shown on Fig. 3b and c). Plot locations within the sites varied between the measurement years; thus each plot was sampled only once. We recorded the coordinates of both occupied and un-occupied bushes from each plot with a GPS unit. All galls from each occupied bush in each plot were collected in February and March each year. We stored the collected galls individually in plastic cups under standard laboratory conditions until insects began emerging. Specimens were collected as they emerged and preserved in 70% ethanol for identification.

2.2. Habitat patches and host-plant networks

Host-plant networks (see Fig. 3d and e for examples) were constructed as flow networks (Proulx et al., 2005) with individual rose bushes as nodes. Between node pairs there was a link if at least one of them contained at least one gall. Link flow was calculated in a three-step process based on the number of rose galls and the distance between pairs of rose shrubs. The distance between bushes was measured from centre to centre. We treated large clonal patches as a single bush if they had discrete and obvious boundaries in the field. In the first step we calculated the mean number of galls for each pair of shrubs from a plot, and the distances between each shrub pair shrubs. We then divided the distance between nodes by the mean number of galls in that pair of