

A bridge too far for conservation?
Considering contemporary evolution in conservation of fragmented
populations

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Introduction

Biodiversity is declining on a global and rapid scale, and extinction of rare and threatened species is increasingly common. Anthropogenic influences are an important factor in contemporary extinction. The four most important anthropogenic causes of the declining biodiversity are described as the 'evil quartet', by Diamond (1975): habitat degradation, loss and fragmentation, overharvesting, invasive species, and chains of extinction.

Many biologists consider habitat fragmentation to be the largest threat to biodiversity (Fletcher, et al. 2018). Habitats are lost and fragmented at an increased rate. Urbanization, such as roads and expanding cities, and food production (e.g., monocultural agriculture), are of great influence (Ruell, et al. 2012, Ralls, et al. 2017). Habitat fragmentation results in populations being separated and eventually isolated. This isolation could lead to limited or no gene flow, which is associated with a loss of genetic diversity, decreased fitness, and survival (Blanton, et al. 2019). Small isolated populations might lose genetic diversity and suffer inbreeding depression (i.e. loss of fitness) (Huisman, et al. 2016, Lopez, et al. 2009, Lino, et al. 2018). Eventually, this could lead to reduced adaptive capacity due to a smaller gene pool and even increased extinction risk (Ralls, 2017). However, there is no clear consensus on this link between isolation and the loss of genetic diversity.

Predicting whether a population will survive, go extinct, or even thrive in a certain (changed) environment, is a large part of conservation. Determining which conservation strategy to apply has been shown a struggle throughout the years. As the effects of fragmentation became known, the urge for a proper conservation strategy became apparent. In the 1970s and 1980s, the Single Large Or Several Small (SLOSS) theory has been debated extensively (Simberloff and Abele 1984), referring to whether connecting fragmented habitats would be the best strategy. These connections are also known as corridors. Furthermore, habitat protection or inaction has been (successfully) applied and, as one might expect, debated (Ralls, et al. 2017, Stockwell, Hendry and Kinnison 2003).

The lack of consensus suggests an incomplete understanding of the processes regarding fragmentation. Few scientists suggest a shift in the paradigm of conservation strategies, taking into account the genetic processes and eco-evolutionary dynamics of isolated fragmented populations (Love Stowell, Pinzone and Martin 2017, Ralls, et al. 2017)). Eco-evolutionary dynamics suggest an interaction but should be interpreted as evolutionary processes on an ecological time scale. The process of genetic changes on such a short time scale, observable during a (human) lifetime, is also known as contemporary evolution. Increased scientific interest and a growing body of evidence emphasize the importance of considering contemporary evolution when determining a conservation strategy (Ralls, et al. 2017).

This paper aims to discover the role of contemporary evolution in fragmented populations and to provide advice for (re)connecting or fragmenting populations. The main question is: *Should contemporary evolution be considered in connecting fragmented populations? And if so, when is connecting fragmented populations based on contemporary evolution desired?*

In the first chapter fragmentation and current conservation strategies are explained. In the second chapter, contemporary evolution and the role in ecological systems is described. Then, in chapter three the influence of fragmentation on contemporary evolution is explained with several examples. In chapter four the main questions are answered, to be concluded and discussed in the last two sections.

1. Habitat fragmentation

1.1 How does fragmentation arise and affect populations?

Species distribution has always been uneven across the globe. Species live in suitable habitats divided over ranges. However, these habitats are increasingly threatened by fragmentation and degradation (Harrison 1991, Margan, et al. 1998, Nilsson 1978). Fragmentation of populations and ecosystems can arise from natural causes, such as volcanic eruptions, river flow change, or forest fires. However, anthropogenic causes, such as deforestation, urbanization, and intensive agriculture, are increasingly influential (J. M. Diamond 1989, Haddad, et al. 2015, Nilsson 1978, Fritz, et al. 2017). Accelerated climate change due to anthropogenic influences, such as melting polar ice, desertification, and higher or more extreme temperatures, can increase the frequency and/or intensity of natural causes (Opdam en Wascher 2003). This can result in populations driven to alternative habitats with other conditions and different (local) selective pressures (e.g., predators, food availability, and competition) (Burnham en Burnham, W. A. 2012, Luigi D'Andrea 2009, Kooij, Engelhard en Righton 2016).

Habitat fragmentation is associated with small population sizes. If the connection between subpopulations is too weak, they can suffer (genetic) isolation by distance (IBD) and local adaptation (isolation by adaptation, IBA) (Zhao, et al. 2013) Whether isolation occurs, depends on the mobility of the species and the proximity of other suitable habitats. If a population is isolated, limited or no gene flow between the (sub)populations occur. (Haddad, et al. 2015, Nilsson 1978, Ruell, et al. 2012). A meta-analysis by Lino et al. (2018) detected an “overall decrease in allelic diversity, allelic richness, observed heterozygosity, and expected heterozygosity in mammalian species that live in situations of high habitat fragmentation”.

There are several theories to describe the dynamics of isolated biotas. The Theory of Island Biogeography was one of the first theories, using extinction and immigration rates of islands to describe the dynamics comparable to ecosystems (MacArthur en Wilson 1967). The dynamics of fragmented populations on land were long predicted using this theory (Nilsson 1978). However, terrestrial fragmented populations are not isolated by water. Haddad et al. (2015) concluded that those fragmented habitats may be surrounded by suitable matrices for some species, instead of inhabitable borders. This results in a range of suitable habitats. Levins (1969) proposed a theory to account for these complex fragmented systems. This Metapopulation Theory provides a framework for understanding and predicting the dynamics of fragmented populations. A metapopulation consists of multiple (sub)populations connected by dispersing individuals. This acknowledges the existence of isolated populations as a part of this model. The model has a few key elements, often used in complex and more realistic models. The equation of this model expresses the proportion of habitat patches being occupied, using the colonization, dispersal, and extinction rates (Levins 1969).

Different structures of metapopulations have been described, with as four main types (from most to least extinction resistant): Patchy, Core-satellite, Levins's classic, and Non-equilibrium (figure 1) (Harrison 1991). Metapopulation analysis proved to be an important addition to population

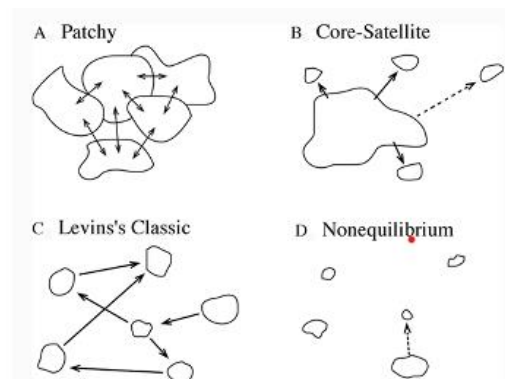


Figure 1: Metapopulation types. A to D ranging from most to least extinction resistant. (Harrison 1991)

dynamic research, for example in the Florida scrub jay. The Florida scrub jay are known for existing in fragmented populations. The population size did not raise the need for immediate action (around 4000 pairs), however, the distribution of the pairs was alarming. Six of the 42 subpopulations were relatively extinction-resistant, while at least half were the unsafe non-equilibrium type (Breininger, Burgman en Stith 1999). Non-equilibrium metapopulations are associated with recent anthropogenic disturbances and receive increasing scientific attention.

Several genetic processes determine the persistence or extinction of fragmented isolated populations. First, small isolated populations suffer from a decrease in genetic diversity. Homogenization of the gene pool due to limited gene flow can lead to inbreeding (Lopez, et al. 2009). When inbreeding is only 10%, the fitness is reduced by 45%, possibly leading to inbreeding depression (i.e., loss of fitness due to inbreeding) (Love Stowell, 2017). An example was shown in wild red deer. Lifetime breeding success (a proxy for fitness) was reduced by 82% in females and 95% in males when the inbreeding coefficient was 0.125, compared to individuals with no inbreeding (Huisman, et al. 2016). Second, genetic drift leads to the fixation of deleterious alleles (Wang, et al. 1999). Last, an extinction vortex might occur due to the accumulation of deleterious alleles and inbreeding depression (Crooks, et al. 2017, Wang, et al. 1999). Extinction risk is greater with more fragmentation, as has been quantified for over 4000 terrestrial species. The risk was elevated due to smaller ranges and few suitable habitats within these ranges. Often highest-suitable habitats were outside the researched protected areas, increasing the extinction risk even further (Crooks, et al. 2017). However, fragmentation does not always lead to the loss of genetic diversity. For example, bobcat populations with different degrees of fragmentation were sampled on the East and West Coasts of the US. It was hypothesized that the closer surrounding urbanization occurred, the less functional connectivity (i.e., gene flow and genetic diversity) was observed. Lower genetic diversity was found in more isolated populations. Yet, some more isolated populations showed higher genetic diversity than less isolated populations. The amount and genetic diversity of possible migrants presumably influence the genetic composition of populations as well (Ruell, et al. 2012). As genetic diversity largely determines evolutionary adaptation, this shows fragmentation isn't the only actor.

1.2 How are fragmented populations currently conserved?

To describe the current conservation practice, a short recap of the past is necessary. Fragmentation has been identified as a primary threat to biodiversity. The urgency for strategies to conserve species on the verge of extinction increased.

SLOSS debate

In the 1970s and 1980s, Single Large or Several Small (SLOSS) was intensively debated. This debate is about the preferred size and layout of a reserve to support species. Diamond (1975) suggested a single large reserve, as a larger area could support more species and small areas would increase the extinction rate. This theory was challenged, as it relies on nested species composition and because of the unavailability of empirical data to prove that fragmentation would induce extinction (Simberloff en Abele 1984). Although there is still no consensus in this debate, the proposal that the outcome depends on situation-specific factors is generally accepted (Margan, et al. 1998, Lindenmayer, et al. 2014). The SLOSS discussion paved the road to fragmentation research and associated conservation practices. Currently, several conservation practices are used. Inaction and habitat protection are common, but considered insufficient to prevent fragmented populations from extinction. (Alagador, et al. 2012, Ralls, et al. 2017, Love Stowell, Pinzone en Martin 2017). Active and passive genetic restoration are increasingly used (Alagador, et al. 2012, Hilty, et al. 2019, Love Stowell, Pinzone and Martin 2017, Bouzat, et al. 2009). Considering fragmentation is linked to decreased genetic diversity, passive and active restoration is a logical approach. Active restoration (i.e. deliberately mixing

populations) can increase genetic diversity, reduce inbreeding depression, and raise population size (Johnsson, et al. 2010, Bouzat, et al. 2009, Neuwald en Templeton 2013). As “active” implies, species and or individuals are to be translocated. A commonly described (successful) example is the Florida panther (*Puma concolor coryi*), where eight female pumas (*Puma concolor stanleyana*) were introduced into the declining population, resulting in increased population size, genetic diversity, and survival rates (Johnsson, et al. 2010). As fragmentation increases, this is presumably not a maintainable practice.

Passive restoration, known as corridors, can restore the gene flow between populations (Alagador, et al. 2012, Hilty, et al. 2019). Gene flow can have positive effects on population size and genetic diversity (Swindell and Bouzat 2006). However, the adaptive potential seems to suffer from connecting isolated populations (Swindell and Bouzat 2006). Yet corridors are suggested as one of the main conservation strategies for fragmented populations (Ralls, et al. 2017, Love Stowell, Pinzone en Martin 2017, Sanderson, et al. 2003). Corridors (or connectivity restoration) are not simply a bridge or tunnel connecting two roadsides, but a complex planning region. Human-altered and natural areas often occur in a matrix (Sanderson, et al. 2003). Specificity is very important, a corridor for one species might form a barrier for another (Alagador, et al. 2012, Van Schalkwyk, et al. 2020, Simberloff en Cox 1987, Stockwell, Hendry en Kinnison 2003).

2. Contemporary evolution

Contemporary evolution is the genetic change on a short time scale, perceivable within relatively few generations (Moya-Laraño, et al. 2014). Also described as rapid or adaptive evolution, it can occur as a genetic adaptation to a changing environment (e.g., as a result of anthropogenic disturbances). Some clear examples might be bacterial evolution towards antibiotic resistance, as this has been a threat to existing infection treatments (Wheatley, et al. 2021), or rapid evolution in influenza viruses (Gorman, Bean en Webster 1992). Another example is pests developing resistance against pesticides, posing a threat to food production (and food security) (Fritz, et al. 2017).

Evolution has long been regarded as a slow process, spanning over many generations and hundreds of years, whereas phenotypic plasticity or adaptation was viewed as the primary short-term mechanism to adapt to a changing environment due to (natural) disturbances. The most famous case is melanism in the peppered moth in the 19th century (Tutt, 1896). However, evidence that adaptation can be genetically based is expanding, as already proposed by Haldane (1957). The amount of genetic variation/adaptation exceeded the expected amount by natural selection through perturbations (Stockwell, Hendry en Kinnison 2003). This vastly induced research on contemporary evolution in the last three decades (Ralls, et al. 2017). Stockwell et al. (2003) proposed the trajectories of populations of a certain size in relation to contemporary evolution after a disturbance (figure 2). Population size declines

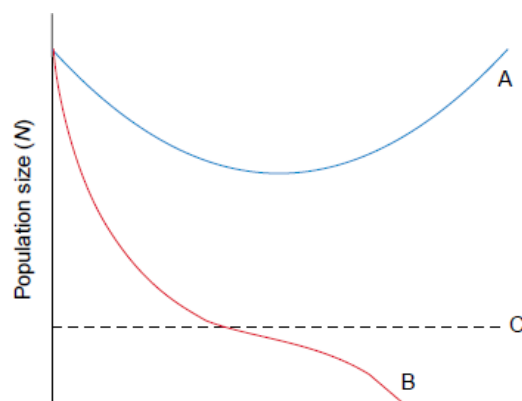


Figure 2: Two scenarios for population trajectories under selective pressures from a changing environment. A presents adaptation and results in population recovery. B presents selective pressure that is strong enough to increase the level of extinction or to a high demographic risk of extinction (Stockwell, Hendry en Kinnison 2003).

under selective pressures. A presents adaptation with increased fitness and survival, resulting in population recovery. With B however, selection pressure is very strong, so strong it might decline to demographic extinction, as depicted by C.

Contemporary evolution plays a role on the ecological time scale, possibly affecting ecosystem functioning and vice versa (Kinnison en Hairston Jr 2007). Uncovering the difference between plasticity and genetic adaptation proved to be complex, and is often intertwined (Rudman, et al. 2018, Collyer, et al. 2007, Ghalambor, et al. 2007, Keller en Taylor 2008).

Phenotypic plasticity can drive directional selection, as shown in pupfish (Collyer, et al. 2007), guppies (Gordon, Hendry en Reznick 2017), and blackcaps (Rolshausen, et al. 2009). A shift of plasticity optimum and mean of traits are observed. This indicates an ecological influence on evolutionary processes (Ellner, Geber en Hairston Jr 2011).

Among many taxa, eco-evolutionary processes as a result of phenotypic adaptation are observed. A few of those cases are:

Blackcaps

Central European Blackcaps were reproductively isolated due to division in their migration route. The genetic divergence occurred in <30 generations and was greater than the allopatric blackcap divergence, which was driven by an 800km distance (Rolshausen, 2009).

Fish

Guppies: Switched from high to low-level predation. After nine years, the guppies genetically diverged from their high predation-adapted ancestors. A change in phenotypic plasticity and life history was observed. Litter size and offspring weight changed, as well as plastic food availability response (Gordon, Hendry en Reznick 2017).

Pupfish: body shapes of pupfish are correlated to the salinity of their habitat. Saline water results in slender bodies, whereas brackish water results in deep-bodied fish (i.e. a body shape wider than its length). Both 30 years and 1 year previously, 'saline origin'-populations were introduced into brackish lacustrine water. Both populations showed body-shape divergence, however, the 30year old population showed significant divergence (Collyer, et al. 2007).

Cichlid fish: One of the most studied species concerning speciation and genetic divergence. This species, *Cynotilapia afra*, had diverged into a genetically and phenotypic different species, located north and south of Thumbi West Island. This divergence was measured over two decades (Todd Streelman, et al. 2004).

Insects

The tobacco budworm (*Heliothis virescens*) lives on and is a pest to cotton plants. To deal with this pest, Bt-toxin-producing cotton plants were increasingly cultivated. However, genetic differentiation of the insecticide target in the genome was soon after observed. The adapted budworm could deal with Bt-toxin produced by the cotton plant (Fritz, et al. 2017) .

3. How does fragmentation affect evolutionary adaptation? Promote or constrain?

Fragmentation promotes evolutionary adaptation, as shown in many cases (Olsen, Evju and Endrestol 2018, Rudman, et al. 2018, Pelletier, Garant and Hendry 2009, Shefferson and Salguero-Gómez 2015, Chen, et al. 2018, Fletcher, et al. 2018). As described, it can have a severe impact on populations and their persistence (Wilcox and Murphy 1985, Nilsson 1978). As novel local selective pressures arise, the need for adaptation conjointly rises. Small population size and lower genetic diversity can disturb and constrain evolutionary adaptation, as stochastic processes/genetic drift and inbreeding

depression might get the upper hand resulting in maladaptation and/or extinction (Wang, et al. 1999, Harrison 1991).

Yet, fragmented populations do show effective adaptation, for example in the white-footed mouse in New York. The white-footed mouse lives in the forest fragments surrounded by urbanization. The adaptation of specific genes is compared across rural and urban populations. The urban white-footed mice have adaptations in genes associated with immune response, reproduction, and metabolism of foreign chemical compounds (i.e. xenobiotics) (Harris, et al. 2013).

Some studies argue that fragmentation generally constrains evolutionary adaptation, since populations are often inbred and lose genetic diversity due to genetic drift (Ralls, et al. 2017, Blanton, et al. 2019, Stockwell, Hendry and Kinnison 2003, LaRue, Chambers and Emery 2017, Kinnison and Hairston Jr 2007). An example in *Drosophila melanogaster* shows that fragmentation does constrain adaptation. Populations of *Drosophila melanogaster* were either (sub)divided or undivided and introduced to unfamiliar conditions and allowed to breed for six generations. Combined with limited gene flow, the fragmented populations showed reduced adaptive capacity, as this is divided over the subpopulations rather than present in one (larger) population (Bakker, et al. 2010). Many different factors determine evolutionary adaptation, such as fragmentation size, distance, habitat amount, and quality (Lopez, et al. 2009, Ruell, et al. 2012, MacDonald, et al. 2018, Nilsson 1978, Breininger, Burgman en Stith 1999). There is no consensus due to the absence of a large-scale meta-analysis and the complexity of these dynamics.

4. Is restoring connectivity of fragmented populations recommended when considering contemporary evolution?

Corridors are applied to prevent inbreeding and fitness decline of fragmented populations, as mentioned in chapter 1. However, not all populations are subject to the same conditions. This poses the question: when should we aim to (re)connect populations and when should we leave or even stimulate fragmentation?

Ralls et al. (2017) called for a paradigm shift in the genetic management of these populations. They described how inaction is often the default conservation strategy and should be renounced. An important criterium is limited outbreeding. A decision-making process scheme was proposed for the genetic management of small isolated populations, see figure 3.

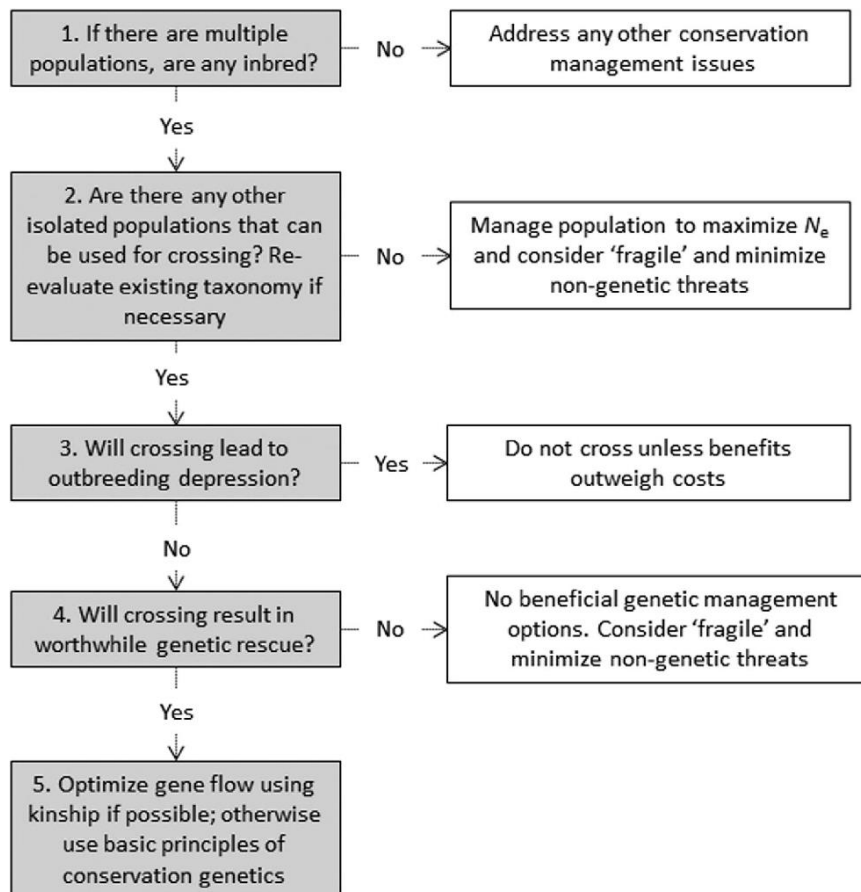


Figure 3: Decision scheme for genetic management of fragmented plant and animal populations N_e is the effective population size, i.e. the number of individuals that would result in the same loss of genetic diversity, inbreeding, genetic drift, or coalescence if they behaved in the manner of an ideal population (Ralls, et al. 2017).

As a supplement to this decision-making scheme, the conditions for reconnection, fragmentation inaction, and stimulation are outlined below.

Reconnection

If the population is too small to persist, inbreeding depression signs occur, deleterious alleles spread through the population rapidly, and adaptive potential/capacity is not large enough. Connecting populations might concern some, as the taxonomic integrity and naturalness of species are at risk, and cultural reluctance to genetically 'mix' populations and create hybrids is present (Love Stowell, Pinzone en Martin 2017). With (re)connection, dispersal and recolonization of suitable habitats are increased, as well as increased genetic diversity and potential spread of adaptive alleles (Alagador, et al. 2012, Olsen, Evju en Endrestol 2018). However, (adapted) populations can produce fewer fit hybrids, unfavourable for the fitness and survival rates of the population. Local adaptation can be lost, but this adaptation is often not substantial and the loss manageable (Ralls, et al. 2017).

Inaction

If the population is large enough to maintain genetic diversity and shows little to no signs of inbreeding with fitness decline, fragmentation can subsist. This also depends on whether adaptive capacity is large enough to overcome selective pressures, as depicted in figure 2. If a population is locally adapted and genetically distinct from other populations, inaction is advised to prevent outbreeding depression.

Stimulation

This might be controversial, as much fragmentation occurs due to human disturbance and is seen as harmful and immoral (Stockwell, Hendry en Kinnison 2003). Yet some cases might benefit from active fragmentation. Obviously with thorough research and consideration. These effects are not studied intensively yet, so it is mostly speculation. One possible scenario is allopatric species that are not completely isolated and form fewer fit hybrids (Ralls, et al. 2017, Love Stowell, Pinzone en Martin 2017). Other (speculative) scenarios could be: a disease or deleterious allele is affecting a population, dividing this population could be a possible rescue solution. If invasive species thriving and harmful to native species, fragmenting their habitat might increase inbreeding and decline their fitness and survival rates, resulting in population decline or even extinction. This could be a solution for persistent pests for example.

Conclusion

The main question of this review was: *Should contemporary evolution be considered in connecting fragmented populations? And if so, when is connecting fragmented populations based on contemporary evolution desired?*

To summarize, fragmentation can have detrimental effects on populations, but can also stimulate local adaptation through contemporary evolution and increase fitness and survival rates.

Contemporary evolution is no longer considered to be rare and observed in many (fragmented) populations. With increasing fragmentation and rapid local adaptation present in many taxa, connectivity strategies need to be well considered, as it is very case-specific. Cases with rapid and proper adaptation might occur, but also maladapted and inbreeding cases.

There is still no clear consensus and relatively few frameworks available. However, there are key elements recognized.

To determine a connectivity strategy, the following criteria need to be considered: population size, genetic diversity, inbreeding (coefficient) and fitness, genetic distinct and local adaptation.

Discussion

The question that remains to be answered: if you increase connectivity and gene flow, and preserve genetic diversity, will you limit current local adaptivity or aim for future adaptivity? (Stockwell, Hendry and Kinnison 2003) It is very case-dependent and needs more fundamental research to be answered.

Contemporary evolution and implementing it in conservation biology is still relatively new and unexplored. Therefore, definitions are not always identical. Fragmentation is described as division of habitats and populations, but is often used interchangeable with degradation. Decoupling these terms can give a more reliable and defined result, as shown in butterfly species (MacDonald, et al. 2018). Other terms that are coupled, are fragmentation and urbanization. Even though their relationship might seem undeniable, the effects of fragmentation are not always explained by urbanization, as for example shown in bobcats (Ruell, et al. 2012) and plants (Dubois en Cheptou 2016). Further research to decouple and define (the relationship between) these terms is necessary to build a proper framework for connectivity strategies for fragmented populations.

Another factor that might play a role and is not always included or considered important, is patch size (Collins, Holt and Foster 2009). An area large enough for one species with the minimal viable population, may be too small for another (Sanderson, et al. 2003).

References

- Alagador, Diogo, Maria Triviño, Jorge Orestes Cerdeira, Raul Brás, Mar Cabeza, and Miguel Bastos Araújo. 2012. "Linking like with like: optimising connectivity between environmentally-similar habitats." *Landscape Ecology* 291-301.
- Bakker, J., M. E. C. Van Rijswijk, F. J. Weissing, and R. Bijlsma. 2010. "Consequences of fragmentation for the ability to adapt to novel environments in experimental *Drosophila* metapopulations." *Conservation Genetics* 435-448.
- Blanton, Rebecca E., Mollie F. Cashner, Matthew R. Thomas, Stephanie L. Brandt, and Michael A. Floyd. 2019. "Increased habitat fragmentation leads to isolation among and low genetic diversity within populations of the imperiled Kentucky Arrow Darter (*Etheostoma sagitta spilotum*)." *Conservation Genetics* 1009-1022.
- Bouzat, Juan L., Jeff A. Johnson, John E. Toepfer, Scott A. Simpson, Terry L. Esker, and Ronald L. Westemeier. 2009. "Beyond the beneficial effects of translocations as an effective tool for the genetic restoration of isolated populations." *Conservation Genetics* 191-201.
- Breining, David R., Mark A. Burgman, and Bradley M. Stith. 1999. "Influence of Habitat Quality, Catastrophes, and Population Size on Extinction Risk of the Florida Scrub-Jay." *Wildlife Society Bulletin* 810-822.
- Burnham, K. K., and Burnham, W. A. 2012. *The history and range expansion of peregrine falcons in the thule area, northwest greenland*. Copenhagen: Museum Tusulanum Press.
- Chen, Yiyong, Noa Shenkar, Ping Ni, Yaping Lin, Shiguo Li, and Aibin Zhan. 2018. "Rapid microevolution during recent range expansion to harsh environments." *BMC Evolutionary Biology*.
- Collins, Cathy D., Robert D. Holt, and Bryan L. Foster. 2009. "Patch size effects on plant species decline in an experimentally fragmented landscape." *Ecology* 2577-2588.
- Collyer, Michael L., Craig A. Stockwell, Dean C. Adams, and M. Hildegard Reiser. 2007. "Phenotypic plasticity and contemporary evolution in introduced populations: evidence from translocated populations of white sands pupfish (*Cyprinodon tularosa*)." *Ecological Research* 902-910.
- Crooks, Kevin R., Christopher L. Burdett, David M. Theobald, Sarah R. B. King, Moreno Di Marco, Carlo Rondinini, and Luigi Boitani. 2017. "Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals." *PNAS* 7635-7640.
- Diamond, J. M. 1989. "Overview of recent extinctions." In *Conservation for the Twenty-first Century*, by D. Western and M. C. Pearl, 37-41. Oxford University Press.
- Diamond, Jared M. 1975. "The Island Dilemma: Lessons of Modern Biogeographic Studies for the Design of Natural Reserves." *Biological Conservation*.
- Dubois, Jonathan, and Pierre-Olivier Cheptou. 2016. "Effects of fragmentation on plant adaptation to urban environments." *Philosophical Transactions to The Royal Society B*.
- Ellner, Stephen P., Monica A. Geber, and Nelson G. Hairston Jr. 2011. "Does rapid evolution matter? Measuring the rate of contemporary evolution and its impact on ecological dynamics." *Ecology Letters* 603-614.
- Fletcher, Robert J., Raphael K. Didham, Cristina Banks-Leite, Jos Barlow, Robert M. Ewers, James Rosindell, Robert D. Holt, et al. 2018. "Is habitat fragmentation good for biodiversity?" *Biological Conservation* 9-15.
- Fritz, Megan L., Alexandra M. DeYonke, Alexie Papanicolaou, Stephen Micinski, John Westbrook, and Fred Gould. 2017. "Contemporary evolution of a Lepidopteran species, *Heliothis virescens*, in response to modern agricultural practices." *Molecular Ecology* 167-181.

- Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. "Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments." *Functional Ecology* 394-407.
- Gordon, Swanne P., Andrew P. Hendry, and David N. Reznick. 2017. "Predator-induced Contemporary Evolution, Phenotypic Plasticity, and the Evolution of Reaction Norms in Guppies." *Copeia* 514-522.
- Gorman, O.T., W.J. Bean, and R.G. Webster. 1992. *Evolutionary Processes in Influenza Viruses: Divergence, Rapid Evolution, and Stasis*. Vol. 176, in *Genetic Diversity of RNA Viruses. Current Topics in Microbiology and Immunology*, by J.J. Holland. Heidelberg: Springer Berlin.
- Haddad, Nick M., Lars A. Brudvig, Jean Clobert, Kendi F. Davies, Andrew Gonzalez, Robert D. Holt, Thomas E. Lovejoy, et al. 2015. "Habitat Fragmentation and its lasting impact on Earth's ecosystems." *Science Advances*.
- Harris, Stephen E., Jason Munshi-South, Craig Obergfell, and Rachel O'Neill. 2013. "Signatures of Rapid Evolution in Urban and Rural Transcriptomes of White-Footed Mice (*Peromyscus leucopus*) in the New York Metropolitan Area." *PLoS ONE*.
- Harrison, Susan. 1991. "Local extinction in a metapopulation context: an empirical evaluation." *The Linnean Society of London* 72-88.
- Hilty, Jodi A., Annika T. H. Keeley, William Z. Lidicker Jr, and Adina M. Merenlender. 2019. *Corridor Ecology*. Second Edition. Washington: Island Press.
- Huisman, J., L.E.B. Kruuk, P.A. Ellis, T.H. Clutton-brock, and J.M. Pemberton. 2016. "Inbreeding depression across the lifespan in a wild mammal population." *PNAS* 3585-3590.
- Johnsson, Warren E., David P. Onorato, Melody E. Roelke, E. Darrell Land, Mark Cunningham, Robert C. Belden, Roy McBride, et al. 2010. "Genetic Restoration of the Florida Panther." *Science* 1641-1645.
- Keller, Stephen R., and Douglas R. Taylor. 2008. "History, chance and adaptation during biological invasion: separating stochastic phenotypic evolution from response to selection." *Ecology Letters* 852-866.
- Kinnison, Michael T., and Nelson G. Hairston Jr. 2007. "Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence." *Functional Ecology* 444-454.
- Kooij, Jeroen van der, Georg H. Engelhard, and David A. Righton. 2016. "Climate change and squid range expansion in the North Sea." *Journal of Biogeography* 2285-2298.
- LaRue, Elizabeth A., Sally M. Chambers, and Nancy C. Emery. 2017. "Eco-evolutionary dynamics in restored communities and ecosystems." *Restoration Ecology* 19-26.
- Levins, R. A. 1969. "Some demographic and genetic consequences of environmental heterogeneity for biological control." *Bulletin of the Entomological Society of America* 237-240.
- Lindenmayer, David B., Jeff Wood, Lachlan McBurney, David Blair, and Sam C. Banks. 2014. "Single large versus several small: The SLOSS debate in the context of bird responses to a variable retention logging experiment." *Forest Ecology and Management* 1-10.
- Lino, Ana, Carlos Fonseca, Danny Rojas, Erich Fischer, and Maria João Ramos Pereira. 2018. "A meta-analysis of the effects of habitat loss and fragmentation on genetic diversity in mammals." *Mammalian Biology* 69-76.
- Lopez, Sébastien, François Rousset, Frank H. Shaw, Ruth G. Shaw, and Ophélie Ronce. 2009. "Joint Effects of Inbreeding and Local Adaptation on the Evolution of Genetic Load after Fragmentation." *Conservation Biology* 1618-1627.
- Love Stowell, Sierra M., Cheryl A. Pinzone, and Andrew P. Martin. 2017. "Overcoming barriers to active interventions for genetic diversity." *Biodiversity Conservation* 1753-1765.

- Luigi D'Andrea, Olivier Broennimann, Gregor Kozłowski, Antoine Guisan, Xavier Morin, Julia Keller-Senften, François Felber. 2009. "Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae)." *Journal of Biogeography* 1573-1587.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press.
- MacDonald, Zachary G., Iraleigh D. Anderson, John H. Acorn, and Scott E. Nielsen. 2018. "Decoupling habitat fragmentation from habitat loss: butterfly species mobility obscures fragmentation effects in a naturally fragmented landscape of lake islands." *Oecologia* 11-27.
- Margan, Sienna H., Roderick K. Nurthen, Margaret E. Montgomery, Lynn Woodworth, Edwin H. Lowe, David A. Briscoe, and Richard Frankham. 1998. "Single Large or Several Small? Population Fragmentation in the Captive Management of Endangered Species." *Zoo Biology* 467-480.
- Moya-Laraño, Jordi, José Román Bilbao-Castro, Gabriel Barrionuevo, Dolores Ruiz-Lupión, Leocadio G. Casado, Marta Montserrat, Carlons J. Melián, and Sara Magalhães. 2014. "Chapter Three- Eco-Evolutionary Spatial Dynamics: Rapid Evolution and Isolation Explain Food Web Persistence." In *Advances in Ecological Research*, by Jennifer Rowntree, Guy Woodward Jordi Moya-Laraño, 75-143. Academic Press.
- Neuwald, Jennifer L., and Alan R. Templeton. 2013. "Genetic restoration in the eastern collared lizard under prescribed woodland burning." *Molecular Ecology* 3666-3679.
- Nilsson, S. G. 1978. "Fragmented Habitats, Species Richness and Conservation Practice." *The Royal Swedish Academy of Sciences* 26-27.
- Olsen, Siri Lie, Marianne Evju, and Anders Endrestol. 2018. "Fragmentation in calcareous grasslands: species specialization matters." *Biodiversity Conservation* 2329-2361.
- Opdam, Paul, and Dirk Wascher. 2003. "Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation." *Biological Conservation* 285-297.
- Pelletier, F., D. Garant, and A. P. Hendry. 2009. "Eco-evolutionary dynamics." *Philosophical Transactions of the Royal Society B* 1483-1489.
- Ralls, Katherine, Jonathan D. Ballou, Michele R. Dudash, Mark D. B. Eldridge, Charles B. Fenster, Robert C. Lacy, Paul Sunnucks, and Richard Frankham. 2017. "Call for a Paradigm Shift in the Genetic Management of Fragmented Populations." *Conservation Letters* 1-6.
- Rolshausen, Gregor, Gemot Segelbacher, Keith A. Hobson, and Martin H. Schaefer. 2009. "Contemporary Evolution of Reproductive Isolation and Phenotypic Divergence in Sympatry along a Migratory Divide." *Current Biology* (2009) 2097-2101.
- Rudman, Seth M., Matthew A. Barbour, Katalin Csilléry, Phillip Gienapp, Frederic Guillaume, Nelson G. Hairston, Andrew P. Hendry, et al. 2018. "What genomic data can reveal about eco-evolutionary dynamics." *Nature Ecology & Evolution* 9-15.
- Ruell, E. W., S. P. D. Riley, M. R. Douglas, M. F. Antolin, J. R. Pollinger, J. A. Tracey, L M. Lyren, E. E. Boydston, R. N. Fisher, and K. R. Crooks. 2012. "Urban Habitat Fragmentation and Genetic Population Structure of Bobcats in Coastal Southern California." *The American Midland Naturalist* 265-280.
- Sanderson, James, Keith Alger, Gustavo A. B. da Fonseca, Carlos Galindo-Leal, Victor Hugo Inchausti, and Karl Morrison. 2003. *Biodiversity Conservation Corridors: Planning, Implementing, and Monitoring Sustainable Landscapes*. Washington: Conservation International.
- Shefferson, Richard P., and Roberto Salguero-Gómez. 2015. "Eco-evolutionary dynamics in plants: interactive processes at overlapping time-scales and their implications." *Journal of Ecology* 789-797.

- Simberloff, Daniel, and James Cox. 1987. "Consequences and Costs of Conservation Corridors." *Conservation Biology* 63-71.
- Simberloff, Daniel, and Lawrence G. Abele. 1984. "Conservation and Obfuscation: Subdivision of Reserves." *Oikos* 399-401.
- Stockwell, Craig A. , Andrew P. Hendry, and Michael T. Kinnison. 2003. "Contemporary evolution meets conservation biology." *Trends in Ecology and Evolution* 94-101.
- Swindell, W.R., and J.L. Bouzat. 2006. "Gene flow and adaptive potential in *Drosophila melanogaster*." *Conservation Genetics* 79-89.
- Todd Streelman, J., S. L. Gmyrek, M. R. Kidd, C. Kidd, R. L. Robinson, E. Hert, A. J. Ambali, and T. D. Kocher. 2004. "Hybridization and contemporary evolution in an introduced cichlid fish from Lake Malawi National Park." *Molecular Ecology* 2471-2479.
- Van Schalkwyk, J., J. S. Pryke, M. J. Samways, and R. Gaigher. 2020. "Corridor width determines strength of edge influence on arthropods in conservation corridors." *Landscape Ecology* 1175-1185.
- Wang, Jinliang, William G. Hill, Deborah Charlesworth, and Brian Charlesworth. 1999. "Dynamics of inbreeding depression due to deleterious mutations in small populations: mutation parameters and inbreeding rate." *Genetic Restoration Cambridge* 165-178.
- Wheatley, Rachel, Julio Diaz Caballero, Natalia Kapel, Fien H. R. de Winter, Pramod Jangir, Angus Quinn, Ester del Barrio-Tofino, et al. 2021. "Rapid evolution and host immunity drive the rise and fall of carbapenem resistance during an acute *Pseudomonas aeruginosa* infection." *Nature Communications*.
- Wilcox, Bruce A., and Dennis D. Murphy. 1985. "Conservation strategy: the effects of fragmentation on extinction." *American Naturalist* 879-887.
- Zhao, Yao, Klaas Vrieling, Hui Liao, Manqiu Xiao, Yongqing Zhu, Jun Rong, Wenju Zhang, et al. 2013. "Are habitat fragmentation, local adaptation and isolation-by-distance driving population divergence in wild rice *Oryza rufipogon*?" *Molecular Ecology* 5531-5547.