1. PUBLISHABLE SUMMARY

Old-field recolonization under selective defaunation: a spatially-explicit individual-based simulation model

Land use changes and defaunation are two major drivers of global change which combined effect is poorly understood. In particular, increased levels of land abandonment worldwide are leading to noticeable changes in landscape cover. Such 'old-fields' can return to their historical state, to be transformed into non-historical 'hybrid' states, or reach a 'novel' state; thus, the consequences of land abandonment for biodiversity are critical and varied. If and how old fields are colonized depend in a first stage by the arrival of seeds which, in turn, is contingent on the density and identity of seed vectors. In the case of animal-dispersed plants, the strength and spatial pattern of the seed rain can be strongly impinged by defaunation.

Our study site, located within the Doñana National Park (SW Spain), was used for intensive cow grazing until 1996, when the land was expropriated, the cows removed and, afterward, protected by the National Park Service. Whether this old field will return to its historical state (i.e. a Mediterranean shrubland) or will be transformed into a different state is an enigmatic and complex enquiry. Several lines of evidence suggest that new combinations of species are occurring. Based on large datasets collected during the last two decades (concerning disperser movements, disperser fruit consumption rates, fruiting plant distribution, and crop sizes), we built an individual-based spatially explicit simulation model to evaluate the effect of rarefaction of different seed dispersers (frugivorous mammals) in the recolonization of this old-field by the endozoochorous Iberian pear *Pyrus bourgaeana*.

Thus, the general objective of the project is to simulate the complex process old-field colonization by endozoochores using a combination of plant demography with rule-based and spatially-explicit modelling and animal movement. This general objective contains four specific objectives:

i) Using spatial point pattern analyses (SPPA), to describe the observed spatial structure of the mammal-generated seed rain in the area and to identify the level of spatially contagious seed dispersal.

ii) To develop a spatially-explicit, individual-based model that simulate the distribution and dynamics of both endozochores at the old field, as determined by the movement of their dispersers and seed retention times, the resulting seed rain.

iii) To optimise the, thus, to indirectly identify potential missing processes or parameters in the models.

iv) Using extensive simulation experiments, to investigate the spatial and demographic consequences of contrasting realistic scenarios and to propose a general model for the colonization of old fields by animal-dispersed plants that accounts for the movements of dispersers.

RESULTS

This section includes results archived so far concerning *i*) the final (i.e. published) spatial analyses of the mammal-generated seed rain and two subsection, and *ii*) the unpublished results from simulation experiments performed with our spatially-explicit individual-based model *DisPear*.

Spatial structure of the mammal-generated seed rain

We investigated mechanisms of seed aggregation using techniques of spatial point pattern analysis. To this end, we used spatial data and seed composition of fecal samples of five frugivorous mammals that were systematically collected during two consecutive dispersal seasons in three Mediterranean shrublands in southwestern Spain (Fig. 1).

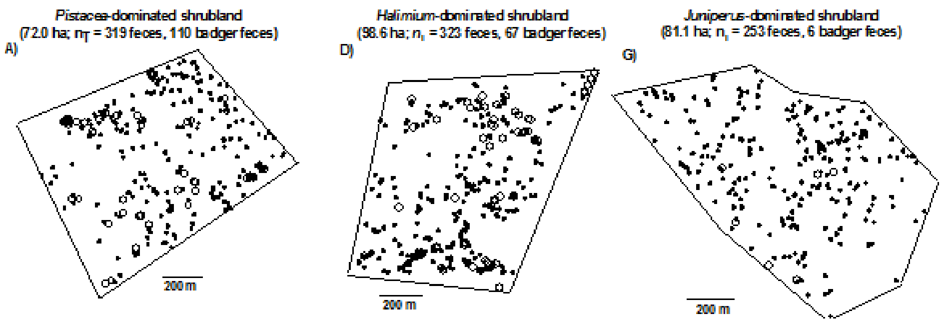

Figure 1: Spatial distribution of mammal feces in each of the three studied shrublands; study area size, total number of feces (n_T), and number of badger feces (represented by large circles) are given. The three study areas were: A) A *Pistacia*-dominated shrubland where the evergreen *Pistacia lentiscus* L., growing alone or in small clumps, is the most frequent shrub, D) A *Halimium*-dominated shrubland near the marsh border, dominated by *H. halimifolium* and *Ulex* spp, and G) A *Juniperus*-dominated shrubland located in a dune area dominated by *Juniperus phoenicea* subsp. *turbinata* (Guss.)

Our approach revealed three hierarchical and complementary mechanisms of seed aggregation acting at different levels and spatial scales. First, frugivores tended to deliver their feces highly aggregated at small and intermediate spatial scales, and the overall pattern of fecal delivery could be described well by a nested double cluster Thomas process (e.g. Fig. 2A). Second, once the strong observed fecal aggregation was accounted for, the distribution of mammal feces containing seeds was clustered within the pattern of all feces (i.e., with and without seeds), and the density of fecal samples containing seeds was higher than expected around other feces containing seeds in two out of the three studied seed disperser networks (e.g. Fig. 2B). Finally, at a finer level, mark correlation analyses revealed that for some plant species pairs, the number of dispersed seeds was positively associated either at small or large spatial scales (e.g. Fig. 2C).

Our approach revealed for the first time how contagious seed dispersal in complex seed-isperser networks can arise by means of complementary proximate mechanisms acting synergistically at a range of spatial scales, and we provided a robust approach that can be applied widely to many other seed-dispersal systems (for reviews, see Schupp et al. 2002, Kwit et al. 2007). For instance, mapped multispecific seed rains generated by rodents (e.g., Beck and Vander Wall 2010), ants (e.g., Fedriani et al. 2004), and diverse diplochorous systems (sensu Vander Wall and Longland 2004) are likely to benefit from our approach. Further research is needed on the population and community consequences of contagious seed dispersal, and to assess the consistency of patterns reported here (e.g., nested double-cluster Thomas process, the importance of single disperser species on overall seed rains) over a broader range of systems. Despite the relative invariant patterning of seed clustering, our study also shows that some attributes of endozoochore seed rains (e.g., intensity, scales of aggregation) are likely to be variable in space and time as a consequence of changes in the ecological context (Agrawal et al. 2007) in which seeds and their dispersers interact.

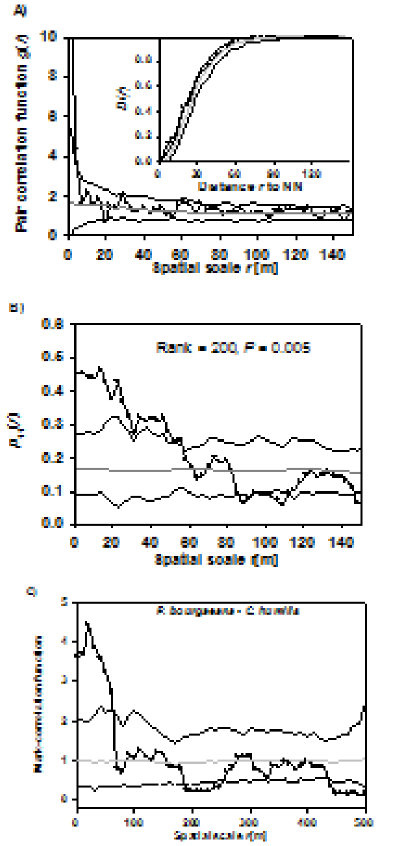

Figure 2: Three examples of each of the three potential mechanism of seed aggregation. A) aggregation of mammal fecal samples following a Tomas process double cluster, B) aggregation of fecal samples with seeds within the overall sample of feces (i.e. with and without seeds, and 3) spatial positive association in the number of seeds for some species pairs.

More details concerning the methods and results on contagious seed dispersal by mammals are available at Fedriani and Wiegand 2014 (Ecology 95: 514-526).

Modelling old-field recolonization: preliminary results

Preliminary results indicate that both severity and selectivity of defaunation (i.e. the relative proportions of different disperser species) have major effects on the dispersal kernel and level of seed clustering (Fig. 3). Furthermore, old-field level of attraction strongly affected the pace of woody recolonization.

Given that badgers are more frugivorous than foxes, our preliminary simulation experiments indicated that selective defaunation (i.e. lower proportion of badgers) has a detrimental effect on the number of dispersed seeds (Fig. 3 A). Similarly, the reduction in number of dispersed seeds with higher old-field attraction level could be predicted, given that none fruiting *P. bourgaeana* is located within this habitat. Interestingly, however, dispersal distance declined in a rather linear fashion with old-field attraction (Fig. 3B). This unexpected result may be a consequence of lower number of seed dispersed and thus lower number of rare long-distance dispersal events. Selective defaunation had only a small effect on dispersal distance; the higher badger abundance the lower dispersal distance. This is likely related to the fact that badgers spent less time in the old-field away from fruiting *P. bourgaeana* trees and, thus, they do less long-distance dispersal as compared to foxes. These simulation analyses will be expanded and publish soon.

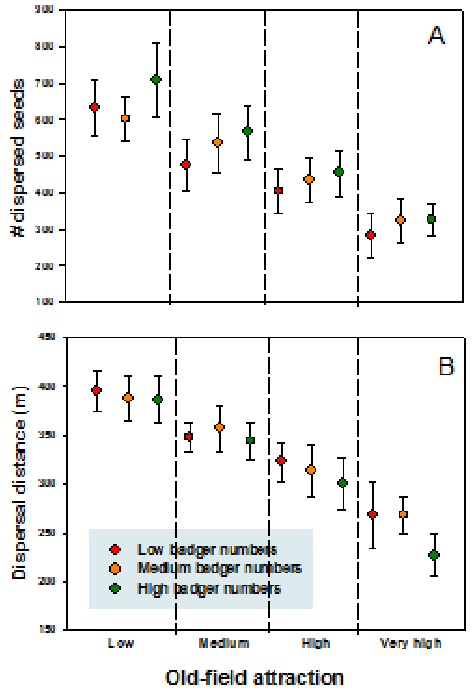

Figure 3: Effect of selective defaunation (i.e. relative number of badgers) and Old-field attraction on two important components of the dispersal kernel, the intensity or number of dispersed seeds (A) and the dispersal distances (B).

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Expected final results and their potential impact and use

Socio-economic changes and the decline of agricultural practices, pastoralism, and forest activities are causing increased levels of land abandonment worldwide and, in particular, throughout the European backcountry. This trend is likely to be accentuated the next decades in Europe and elsewhere. In the case of animal-dispersed plants, the recolonization of oldfield can be strongly limited by defaunation. Our model *DisPear* thus helps to understand the recolonization process of an oldfield in southern Spain under different sceneries of selective defaunation. Therefore, it is useful **from an applied perspective** to predict the effects of global change at the landscape levels. Importantly, our model *DisPear* is easily applicable to other species and landscapes; always that critical empirical data is available. Thus, *DisPear* will likely be useful to investigate the colonization process of oldfields elsewhere. On the other hand, given the complex dynamics of animal-dispersed plants in old fields and the need of modelling to integrate all processes involved in plant life cycles (scale and shape of dispersal kernels, plant demography parameters) this project make also an impact **from a scientific/technical perspective** providing a comprehesive framework to study and simulate the recolonization of oldfields easily applicable to many other similar system.