

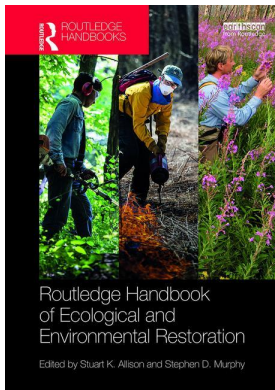
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### **The Principles of Restoration Ecology at Population Scales**

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# 3

## THE PRINCIPLES OF RESTORATION ECOLOGY AT POPULATION SCALES

*Stephen D. Murphy, Michael J. McTavish and Heather A. Cray*

### **Restoration at population scales cannot be done in isolation**

While restoration ecology is probably best considered as a cross-scalar effort, its origins and practice are often firmly in the camps of the more disciplinary levels of domains like population ecology. When we use the term ‘cross-scalar’, we refer to the notion that ecosystem functions (processes like nutrient and water cycling or interactions between organisms and their environment) and structures (the genetic and species diversity of organisms or the size and physiognomy of habitats) are not definable or restricted to molecular, population, community, landscape, or ecological regime domains. One recent paper that captures this nicely is Rose *et al.* (2015). They examined cross-scalar ecological restoration impacts on fish populations and communities in the context of ecological modelling (a topic of much discussion in this chapter). Their main message was that successful restoration ecology starts with an understanding and communication of the major steps involved at different scales – population, community, and landscape – and they fulfilled a much more ambitious objective of discussing all of these in terms of best practices for management within restoration ecology. We will restrict ourselves here to population scales, but that context by Rose *et al.* (*ibid.*) is what ultimately drives these discussions.

We can conceptualize that restoration ecology is really about the changes in evolutionary ecology – how drivers like natural selection, genetic drift, and phylogenetic constraints are changed by humans and how humans may then try and manipulate them further to repair ecosystem damage. However, the traditional oeuvre of restoration ecology is still entrenched in population scales – rescuing endangered species – because legal instruments tend to focus solely on this scale. There is focus at ecological community scales because the pioneers of restoration ecology were mainly from that school of thinkers – Aldo Leopold, John Curtis, Norman Fasset, and others were often focused even further on prairies and the community drivers like fire. This book as a whole will not restrict itself to population scales but it is important that a chapter be devoted to reviewing and discussing these given their prominence. Our cue is the classic paper by Montalvo *et al.* (1997) – the paper is nearing its twentieth anniversary but it is so well written that the ideas it reviews and the notions it inspired are relevant today; readers will see that this chapter builds on their excellent strategic paper.

## **The fundamentals of understanding population dynamics: Genetics and evolution**

We start with some reminders of basic terms because we have found that not all restorationists will have a strong background in ecology. The basis of ecology is evolution and its theories; we cannot do justice to the complexity of the contemporary theoretical framework.

Evolution is the change in the frequencies of heritable genes over time. This will be influenced by factors including: mutations incurred during mitosis, random gene assortments during meiosis (producing gametes) and recombination during fusion of gametes, the relative benefit or detriment created by genes interacting with and within the whole environment during each generation or cohort, the response of genes to drivers that favour some over others (selection – natural and human directed), the response of genes to random influences like some organisms dying because of an accident while some less robust ones happen to survive (genetic drift), the interactions of genes with each other and the varied influences on the expression of genes (many mechanisms like epistasis and pleiotropism) and the constraints on gene inheritance and structure imposed by the evolutionary history and developmental processes (roughly, evolutionary developmental biology – ‘evo-devo’).

We can speak of genes in terms of their encapsulation in genotypes (all the genes in an individual), their expression in individuals (phenotypes), and the entire genetic complement of a species (a genome). While there is tendency to limit evolution to the concept of the non-random factor of natural selection favouring well-adapted genes/genotypes/phenotypes, this is not correct because the preponderance of neutral mutations and the influences of genetic drift, interactions, and evo-devo are quite important. Despite breathless reporting to the contrary, most organisms’ genetic complement and their expression is not a history of optimization or excising useless or even detrimental genes or gene products. Organisms are filled with junk DNA that does no harm and thus is not selected out, genes that are co-opted but suboptimal for functionality, and functions and structures that are reflections of evo-devo (like the human eye – the octopus eye is much more efficient and reflects an evolutionary history less constrained than our own).

### **But what is a population – how do we define or delineate it?**

Traditionally, populations are considered to exist when there are a group of phenotypes that contain genotypes that are similar enough to allow for successful sexual reproduction and survivorship of offspring. As readers will discover, this is problematic for many organisms because they do not require sexual reproduction to survive. Further, populations are normally considered to be constrained and defined by some form of sympatry – they live near enough to one another to interact with some regularity and likelihood of breeding. This compounds the problem because this still relies on the notion of sexual reproduction and now it refers to some vague notion of being close enough to likely breed.

If we now think of populations as being genetically similar enough to breed, we probably assume they are from the same species – defined again in terms of being able to produce viable offspring. But species are not immutable (evolution eventually or even suddenly leads to new species arising from ancestral ones), there are some that are classified as different species yet produce viable cross-species hybrids, and some species are rarely – perhaps never – sexual. Species were often defined more by morphological characteristics that belie the complexity of breeding systems and the molecular basis of life.

Still, one can argue that many populations (and the species they are part of) are reasonably well-defined in the sense that many species do reproduce sexually – often or not, that relative

to the vast diversity of life on Earth, many species are well defined enough genetically and phenotypically that they do not mate or produce viable hybrids, and that populations often are definable by studying the gene identities and frequencies, and the barriers to interaction. Practically, restoration ecologists often do not consider the nuances of what a population actually represents and it may not matter to success in many cases; however, we would be remiss in not alerting readers – even beginners – to the issues that arise because nature is not as easily compartmentalized as humans would like it to be.

### **What is population ecology?**

Population ecology bleeds into other scales of restoration ecology because it is based on genetic assortment, differentiation and diversity; ultimately these are the bases for how we define species and hence how we track how species interact to form ecological communities. Because populations are affected by spatial factors as well as time, we can examine populations at landscape scales (meta-populations – populations that are separated spatially and their interactions are defined by their ability to overcome spatial constraints or take advantage of spatial facilitations like physical corridors connecting habitats). In restoration ecology, populations are not treated any differently than in general ecology. We can start with the basics of population dynamics – the main demographic variables of birth, death, migration rates.

### **How do we measure demographic variables when studying restoration of populations?**

While eponymous and therefore self-explanatory, the actual study of birth, death, migration rates in restoration ecology reveals some nuances. An important concept is that unlike humans, ‘birth’ in the many organisms that a restoration ecologist studies has multiple meanings. It can mean what humans expect – two individuals mate; their genes were randomly assorted during meiosis and recombination, providing increased genetic diversity as long as the two who mated are relatively unrelated. But many organisms have more complex mating behaviours. Some plants self-fertilize while others cannot. Many organisms reproduce asexually: fission, budding, fragmentation, sporogenesis, agamogenesis (no male gamete needed), and a large range of vegetative reproduction in plants.

The range of mating systems found in organisms can make birth rates hard to discern since some of these processes happen many times in a short period (short generation times) and others take much longer – it is not a case where one calendar year or even one generation truly form a unique cohort of individuals. Even death can be hard to measure; it can be difficult to detect when cryptic organisms die (it is not easy to measure bacterial death rates for example) and even with organisms like plants, algae, or fungi, do we measure death rates based on when the genetically unique individual (‘genet’) finally dies or when a given asexually reproduced ‘ramet’ dies? And can we easily tell the difference between death and dormancy – this is not easy with organisms that undergo sporogenesis or ones with some type of dormancy, especially if the dormant structure is hidden, like a seed or spore, or a tuber, corm, or rhizome that is underground. Migration can be fuzzy too – pollen and asexual forms can travel on wind, animals, or human conveyances long distances and it can be hard to track them at all, much less their success at fertilization (pollen) or survival.

For a restoration ecologist, the basic information needed to gauge the need for restoration and the success of restoration can be more elusive than the layperson realizes – it is challenging, though there are useful approaches and we can measure population dynamics. Restoration

ecologists can use standard tools like molecular markers to track the origins and dispersal of genes within genotypes of populations. Still, even with modern techniques for markers, it can still be very expensive and requires gaining an adequate sample of source and destination populations. Indeed, the basic goal that was perhaps implicit in the origins of restoration ecology is the same today, except more explicit – we want heterogeneity and variation at the genetic and phenotypic level of source and destination populations.

Falk *et al.* (2006) provided a detailed review of the measurements used by restoration ecologists studying population dynamics in order to meet the goal of genetic and phenotypic diversity.

Intriguingly, there is an operational caveat to a goal of population-level diversity – if a site is extremely degraded and therefore in dire need for ecological restoration, it may be useful to introduce populations that are less diverse and more amenable to being able to establish under extreme conditions. Populations of organisms that are able to sequester compounds like organo-metals, polyaromatic hydrocarbons, or concentrated acids often have low genetic diversity because only a few will survive under such extreme selection pressures. Such conditions tend to favour homozygosity for alleles on genes that confer an ability to sequester toxins. This creates an apparent ‘stress paradox’ because such homozygosity reduces potential adaptation response so stress-tolerant genotypes should go extinct quickly. Ironically, once stress-tolerant genotypes and phenotypes have reduced toxicity to levels other organisms can withstand they create a new successional pathway that actually dooms the stress-tolerant populations.

However, the low genetic and phenotypic diversity is not as low as some might assume. This is because during the time they are under stress from toxicity, they survive because mutation rates will increase under stress – some will be able to adapt to successively less toxic conditions, sexual recombination increases under stress – there will be new genetic combinations also able to adapt successively to less toxic conditions, and many have transposons that allow for rapid mobile response to new environmental conditions. Genetic linkage, epistasis, pleiotropism, and phenotypic plasticity can also allow for some increases in genetic or phenotypic diversity even while the overall genetic diversity is still low under stressful conditions. The paradox is that the same selection pressures can favour low genetic diversity because it augments survival during stress and yet favours increases in diversity – and that latter outcome then helps some part of each organism’s genotype remain in the population once conditions are less stressful.

The larger principle the stress paradox portends is the practical question of how one copes with inbreeding and outbreeding depression. Inbreeding depression occurs when organisms that have very similar genetic compositions – they are close relatives – mate and their offspring survive and mating between close relatives (and their genotypes) is rampant. While some plants are extreme inbreeders – self-compatible and mate with themselves – many organisms have biochemical and behavioural barriers that discourage or prevent inbreeding.

Bear in mind that the need for ecological restoration is often created because populations of a species have become very low – and inbreeding then is a means of last resort, even with attendant problems. The main problems arise because the genetic diversity of a population is so low that:

- It is vulnerable to extinction because if the environment changes, the entire population may be disfavoured by natural selection.
- Genetic drift can have disproportionate impacts in that some desirable genes may be lost because of random factors – this is a small risk if the genome has many genes and alleles but is a large risk if there are few to begin with.

- Deleterious mutations can accumulate quickly in low diversity populations. This creates a genetic bottleneck – the low genetic diversity hampers the survival of populations and perhaps the entire species if it is a widespread occurrence.

The response of restoration ecologists to this situation is usually to either translocate new genotypes from nearby populations or to begin a captive breeding or nursery programme using new genotypes from nearby populations. The latter is used if the situation is so dire that there is a need to ensure that successful mating of unrelated organisms occurs. However, if the numbers of organisms of a species is already so low that genetic diversity is practically nil, then the efforts will fail.

There is some promise that if DNA can be extracted from samples of preserved (dead) specimens from museum collections, then it can be reintegrated into a modern genome of species or at least populations. This is still in early stages but one can read about efforts to bring about ‘de-extinction’ of species such as the thylacine. For now, the best one can do if populations are too low worldwide is to promote hybridization between closely related species (not individuals) if their chromosomes will align properly during fertilization and produce viable offspring. Both methods can be controversial even under desperate circumstances and some argue that they are not ethical under any circumstances; it is not true restoration because the original species will still be extinct, it is not true restoration if the hybrids would not exist outside of a breeding programme (species are not sympatric), or it delays the inevitable extinction while risking source populations or introducing a new type of species to environments where it may disrupt existing community-level interactions. And this assumes hybrids are viable. In cases like *Panthera*, most male hybrids are sterile but a few are fertile – like the males produced from female lions and male leopards.

The hybrid question underscores a problem often neglected by restoration ecologists – outbreeding depression; this occurs when two organisms are from populations that should or could be able to produce offspring, but (a) they cannot do so at all because their chromosomes are not able to align during fertilization, (b) they produce sterile offspring for similar reasons, (c) they produce weak offspring because the chromosomes align poorly, causing genetic damage, or (d) they produce offspring poorly suited to local conditions.

This is why restoration ecologists must focus on source populations – and here the question of the provenance, manipulating source populations, and the genetic differentiation of those populations is of great concern for any organism – plant, animal, fungi, or otherwise (Hufford and Mazer 2003; Rice and Emery 2003; McKay *et al.* 2005; Armstrong and Seddon 2007; Weeks *et al.* 2011). They often should be geographically close on the assumption that most dispersal is relatively slow and local so that even if several hundred years have passed since populations migrated, there has still been some gene flow between them and they are not so isolated as to be nearing the point where their local genomes are too divergent or even nearing speciation thresholds. This may not apply to long distance migrants and even apparently sedentary organisms like plants can have some long distance dispersal via pollen, seeds, or vegetative structures like pieces of rhizomes being transported by wind, water, animals or human conveyances.

Restoration ecologists also have to take care in how they measure the state and function of populations. If one uses proper sampling techniques – and what is proper depends on the context of the research or desired outcome of restoration – it is feasible to census most populations. For herbs and forbs, we probably will use a stratified random sample using transects and quadrats and strive to minimize sampling bias, including autocorrelation. For many animals, we will do some form of mark and recapture or mark and monitoring via radio-collars, barcodes, drones, airplanes, or satellites; again, we will strive to minimize bias but must be aware that our

initial capture can make an animal trap shy or trap happy should we want to repeat their capture for measurements. If we're doing monitoring from aircraft, we will have to be careful – and be able – to determine which animals we've already counted in a given period of time so we do not repeat counts and over-estimate population sizes.

But a census only tells us how many. It does not tell us if the population is viable. For that, we need to determine the effective population size – how many are fertile now and currently able to breed successfully, how many actually do breed successfully, and how many future organisms should be able to breed successfully. Depending on breeding system, we may need to know how many female or female-expressed organisms exist and then the same for males/male-expressed organisms. It may appear odd to see the word 'expressed' but we remind readers that many organisms are not dioecious – they have mixed expressions of what humans would call genders and even humans and other dioecious species have some range of expression of sexual organs (and behaviour in animals).

Thus, we can census (determine  $n_{\text{sampled}}$  and  $N_{\text{estimated}}$  – the sampled and estimated total population!). We can sample more thoroughly and determine  $N_e$  – the effective population size that, usually, represents the number of organisms that do mate and produce viable and fertile offspring – though it can represent potential numbers that are known to be able to mate. This would be further enhanced in populations more reliant on sexual reproduction if we also knew the numbers of female and male individuals or the relative expression of functional female and male reproductive capacity – an extended  $N_e$ .

### **Population models in restoration ecology**

We want to use our samples of populations in restoration ecology – and conservation ecology, for that matter – to help us determine if our restoration efforts are likely to bear success, if they are bearing success, or if they did bear success. For that, we usually use several approaches but we often will model our populations – we create population models that either represent what has happened to population dynamics already or we predict what might happen to population dynamics in the future. This could mean that we represent populations mathematically and stop there. It could mean that we use that mathematical expression further – we try to create scenarios or perhaps even more concrete predictions about the likely future of the size or composition of populations. These still will be tied to the mathematical functions but they will normally become more complex mathematically and more realistic ecologically.

These population models can be expressed in different ways. One approach with a long history is to use matrix algebra – a means of expressing and calculating repeated algorithms. This was quite useful in the eras before personal computers were economical, powerful, and ubiquitous and even after that, the structure of matrices is very similar to how even modern analysis programs input data. At the risk of your editors seeming even older than we are, the prehistoric era before the advent of small, powerful, personal computers lasted until the mid-1990s in many places – and still exists in some regions today. This is another reason the matrix algebra approach is still used today – it allows for consistency in data expression and analysis across the decades of data collection and recording where matrices were used for most of that time period. The ability to use the same basic approach is important for reasons clear to anyone who experiences the frustration of new devices that are not backwards-compatible. This is why the literature is replete with references to population models that are based on such arcane terms as 'the Leslie matrix' or 'the Leftkovich matrix'.

The core of population models is not so much their mathematical expression as their assumptions. 'The Leslie matrix' and 'the Leftkovich matrix' differ on that basis. We usually

start with the simplest population model – a linear relationship that adds organisms born or immigrating and subtracts organisms dying or emigrating during a time interval expressed as  $(t, t + 1)$

$$N_{t+1} = N_t + B_{(t,t+1)} - D_{(t,t+1)} + I_{(t,t+1)} - E_{(t,t+1)}$$

Again, it is very difficult to sample even these variables accurately. We might try to write a model that focuses on the main outcomes of population dynamics of one gender – as if all species were dioecious; this often is focused on females because there usually are fewer female gametes in populations as they are more expensive, energetically, to produce:

$$N_{t+1} = N_{t(\text{reproductive females})} \times S_{t,t+1(\text{reproductive females})} + N_{t(\text{pre-reproductive females})} \times S_{t,t+1(\text{pre-reproductive females})} \\ \times [S_{t,t+1(\text{pre-reproductive females})} / S_{t,t+1(\text{reproductive females})}]$$

In this model,  $N$  is the number of females and  $S$  is the survival rate of females. The measurements are based on current measurements (now =  $t + 1$ ) and prior measurements, generally expressed as an interval between now ( $t + 1$ ) and the earlier time ( $t$ ) (that interval is often assumed to be annual – one year – or one reproductive/breeding cycle).

This can be simplified further if the measurements exclude any possible immigrants or emigrants and also assume that resources are not limited. In fact, those assumptions – combined with the exclusive focus on one gender expression (female) – are the basis for the often cited Leslie population model (also called the Leslie matrix model if matrix algebra is used). This is what leads to an exponential population growth model – which is not realistic but just like learning to count, this is what allowed population ecologists to build more sophisticated and realistic population models.

The first step in that history was to focus more on the stages rather than ages. Instead of assuming that all organisms' life history was tethered to human calendars or even a seasonal cycle, the Leslie model was modified to account for the basic difficulty in properly calculating the age of many organisms, the fact that many organisms reach reproductive maturity based on their size-stage (usually this occurs once they have enough resources to reach a certain size) rather than age, the ability of many organisms to effectively 'age backwards' in the sense that they might reproduce vegetatively and the daughter organisms are clones but smaller than the parent or they could become dormant. This more advanced approach is called the Leftkovich model of population dynamics.

While both of the above models were – and still are – popular because of their simplicity, that is their very drawback. Again, they usually focus on one expressed gender, do not consider any resource limitation, and do not consider the existence of immigration or emigration. Both therefore assume that any age or stage are subject to the same fecundity, mortality, and growth rates – all of those are also not true in most cases.

More traditionally, we express population changes in mathematical notation that focuses on the key variables of  $N$  (symbolizing actual population size in this case), the constant, intrinsic growth rate ( $r$ ) of a population, and the carrying capacity,  $K$ . While this still simplifies the ecological world by assuming that  $r$  and  $K$  are constants – they never change regardless of genetics or environment – this leads to useful approaches in population modelling. While  $r$  is not really a constant, we can conceptualize  $r$  as representing the maximum growth rate of a population – which can happen in the real ecological world, if only for a short time; it can be expressed as the exponential growth rate:



$$N_{t+1} = N_t + rN_t$$

Any population growing near the maximum value of  $r$  is likely to be one that is, not surprisingly, termed ‘ $r$ -selected’. This means that there are periods of time when it is evolutionary advantageous to produce massive numbers of offspring quickly – short generation times exist. Bacteria are an obvious example; so too are fungi. Plants that have annual lifecycles are slower but consistent with this model. In no case is the growth rate maintained at maximum  $r$  – competition within or between species for resources, diseases, predation, herbivory will all contribute to a slowing of the population growth.

Some of these causes may be a function of density – how many organisms exist in a given space; if so, they are density-dependent variables and this means the probability of the variable affecting population dynamics increases with density. Diseases would be one example. Of course a variable may be density-independent and there will be more variation in the probability it will affect a population. This is often the case with abiotic limits to population growth – a drought’s impact is not dependent on the population density if the drought is wide-spread and the occurrence of a drought is not completely deterministic and is therefore not predictable either. This latter notion alludes to yet another broader issue – whether populations are more affected by deterministic (non-random or at least constrained) variables or stochastic (‘random’) variables.

A restoration ecologist can exploit this knowledge. If the organisms are beneficial, then it may be inexpensive and fast to establish key components of ecosystems in restoration ecology. And this is usually true. A useful strategy in restoration ecology is to introduce beneficial bacteria, fungi, and annual plants – among other  $r$ -selected organisms – to a degraded start to speed the whole process. We still need to be careful about source material and maximize genetic diversity within species’ populations and we’d need to spread the material around but this is a major first step in ecosystem restoration. We need to quickly increase populations of desirable organisms and ones – like bacteria and fungi – that will be needed to re-initiate and maintain processes like nutrient cycling. This is what our research group does – if we compare success of restoration at sites where we ‘inoculate’ soil with beneficial bacteria and fungi versus sites where we do not and simply hope these re-colonize from nearby source populations, the inoculated sites are restored much quicker. Here we measure the pace of ecological restoration as a functional response of  $\text{NO}_3$  concentrations in what was a situation where it was an eroded, depleted soil; we planted 12 herbaceous and forb species at a site where 6 replicates were inoculated and 6 were left un-inoculated as a control. [Figure 3.1](#) has been simplified (no error bars) for presentation as an example but the variation was such that by the time 2012 arrived, the inoculated sites had significantly higher concentrations of the limiting resource of  $\text{NO}_3$ .

To be more realistic, we should acknowledge that populations will in fact be limited by some factors – resources, diseases, random events. Considering this, there is a fundamental equation – the Verhulst equation – that expresses population dynamics as the population change based upon the interaction of the maximum population growth rate and resource limitation, as represented by the carrying capacity. One version of the equation can be symbolized as follows:

$$N_{t+1} = rN_t(1 - N_t/K)$$

This creates a curve that is also known as the logistic equation – it is a sigmoidal shape that shows a rapid growth phase that is truncated at an asymptote. The example shown in [Figure 3.2](#) is a more realistic one than is often shown in textbooks where there is a perfect logistic curve – that really never happens with real data. The example is still a simple one where fungal

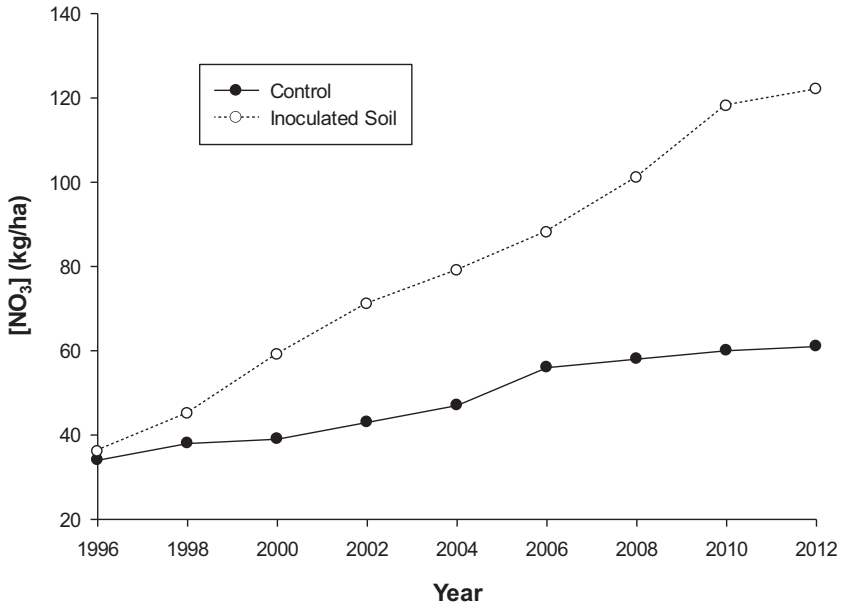


Figure 3.1 The contrast between the amount of  $\text{NO}_3$  accumulated in soil that was/was not inoculated with symbiotic and transformational bacteria and fungi

Source: Murphy (unpublished data)

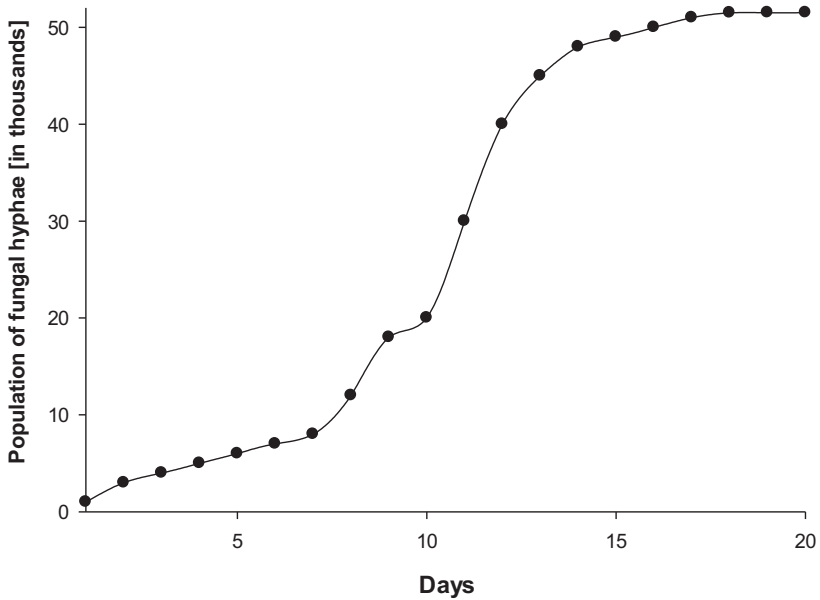


Figure 3.2 Logistical growth in a population of fungal hyphae grown in petri dishes

hyphae were grown in petri dishes from an initial population of 1 hypha (and spores that will produce hyphae since they are given nutrients in the petri dishes); not all species of fungi will show logistical growth in their hyphae but this species – *Ischoderma resinosum* – does (under laboratory conditions, at least).

The asymptote (here at about 51,000 hyphae between 15–20 days) occurs when the carrying capacity is reached; again, reaching carrying capacity is caused by the real-world limitations like resource scarcity or disease – in this example, it was because the nutrients provided were nearly used up and so was the space available.

The theoretical distribution does not allow the population to exceed the asymptote at  $K$ ; in reality, populations can overshoot this theoretical cap and they may even ‘crash’ to a much lower population if they die en masse in a short period of time.

For a restoration ecologist, this means we need to consider how many restored populations – and their size – an ecosystem can support. If we have too much of a good thing – introduce too many organisms – we might exceed  $K$  and create a serious problem if the population crashes because the excess over-consumed resources at a level that precludes recovery of the population and/or affects populations of other species. It also means that some of the populations we restore will be ones that will need to be able to compete with the faster growing  $r$ -selected populations; often, we wait until the  $r$ -selected populations have re-established ecosystem conditions that support the  $K$ -selected populations to avoid that competition and possible thwarting of restoration in the typical ecosystem where there are more  $K$ -selected populations as an ecosystem matures through time.

Even in harsh conditions where one might expect there to be selection pressures for  $r$ -selected species, the strategy of restoring with  $r$ -selected populations first and waiting several years to restore the  $K$ -selected species works. Our research group has done this in recently abandoned farmlands on sandy soil where water and nutrients quickly are lost once farming stops (Murphy *et al.*, unpublished data). The best approach is to inoculate with fast growing populations of micro-invertebrates, bacteria, fungi, and other protists to re-establish the nutrient and water cycles before the sandy soil erodes or crusts. Once accomplished,  $r$ -selected grasses and herbs are seeded and transplanted to provide a fast-growing population of plants to anchor the soil, and begin returning carbohydrates to the protists and micro-invertebrates via symbiosis or decomposition. The plants feed the soil organisms and then the soil organisms recycle the nutrients so new populations can grow.

Some minor paedogenesis may occur but the basic outcome is that nutrient and water cycles are restored and the soil becomes near capacity for resources. This will allow more  $K$ -selected plant species to colonize if they are near enough or to be seeded or translocated. During this time, macroinvertebrates and perhaps vertebrates will begin to colonize or be able to be restored by human intervention. This will normally be an accelerated process assuming ecological restoration is implemented – rather than just waiting for recolonization from nearby source populations.

If we had simply restored all types of populations at once, failure would likely have been the outcome because the  $K$ -selected species would not have sufficient resources to survive long-term but probably would survive long enough to reduce the ability of  $r$ -selected species to acquire sufficient resources to survive long-term. Another possibility is that simultaneously saturating a site like this with  $r$ - and  $K$ -selected populations will result in some surviving  $r$ -selected populations but these could be undesirable exotic species able to withstand harsher conditions of resource limitation and initial competition with  $K$ -selected species. We have not experienced this type of failure ourselves but have monitored sites where this has happened – in contrast to successful ecological restoration (Figure 3.3).

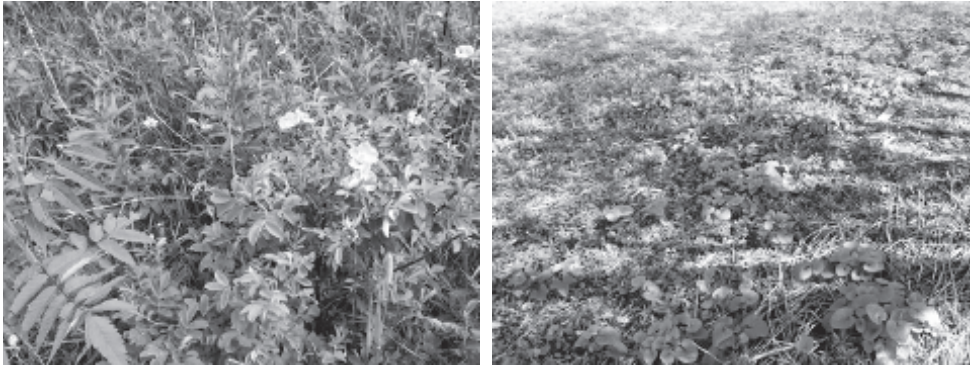


Figure 3.3 On the left is a successful restoration after 10 years of staggered introduction of *r*- and *K*-species' populations. On the right is a failed restoration ecology design that tried to introduce all species simultaneously – the result was dominance by exotic species like *Alliaria petiolata* after 10 years

Aside from the fact that both models maintain all variables as constants and don't yet account for the complexity of birth, death, immigration rates, and emigration rates (temporal variation), they are also oversimplified because they don't account for spatial variation. Population dynamics are influenced by the size of their habitat and the connectivity between habitats, where generally larger and better connected habitats will increase the potential population size. This is why restoration ecologists usually focus on what are called 'spatially explicit population models'. These can be quite simple in that they can represent a geographical area as a simply polygon like a rectangle that is composed of smaller rectangles ('cells') as shown in Figure 3.4.

The one shaded area represents either an individual organism or it could represent a whole population. Modelling population dynamics then depends on the factors already discussed now that spatial dispersion is added into the model. This could be still quite simple – any individual or population can move anywhere in two-dimensional space. It could be a bit more complex and realistic – any individual or population can only move certain distances, certain distances within a certain time, certain directions, or under certain conditions (like it can only move to unoccupied cells). We can then add more conditions – movement is only allowed to

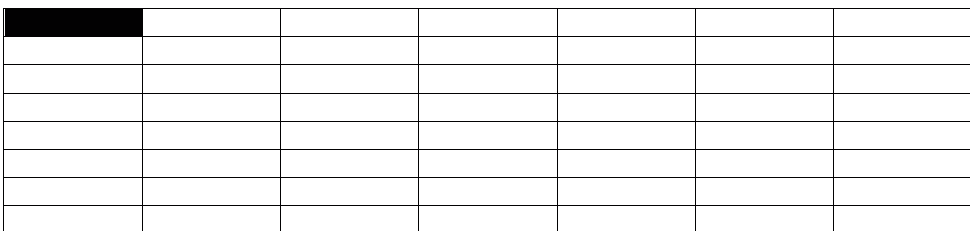


Figure 3.4 A simple 'cellular automata' population surface – two dimensional, simple polygons, and the 'automata' term means that we could program the computer to allow the shaded area to move next to any of the unoccupied cells at any time

cells where the habitat is suitable for survival of a given population or individual. And we can go further still – the space is a two-dimensional complex polygon or it is an actual map of a geographical space (usually mapped with GIS), or it is a three-dimensional map of actual geographical space because there will be abilities to move underground, up into trees, below the water and so on. Our population or individual moves through the world that is familiar and realistic, as in [Figure 3.5](#).

The individual-based models are best because each individual will encounter a range of selection pressures that will shape the population as a whole but even with modern technology of genetic markers, barcoding tags and drones, it can be difficult to do this if populations are large and dense and if their life cycles are complex (e.g. not  $r$ -selected or at least not annual, where all adults die after only one year at most).

We also have to account for the reality alluded to earlier in discussing the Leslie and Leftkovich models – that there will be differential birth, death, immigration, and emigration rates between each cohort of populations. Yes, there will be constraints on how much variation exists – because there is a fundamental value of  $r$  – but unless one is working in a



*Figure 3.5* An actual aerial photograph of a landscape matrix. The ‘cells’ are now a mix of regular and irregular polygons (the farms are more regular – the yards of the housing development are surprisingly irregular because these are estate-type developments), there are physical barriers like roads to movement of some organisms, and the ecological conditions of each part of the matrix will be variable between locales and across time. The ability to restore a population (or several populations) of a species if a farm should be abandoned and restoration desired will be challenged by the complexity of migrations or other interactions of movement of individuals between populations or habitats

laboratory under carefully controlled environmental conditions, each individual in each cohort (age- or stage-based generations within populations) will experience differential selection pressures, causing whole-cohort differences in population dynamics.

This is why population models normally use some form of sensitivity analysis. We test to determine which variables – like birth, death, immigration, or emigration rate – change our population models the most; we determine which variables the population model is most sensitive too. In simpler models, we simply can change these variables across a large range to test sensitivity. We usually constrain that range to ecologically realistic conditions (e.g. if we have never recorded greater than 20 per cent of the population dying in a given time period, that may be considered our worst-case scenario).

However, in restoration ecology, we are usually not dealing with historical or typical conditions existing at the time of restoration so we usually include the extreme values of population variables as best- and worst-case scenarios. Somewhere in between best and worst, we would like to determine the most probable set of circumstances under conditions of restoration versus no restoration. That can be difficult unless we have experience with a given type of ecological restoration already.

Still, a population model will allow us to understand how fast we might expect a restored population to grow, to set goals to maintain a certain size of population over time, and to act if we see populations getting too big or too small as we monitor an ongoing restoration project. The last one is challenging because how do we know when to intervene during restoration – populations might be able to rebound if there is a crash? Once again, our ability depends on experience and early experimentation; this is why we do smaller scale experiments to determine fundamentals of the population under restoration and non-restoration conditions if we have no experience or comparative, reliable, accessible, and appropriate case examples.

In using population models in restoration ecology, we also have to be cognizant of how the variables are constructed. By that, we mean what do the variables represent and what is their mathematical expression. If we are measuring survivorship and fecundity as indicators of success or failure in restoring populations, we have to be careful about including these blithely in a single population model. Survivorship ranges from 0.0 to 1.0 (0% to 100%). Fecundity – especially in *r*-selected populations – might be in the millions numerically. This will distort the relative importance of the two variables of fecundity and survivorship because their mathematical expressions are different – a percentage versus a raw number that grows exponentially. Survivorship is actually more important in the sense that it tells us the outcome of a cohort after restoration and indicates the potential intrinsic growth of a population in the next cohort – granted that emigration by natural means of dispersal or via more restoration intervention will affect the actual outcome. Thus, we test the reality of our population models by measuring elasticity – what is the proportional effect of a variable caused by its mathematical expression and what should be the proportionate effect based on demographic and perhaps ecological importance. Here too the problem of life cycles arises because elasticity will not be constant cohort to cohort.

The formulae for sensitivity and elasticity analysis often are expressed in the mathematical notation of matrix algebra, and can look quite intimidating or cryptic. Expressing these in a wordier but perhaps more tenable fashion, we can calculate sensitivity as:

- $s = d_{\text{population growth rate}} / d_{\text{(population variable)}}$

The ‘d’ symbolizes that this involves calculus – we calculate the partial derivative of a population’s growth rate as it changes with a given population variable. Examples:

- $d_{\text{population growth rate}} / d_{\text{birth rate}}$
- $d_{\text{population growth rate}} / d_{\text{survivorship}}$
- $d_{\text{population growth rate}} / d_{\text{emigration}}$

We can test how  $s$  (sensitivity) varies with each variable above.

We need to determine sensitivity because we then calculate elasticity with that value. The simplified formula for elasticity ( $e$ ) is:

- $e = s \times (\text{population variable measured} / \text{population growth rate})$

This means that elasticity measures the proportional sensitivity of a given population variable.

Remember that we would compare sensitivity and elasticity for all population variables that we measured to understand how the proportional importance/effect of each variable is exaggerated by our analysis, which ones are under-estimated, and which ones are basically accurate.

### Examples of population models used in attempts to restore populations

The population models can get more elaborate but they can become so complex as to be rendered intractable even with modern computing knowledge and technology. However, there are a series of useful elaborations of the basic population models, starting with the exponential and Verhulst logistical model.

One good example is from Cromsigt *et al.* (2001) wherein they compared the utility of several still reasonably simple population models in determining impacts of using source populations of black rhinos that were reasonably stable to restore populations in other areas. They compared how many black rhinos would be needed for success and what translocation of the various numbers of rhinos would do to the source population.

Specifically, it had been determined that in the mid-1990s, the total worldwide black rhino population was 2500 individuals. About 1050 of these were in South Africa where poaching was less common; the rest of Africa had scattered and smaller sub-populations. To restore and thus conserve the species by restoring other African sub-populations, translocating rhinos from South Africa was proposed but this would only work if the source population was really as large as 1050 individuals. There was concern that it may not have been accurate because of risks of double counting when aerial surveys are done and the very issue that there are low population numbers meant expenses in finding them, resulting in high yearly variance in estimates of  $N$  – much less anything like  $N_e$ .

This study used an approach that almost any reasonably educated student in restoration ecology could do by second or third year – they used Microsoft Excel to determine and minimize the errors between census data and their population model data – they basically minimized the sums of squares to generate best estimates of initial size  $N$  that will then be used to predict all  $N(t)$  values. This was to account – as best they could – for any census errors. They then compared several population models:

- exponential model:  $N_{t+1} = N_t + rN_t$
- Verhulst logistic model:  $N_{t+1} = rN_t(1 - N_t/K)$
- Fowler's model:  $N_{t+1} = rN_t(1 - [N_t/K]^a)$
- Verhulst logistic model with translocation of 'h' numbers of rhinos:  $N_{t+1} = rN_t(1 - N_t/K) - h$
- Fowler's model with translocation of 'h' numbers of rhinos:  $N_{t+1} = rN_t(1 - [N_t/K]^a) - h$

' $h$ ' represents the number of rhinos that would be translocated – it can vary from 0 to all of the rhinos available but the realistic numbers would be at least in the double digits so the new population would survive.

' $n$ ' is used to model the real-world situation where as a population of black rhinos gets closer to its carrying capacity,  $K$ , the population is increasingly affected by density of rhinos; it is a way to express that there is a density-dependence that alters population dynamics but that dependence is not usually constant (if it was, then  $n = 1$  and this reduces back to the simpler Verhulst logistic equation because  $x^i = x$ ).

What they found was that the basic Fowler model was the most applicable and accurate but that adding in the even more (potentially) accurate variable of number of translocated individuals only worked for one of the two game reserves they studied. What this told them was that when the translocation variable was not important, the population census was over-estimated because it should have made a difference and improved accuracy of the population model. They also found that the exponential model was almost as good as the Fowler model in the same game reserve where adding the translocation variable did not improve accuracy. This may mean that the population there is still growing as opposed to being near  $K$ .

Generally, they found that each model gave quite different values for the maximum population size – the logistical model indicated that up to 50 per cent of the rhinos could be removed (and translocated) whereas the Fowler model indicated that only 10–15 per cent of the rhinos could be removed (and translocated). Given that translocation can harm the source population if it is too large and insufficient translocation can result in failure in restoration for the target/sink population, this is a very important issue – make a mistake and both source and sink populations of rhinos might drop and you might just become the cure that was worse than the problem. Implicitly, Cromsigt *et al.* (2001) did consider the gender and age variables as well but the basic question of numbers to be translocated was the main issue.

The problem of sufficient translocation to a new target or sink population and the corollary of ensuring sufficient individuals remain in the source population relates to the problem of estimating the minimum viable population (MVP) size – how many organisms are needed to maintain a population that can successfully produce new generations of fertile offspring that continue to survive. Once again, this number should be tempered by our knowledge of the breeding system – if there is (as usual) a minimum and maximum age or stage threshold for reproduction and if sexual reproduction (aside from self-fertilization) is important, then once again we would want to know the extended  $N_e$ . For MVP calculations, one needs to know how much genetic variation exists, how much of this is expressed, whether the genetic and phenotypic expressions are relatively equally distributed and how this is influenced by natural selection, genetic drift, patch size and proximity effects and the probability of stochastic or deterministic factor.

Interestingly, we can provide a 'ballpark' estimate for entire groups of organisms, based on empirical work experience. For example, in using plants to help restore habitats, we tend to harvest and translocate 200+ seeds from a random sample of all dispersal agents (like seeds) except for vertebrate dispersal agents where translocation of 200–500 seeds is a typical range because animals tend to collect them from the same plant (Falk *et al.* 2006). This is not as theoretically sound as we would like and certainly caution is urged until replicate studies that formally study MVP are completed for a given species–environment combination because demographic and environmental variation will affect the number to be translocated.

Finally, we also would like to know whether a population is likely to go extinct sooner rather than later or what the long-term probability of extinction of a population or entire species might be. For this, we turn to population viability analysis (PVA). This relies upon most



of the variables and processes/analyses we already have discussed so an example should help illustrate how this works. Ferreras (2001) and Ferreras *et al.* (2001) studied the Iberian lynx. While we are simplifying the study here, he basically showed that lynx habitat was critically low and that the small  $N$  and  $N_c$  of isolated populations of lynx meant that translocation was needed. Lynx can be too sensitive to allow for successful human transport, hence translocation would be encouraged by some type of habitat restoration within the agricultural landscape and then reconnecting restored or existing habitats via corridors (this steers us into some landscape ecology elements but that is inevitable). However, this begged the question of whether some other management was needed (i.e. reduce mortality in lynx).

Ferreras *et al.* (2001) asked just that broader question – their question focused on whether the goal should be to restore lynx habitat or reduce lynx mortality. They used PVA to model the risk of extinction of this species and then to determine which management options – restoration of habitat, reduced poaching, reduced road kills – were most effective. The standard approach – reduce human-caused mortality – did not sufficiently reduce the risk of mortality of lynx, hence habitat restoration was likely needed. Their study showed the nuances of management needed. Using restoration ecology techniques to improve  $K$  in source populations was effective at reducing extinction risk to lynx. Oddly, these same techniques were not very effective at improving  $K$  and reducing extinction risk if applied to sink populations unless those populations also experienced the total removal of all human-caused mortality – and that is not likely. The most effective method was still to increase connectivity between isolated populations, hence in that sense the outcome of effectively ‘restoring’ habitat by increasing connections between smaller habitats works because it increases one, again effective, larger habitat.

### Summary

Overall, restoration ecologists have many tools at their disposal to examine the outcome and effectiveness of restoration as measured at population scales. There are challenges in terms of gathering sufficient and reliable samples and building population models that capture the range of variation in the expression and meaning of fundamental demographic variables of birth, death, immigration, and emigration. One must be careful in weighting variables (examine elasticity) and determining which ones are more important (examine sensitivity). As molecular scale tools improve, it may become easier to identify and classify the range of genetic and phenotypic variation within populations of different species and this can give restoration ecologists more confidence that their efforts at restoring populations will succeed in reconstituting the diversity needed to support a self-sustaining population that can cope with rapid or slow environmental changes.

### Note

- 1 Often just ‘ $n$ ’ and ‘ $N$ ’ are used, but we prefer terms to be explicit.

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