## Spatially balanced sampling designs are always more precise than random designs for estimating the size of aggregated populations

Population size is a parameter crucially needed for both ecological research and conservation planning. As it is usually impossible to count every individual in a population, ecologists rely on sampling strategies to estimate it. The precision of the resulting population size estimates, i.e. the sampling variance, depends on how the individuals are spatially distributed over the study area, more precise estimates being obtained for populations with spatially homogeneous densities of individuals than for populations with heterogeneous densities. One of the main causes of such a spatial heterogeneity of density is the aggregation of individuals, which can result from limited dispersal capacity or from the patchiness of favourable habitat for example. The goal of our study was to determine the best sampling strategy for populations depending on their level of aggregation and to provide practical guidelines to define this design for a given population in the field. We combined simulations of virtual populations and fieldwork on herbaceous plant species to compare the precision of three sampling designs, i.e. simple random sampling (SRS), systematic sampling (SYS), and spatially balanced sampling (SBS), over wide gradients of densities, aggregations (from repulsion to strong aggregation) and sample sizes.

For the virtual populations, SYS and SBS were always equally or more precise than SRS, with sampling variances lowered by 40% and 20% respectively. This result is explained by a unique property of both sampling methods, whereby the highest precision for a population is always obtained when the average distance between sampling units equals the diameter of the aggregates. We obtained similar results for the natural populations we studied, although SYS and SBS were even more precise than in our simulations, with sampling variance lowered by 75% (SYS) and 60% (SBS) compared to SRS. Aggregate diameters we measured in the field allowed us to identify efficient designs, but not the best possible designs for the studied populations, suggesting that other parameters influence the sampling variance in natural populations with more complex spatial structures than the one we simulated. Meanwhile, we recommend to roughly assess aggregate diameters in the field to build relevant sampling designs for aggregated populations.