

Seed dispersal depends on frugivore biodiversity and on how exclusive frugivores are for fruiting plants and *vice versa*

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Many ecosystem functions, like pollination and organic matter recycling, largely result from animal feeding activity. We know that ecosystems with more animal species usually function better, but we are still ignorant of the reasons for this pattern. We may expect complementarity, that is, different species feeding complementarily on different resources, to explain the link between animal biodiversity and functions. We approach this issue with networks based on the ecological relationships that emerge when animals feed on fleshy fruits, and the function that derives from dropping intact seeds after fruit meals: seed dispersal.

The temperate secondary forest of the Cantabrian range, in N Spain, contains different assemblages of fleshy-fruited woody plants (like holly, hawthorn and bramble) and birds (like thrushes, robins and warblers) across different landscapes. In a large-scale sampling comprising fourteen local landscapes, and during the fall-winter of two consecutive years, we counted birds and fruits to estimate their abundance and diversity. We also monitored birds eating fruits to build bird-plant seed dispersal networks. We further collected seeds dropped by birds, to assess the function of seed dispersal globally.

Our Cantabrian landscapes markedly differed in the structure of seed dispersal networks, in terms of how exclusive frugivorous birds were for fruiting plants and *vice versa*. Landscapes with small birds, like blackcap and European robin, which mostly dispersed seeds of small individual fruits (e.g. bramble, elder), had more specialized networks. The same held true where fruiting was dominated by late-ripening holly, mostly dispersed by wintering redwings. We also found that landscapes harboring more birds from more species received more seeds, which were also more widespread in space. Seed



A Cantabrian seed dispersal network with high complementarity in interactions. Small birds (blackcap, European robin) disperse mostly small-fruited plants (bramble), and dominant fruiting plants (holly) are mostly dispersed by wintering birds (redwing). Artwork and pictures by Daniel García.

dispersal was also affected by network structure: more seeds were found in landscapes with more specialized networks, irrespective of bird abundance and diversity. Therefore, complementarity in ecological relationships between frugivores and plants would contribute to the positive effect of frugivore biodiversity on seed dispersal function.