Annotated Bibliography
Patch Dynamics in Naturally Fragmented Habitats: Implications for Conservation

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The literature below touch upon the basics and application of metapopulations and metacommunities and are an introduction to theories commonly used as a basis for the evaluation of dynamics of naturally patchy habitats.

Anderson, R.C., Fralish, J.S., and Baskin, J.M., editors. 1999. Savannas, barrens and rock outcrop plant communities of North America. Cambridge University Press. Cambridge, UK.

This book is interesting, but not that relevant. This book is a wealth of information on naturally patchy plant communities across North America. Patchiness in these communities is a result primarily of edaphic factors and microclimate. Substrates these communities occur on include sand deposits, granite outcrops, serpentine, limestone, and shale. Interesting and an excellent reference source, but the book is mostly descriptive in its treatments of the plant communities and therefore isn't that relevant to the concept of patchiness since there is not a strong theoretical basis in the descriptions.

Freckleton, R.P. and Watkinson, A.R. 2002. Large-scale spatial dynamics of plants: metapopulations, regional ensembles and patchy populations. Journal of Ecology 90, 19-434.

This is a good paper in general that addresses what constitutes a metapopulation; "a critical review of the application of metapopulation theory to the regional dynamics of plants". It proposes a classification of spatial dynamics of plants at the regional and local scales, and defines metapopulations, regional ensembles, and spatially extended populations. Says that a patchy population is not necessarily a metapopulation.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42, 73-88.

This paper is somewhat dated but is still an excellent theoretical overview of three alternatives to classical metapopulation theory, which Harrison states is exemplified by few metapopulations in the empirical literature. She contrasts classical metapopulations, where sets of populations persist in a balance between local extinction and recolonization, with 1). Mainland-island source-sink metapopulations, 2). Patchy populations, and 3). Non-equilibrium metapopulations.

Harrison, S., and Taylor, A.D. 1997. Empirical evidence for metapopulation dynamics. Pages 27-42 *in* I. Hanski and M.E. Gilpin, editors. Metapopulation biology: ecology, genetic, and evolution. Academic Press, San Diego, CA, USA.

This is a good place to start for gaining some background theory before evaluating naturally patchy population, community, or landscape-level dynamics. This chapter in an edited volume on metapopulation dynamics is a good summary and review that provides a forum for presenting the concepts of metapopulations. It discusses the differences between single-species and multi-species metapopulations, different cases of population dynamics and species interactions, and examines the critical assumptions of classical metapopulation models.

This chapter provides examples where classical metapopulation theory does not describe populations and patch dynamics, and is a good place to review concepts of the theory before reading papers on naturally patchy populations that attempt to apply the theory. The authors also identify criteria for judging empirical evidence on metapopulations.

Templeton, A.R., Shaw, K., Routman, E., and Davis S.K. 1990. The genetic consequences of habitat fragmentation. Annals of the Missouri Botanical Garden 77(1), 13-27.

An interesting paper that discusses the long-term genetic and evolutionary consequences of fragmentation is inferred from studies on populations that have undergone natural habitat fragmentation (historic) in the Ozark Mountains. The authors feature case studies of genetics of relictual populations in naturally fragmented habitats, and make the point that genetic surveys offer a more reliable means for inferring demographic fragmentation that dispersal studies.

The articles by Harrison and Harrison et al. are complex but interesting and approach the dynamics of naturally patchy plant communities from a perspective of large-scale and differential scale patterns of diversity at the community level. The emphasis is on patch dynamics in serpentine habitats.

Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology 78(6), 1898-1906.

This study examined local and regional components of diversity (alpha, beta and gamma diversity) of woody species in a patchy habitat, providing as they put it, a "spatially structured analysis of community diversity". It's a well-written and interesting paper; somewhat complex and needs to be read a few times to really get it, but worth it for the examination of diversity at different spatial scales. This study was one of the first to confirm the prediction that patchiness enhances the differentiation in species composition among sites, as well as one of the few to examine ecological implications of patchiness of serpentine soils.

Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. Ecology 80(1), 70-80.

This is the companion study to the one by Harrison above on woody species diversity, and compares alien, native, and endemic herb diversity patchy and continuous sites within a single habitat and community to analyze the affects of patchiness with respect to predictions of metacommunity theory. This paper addresses diversity in a sparse habitat where competition is not a strong force (not a competition-based metacommunity model). Instead, the study shows results consistent with Holt (1997): spatial structure in the metacommunity arises through the individual species' different habitat breadths, colonization rates, and persistence abilities.

Harrison, S., Maron, J., and Huxel, G. 2000. Regional turnover and fluctuation in populations of five plants confined to serpentine seeps. Conservation Biology 14(3), 769-779.

This study tested a 'classical' metapopulation theory of local extinction and recolonization through the examination of some predictions of metapopulation theory in five plants confined to a harsh and isolated habitat, spring seeps on serpentine soils. The study tested and confirmed that habitat isolation increased the chance of local extinction and decreased the chance of colonization. The purpose here was to address another central issue in metapopulation theory: for rescue and recolonization to be effective, local populations must be close enough to one another to permit dispersal among them. Results suggested that for rare plants in isolated habitats, the spatial configuration of populations may have an important influence on local population persistence.

Harrison, S., Viers, J.H., and Quinn, J.F. 2000. Climatic and spatial patterns of diversity in the serpentine plants of California. Diversity and Distributions 6(3), 153-161.

This 'big picture' study analyzed the spatial distribution and large-scale patterns of diversity across the entire serpentine landscape of California. The naturally patchy, isolated nature of the habitat was hypothesized to either promote plant diversity by enhancing opportunities for speciation, or reduce diversity by increasing rates of extinction. Results indicated that regions with greater average isolation among serpentine outcrops tended to have fewer endemic species, indicating that insularity actually leads to reduced diversity in the serpentine flora. These results are similar to what Harrison found (1997, 1999) in her study of herbaceous and woody serpentine flora.

Harrison, S., and Inouye, B.D. 2002. High beta diversity in the flora of Californian serpentine islands. Biodiversity and Conservation 11, 1869-1876.

This study of alpha, beta, and gamma diversity draws upon the work done by Harrison (1997, 1999; discussed above) by extending the investigation to a larger scale through an examination of the botanical richness of the entire Californian serpentine flora. This is the companion study to Harrison et al. 2000, which looked at alpha diversity. The present study compared (1) overall beta diversity of the serpentine and total floras, (2) the strength of the responses of beta diversity in these two floras to two explanatory factors, geographic distance and large-scale climatic variation. The study hypothesized, and affirmed, that beta or among-region diversity would be higher in the serpentine flora. The serpentine flora showed greater variation across geographic and environmental distance than did the non-serpentine flora, in proportion to its size. Results were consistent with Harrison (1997, 1999), which concluded that the patchiness of the serpentine substrate within a single region led to lower local (within-outcrop) diversity but enhanced among-site (among-outcrop) diversity. Thus the authors' conclusion is that patchiness in this system means that conservation work should protect a network or region of sites.

The series of articles by Wolf and Wolf et al. are interesting in examining conservation dynamics, often from a pollination ecology and population genetics standpoint, of rare plants in naturally patchy habitats. Once again the emphasis is on patch dynamics in serpentine habitats.

Wolf, A., Brodmann, P.A., and Harrison, S. 1999. Distribution of the rare serpentine sunflower, *Helianthus exilis* (Asteraceae): the roles of habitat availability, dispersal limitation and species interactions. Oikos 84, 69-76.

This study by Wolf et al. is similar to the other work by Wolf where she examines persistence of a rare plant on serpentine soils. In this work on the serpentine sunflower, she examines patch occupancy, distribution and pollinator interactions in order to determine "whether limited dispersal is a major influence on the regional distribution of *H. exilis*". Again, a study that examines patch dynamics from a classical metapopulation perspective: is this species subject to a precarious extinction-recolonization balance for persistence? In this case, since most suitable patches were already occupied, the species appears to have a very low rate of extinction, perhaps due to a highly persistent seed bank.

Wolf, A.T., Harrison, S.P., and Hamrick, J.L. 2000. Influence of habitat patchiness on genetic diversity and spatial structure of a serpentine endemic plant. Conservation Biology 14(2), 454-463.

This paper discusses the importance of taking into account the natural distribution of populations, as surprisingly the results of this study on genetic diversity and spatial structure of the rare serpentine morning glory indicated that there was no reduced genotypic diversity or heterozygosity of populations on small, more isolated patches compared with populations on large patches. On the contrary, there was significant diversity of genotypes on isolated serpentine outcrops. The authors conclude that for preserving genetic integrity of the species, conservation should focus on all populations, however small or fragmented.

Wolf, A.T. and Harrison S.P. 2001. Effects of habitat size and patch isolation on reproductive success of the serpentine morning glory. Conservation Biology 15(1), 111-121.

This is a companion paper to the study above, on the same rare species. An excellent general introduction to some of the issues facing research on, and conservation in, naturally patchy or fragmented habitats. This work provides an interesting context for evaluating the features of naturally patchy habitats and how the size and proximity of the patches may influence reproductive success of rare endemic species. In this study, habitat geometry was an important influence on reproductive success. Results indicated that fruit production was significantly lower on small outcrops. While pollinator visitation rates per flower and overall bee abundances were not different, the effectiveness of pollination was lower on small outcrops because sources of compatible pollen were generally farther away than on large outcrops. This study found that spatial factors shaped ecological interactions locally (within 100m), while at the regional scale, outcrop size was a consistent predictor for reproductive fitness in the serpentine morning glory. The authors conclude that conservation measures for naturally patchy species should be aimed at multiple scales, including the microenvironment of individual plants, the configuration of local populations, and the spatial extent of remnant habitats. These various scales are all important even if the target species appear to be pre-adapted to fragmentation of their natural habitat.

Wolf, A. 2001. Conservation of endemic plants in serpentine landscapes. Biological Conservation 100, 35-44.

This summary study of previous research on two rare plants in serpentine habitats evaluates the results from a conservation perspective. The findings support the recommendation that clusters of local populations should be protected for long term conservation of endemic, self-incompatible plant species. Empirical studies such as this analysis suggests that physical features (e.g. microhabitat distribution) and functional characteristics (e.g. pollination dynamics) of the landscape may be equally or more important than habitat area per se in preserving native plant populations. Wolf highlights the need to be aware of spatial dynamics of populations and the importance of local environments in this patchy environment of two self-incompatible, rare plant species.

The references below highlight work on metapopulation and spatial ecology of fauna in a variety of naturally patchy habitats. Oftentimes the purpose of the study was to critically examine, and in some cases refute, predictions of metapopulation theory.

Bleich, V.C., Wehausen, J.D. and Holl S.A. 1990. Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4(4), 383-390.

Fairly interesting. This paper discusses the conservation of mountain sheep in their naturally patchy habitat and the importance of "non-habitat" areas or "stepping stones" to suitable habitat. The authors highlight the importance of the matrix to connect habitat patches.

Bradford, D.F., Neale, A.C., Nash, M.S., Sada, D.W., and Jaeger J.R. 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology 84(4), 1012-1023.

This was a good paper that applied the concepts of metapopulation theory in examining the distribution and patch occupancy of toads in the Mojave Desert. The paper tested two predictions of metapopulation theory: that the incidence of habitat patch occupancy is related to patch size and inversely to patch isolation. In addition, the paper tested a potentially competing hypothesis: that patch occupancy is influenced by local environmental conditions. What they found is a model not of classical metapopulation dynamics, since there was no correlation of patch occupancy with isolation, but of 'patchy populations', where there is frequent dispersal among patches and rarely local extinctions. The paper was also interesting because it examined the effects of environmental conditions on patch occupancy, which is different from many metapopulation studies which often assume that patch quality is uniform.

Darimont, C.T., Price, M.H.H, Winchester, N.N., Gordon-Walker, J., and Paquet, P.C. 2004. Predators in natural fragments: foraging ecology of wolves in British Columbia's central and north coast archipelago. Journal of Biogeography 31, 1867-1877.

This paper was not very relevant to my topic. The study examines the spatial variability of resource use (foraging ecology) by predators (wolves) in fragmented areas.

Driscoll, D.A. 2005. Is the matrix a sea? Habitat specificity in a naturally fragmented landscape. Ecological Entomology 30, 8-16.

An interesting paper, but the hypotheses tested are fairly simple. Paper examines beetle abundance and species richness in two types of forest (the 'patches') and in a surrounding matrix of low buttongrass sedgeland. This paper asks, what is the proportion of patch-specific species in a fragmented landscape? What is the amount of overlap between habitat patches and the surrounding land? An important point that this paper makes, but does not explore further with any additional research or experiments, is that "a high level of habitat specificity does not necessarily imply that metapopulation dynamics occur". The authors go on to point out that species persist in landscapes in a variety of ways, and can form patchy populations, classical metapopulations, etc. It is through the study of how patches and species within those patches function, as well as the spatial distribution of both, that can give more insight into metapopulation theory or other dynamics. The one point this paper CAN make is that "The results of this study are valuable because they show that in at least 40% of the pit-trapped species, metapopulation and island biogeography theory are not important, at least at the scale of forest patches…"

Grant, P.R. and Grant, B.R. 1997. The rarest of Darwin's finches. Conservation Biology 11(1), 119-126.

This article was not that relevant. This article is basically a summary of the conservation status of this species of finch, which occurs in a naturally fragmented distribution in specialized habitats on individual islands in the Galapagos. It is more of a descriptive study of conservation status and current population size, and discusses threats and conservation needs of the species. Not much theory presented except "small and isolated populations are vulnerable to extinction".

Kneitel, J.M. and Miller, T.E. 2003. Dispersal rates affect species composition in metacommunites of *Sarracenia purpurea* inquilines. The American Naturalist 162(2), 165-171.

This paper examines the role of dispersal in determining species composition and diversity in a patchy community, the water-filled leaves of pitcher plants. It's a good paper that tests a theoretical prediction of dispersal frequency and local species richness. The authors in this study manipulated dispersal frequencies, resource levels, and the presence of predators (mosquitoes) among pitcher plant communities. The results were consistent with the model. Increased dispersal frequencies significantly increased regional species richness and abundance while decreasing variance among local communities. Intermediate dispersal frequencies maintained some species in the inquiline communities by offsetting extinction rates. The authors conclude that local community composition and the degree of connectivity between communities are both important for understanding species diversity patterns at local and regional scales.

Leisnham, P.T. and Jamieson, I.G. 2002. Metapopulation dynamics of a flightless alpine insect *Hemideina maori* in a naturally fragmented habitat. Ecological Entomology 27, 574-580.

An interesting paper that tests classical metapopulation theory for a flightless, low-dispersing, low density insect that occurs naturally under slabs of rock that have broken off isolated schist outcrops called tors. The objectives of the study were to determine whether *H. maori* fit the criteria of a true metapopulation by determining the extent of dispersal between local populations and to examine the effect of patch size on immigration and emigration rates among large and small tors over time. This study was interesting because most metapopulation studies have focused on organisms with relatively high dispersal capabilities, while fewer studies have examined species with low dispersal capabilities living in a highly fragmented habitat. The authors concluded that *H. maori* conform to many of the predictions of metapopulation theory even though they are flightless, show relatively low dispersal rates, and occur at low densities. The low dispersal rate between tors and the low frequency of colonization events recorded in the study suggest that the weta on rock tors act like semi-isolated island populations. However, the authors conclude that the population size on large patches, the fact that there is some long-distance dispersal, and the indication that smaller tors are more prone to extinction, indicate that "the dispersal rate can generate enough migrants to potentially colonize or recolonize uninhabited tors" and thus constitutes a metapopulation.

McIntyre, N.E. and Wiens J.A. 1999. How does habitat patch size affect animal movement? An experiment with darkling beetles. Ecology 80(7), 2261-2270.

This article was fair but not terribly relevant. It is interesting for an overview of landscape pattern and how the patterning of the heterogeneity affects the abundance and distribution of organisms and population, community, and ecosystem patterns that follow from distribution and abundance. "Within any landscape, the behaviors of organisms will be influenced by the heterogeneity or spatial patterning of the mosaic and the scale on which landscape pattern is perceived".

Roslin, T. and Koivunen, A. 2001. Distribution and abundance of dung beetles in fragmented landscapes. Oecologia 127, 69-77.

Interesting ideas and introduction, but the paper itself I found difficult to read, understand, and relate the methods and results back to the hypotheses tested. This paper analyses the spatial population structures of a set of closely related dung beetle species that frequently co-occur in a patchily distributed resource: livestock dung in pastures. The study had three objectives: to describe the spatial population structures of different *Aphodius* species, (through data on habitat selection, resource use and migration rates), to relate the spatial population structure of individual species, and groups of ecologically similar species, to contemporary abundance and distribution in two landscapes with different densities of pastures, and to compare the abundance and distribution of beetles before and after 15 years of habitat loss in one landscape. The paper evaluates whether the classical metapopulation concept provides a useful description of the actual population structure and consequent dynamics.