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An introduction to agro-ecology

Introduction

Agriculture, the cultivation of plants and domestication of animals by humans, is approximately 10 000 years old. In evolutionary terms this should be an insignificantly short period of time, but it has not been. Human agricultural activity has changed the world completely; the genotypes of domesticated species have often changed beyond recognition. The relative abundances of species on earth have been altered dramatically, so that previously uncommon weedy grasses (cereals) now dominate vast areas. Even the habitats occupied by wild species have frequently been modified so they now support entirely novel communities of plants and animals. Natural communities from late in succession have been replaced by communities with ecologies more typical of early succession. The move from hunter-gathering to farming has allowed the human population to rise to more than six billion and therefore everything that humans do, every impact that we make on the planet, can be considered as an indirect environmental impact of agriculture. However, the scope of this book is less ambitious as it covers the more immediate direct interactions between agriculture and the environment. The function of agriculture is to direct energy from the sun (including fossil sunlight) into the human food chain. Little of this energy that is utilised by humans is then available for the other inhabitants of our planet. This process involves a great deal of effort to convert natural habitats into agricultural ones and replace wild species with domesticated ones, while natural ecological processes are exerting pressure on the system in the opposite direction. This movement away from the natural situation constitutes one of the direct environmental impacts of agriculture.

This book explores the nature of these impacts, how they can be managed, and whether they can be balanced by farmers and policy makers with our need

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to produce food. To better understand the complexities of the environmental impacts of agriculture, this first chapter explores the origins and ecologies of species that inhabit farmed land. This understanding of the population ecology of single species is developed into looking at competitive interactions between species, which builds into community ecology theory. Finally an understanding of the management and exploitation of biodiversity within the agricultural context are introduced as key themes that are considered further throughout the rest of the book.

Species that inhabit farmed land

Farmed land has only existed for, at most, about 10 000 years, which is very little time for new species to have evolved which are adapted to this relatively new habitat. During this period, selection by humans has produced a range of domesticated crops and animals that are no longer able to survive without the assistance of humans outside the agro-ecosystem. They have been so genetically modified, by hybridisation and selection, that their origins were uncertain until the advent of modern molecular genetics (Hancock, 2005). Although less dramatic, the wild species that co-inhabit farmed land have also undergone sometimes substantial genetic changes. Many of the wild species of the arable agri-environment would have been rare or out of range before the advent of agricultural activity. These plants and animals had evolved in naturally disturbed habitats associated with early succession, such as sand-dunes, retreating glaciers or volcanic lava fields. Such species are known to ecologists as ruderals, they have life-histories characterised by short lifespans, the production of large numbers of small offspring, and they are highly mobile and invest few resources in defence mechanisms. These are the annual weeds of the plant world. Many agricultural invertebrate pests and diseases have similar life-history strategies. Alternatively these problem species can be seen as valuable biodiversity at the base of the food chain for the other larger more charismatic species of farmed land. Determining to what extent we tolerate these non-agricultural species diverting sunlight from the human food chain to the rest of nature is central to how we manage the agri-environment and this is a problem that we will return to again in Chapters 8 and 10 (Figure 1.1).

Until recently pastoral agriculture was based on the grazing of native or semi-natural grasslands or dwarf-shrub communities, but the twentieth century saw an increasing reliance on more productive, agriculturally improved forage systems. These new artificial grass-dominated communities are species-poor. The species they contain are now amongst the commonest on Earth, but their natural ecologies and genetics have been completely changed by agriculture

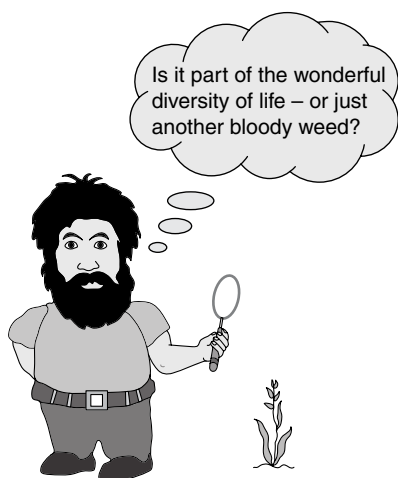


Figure 1.1 When should a species be considered an agricultural pest or be tolerated or even encouraged as valuable biodiversity? The answer to this question is central to how we think about and manage the agri-environment.

(Warren *et al.*, 1998). The plant species that form the basis of both improved and semi-natural pasture systems evolved in non-agricultural grasslands. In Western Europe most grasslands have previously been thought of as transitional vegetation communities, which form part of a succession that would naturally lead to climax woodland. Vegetation succession has been arrested at the grassland stage only because of agricultural grazing. This view has been challenged by Vera (2000) and many now think that the natural vegetation of Western Europe may have included much more grassland than was previously considered. This is significant because it might imply that agricultural habitats regarded as semi-natural may be more natural than previously thought and the species associated with them may have been coevolving for longer. Where the history of agricultural development is much shorter, such as North America and Australia, there is a better understanding of the make-up of the climax communities, whether forest or grassland. In fact remnant tracts of many natural vegetation communities, albeit very small in some cases, do still exist.

Population dynamics of single species

The science of ecology is about understanding why species live where they do and why sometimes they are abundant and sometimes rare. The practice of agriculture is about managing populations of species so that they can be exploited by humans. Therefore, by necessity agriculturalists need to know what species will live where and how well they will thrive. Agriculturalists

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need to understand ecology and need to know what regulates populations. Understanding what processes regulate population sizes underpins selecting stocking rates of livestock, sowing rates of crops, what species can be successfully grown or kept together, plus the biological or chemical control of pests and diseases.

With a single species, in the simplest of all worlds, that is with no overlap of generations, no immigration or emigration from the population and all individuals being hermaphrodite, all of whom successfully reproduce, because resources (food, water, space, sex, etc.) are in excess and disease, predators and competitors are all absent, then:

$$N_{t+1} = N_t R.$$

The population in the next time period (N_{t+1}) = the population now (N_t) multiplied by the maximum number of offspring an individual can produce, R .

These restrictions might seem unrealistically crude; however, the population dynamics of many species of weed and pest of agriculture can at least spasmodically be regulated and mathematically predicted by such exponential explosions in numbers when they exploit a new resource, for example a newly ploughed field. These ruderal species tend to have populations that rapidly increase in numbers and then crash, with the episodic declines usually resulting from agricultural activity, such as ploughing or the application of chemical control.

In most species, the size of the population is regulated by density-dependent processes. That is, as the population size increases competition between individuals of the same species tends to reduce the growth rate of individuals, which affect the age or size at which individuals reproduce, decrease the birth-rate or increase the death-rate. Exactly what combination of these possible effects occurs differs between species, but the outcome of limiting population size always arises. This within species competition for resources, which reduces the size of individuals and over time increases the death-rate of smaller (less competitive) individuals, is responsible for a relationship known as self-thinning in plants (see Figure 1.2) and this effect is behind what determines optimal sowing rates for crops and planting densities for tree crops.

Even if agriculturalists are not consciously aware of the self-thinning rule, they select sowing rates for crops so that the plants are able to grow to a desirable size by keeping levels of intraspecific competition low enough to avoid crop plant mortality. This must be balanced by sowing enough of the crop to obtain an acceptable yield and for interspecific competition to be intense enough to help in suppressing the growth of non-crop plants.

In managed agricultural populations extra resources are used to counter the effects of density dependence to artificially increase birth-rates. Death in

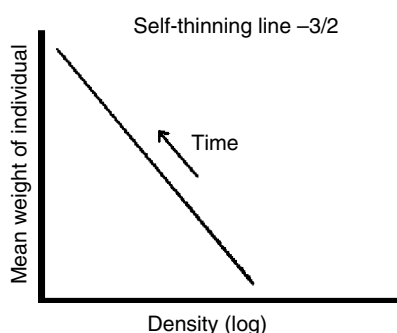


Figure 1.2 As individuals grow over time competition becomes more intense. This results in the death of the weaker/smaller individuals, which reduces the density of the surviving population, which eases competition and allows the surviving individuals to grow larger. Thus both size and population density are interrelated and change over time in accordance with the self-thinning rule. The gradient of the self-thinning relationship $-3/2$ arises from the fact that density (log) is area based and changes as a square whereas weight/volume changes as a cube.

domesticated species tends to escape density dependence by being regulated by harvesting/slaughtering rather than competition. However, the natural processes illustrated in Figure 1.3 do regulate the populations of the wild species that inhabit the agri-environment.

Mathematically, density dependence can be incorporated in population equations, with similar assumptions as before, those of: no overlap of generations, no immigration or emigration from the population and all individuals being hermaphrodite; although competition within a species is represented, the effects of disease, predators and other competitors are again all absent. Under these conditions:

$$N_{t+1} = \frac{N_t R}{(1 + aN_t)^b}$$

As before N_{t+1} represents the population size in the next time period, N_t is the population now and R is the maximum number of offspring an individual can produce. The only new parameters in the density dependence equation are a , which is described by some plant ecologists as ‘the area of isolation’ (that is the area which a plant needs to be able to produce R seeds and beyond which no extra seeds are produced) and b , ‘the coefficient of resources use efficiency’. However, both these values are probably best thought of as simply constants, which just happen to be useful in predicting the size of the population next year. The effect of variation in the value of parameter b on the population size in the following time period can be seen in Figure 1.4. Species with low b and R values and hence relatively stable populations are associated with late succession, such

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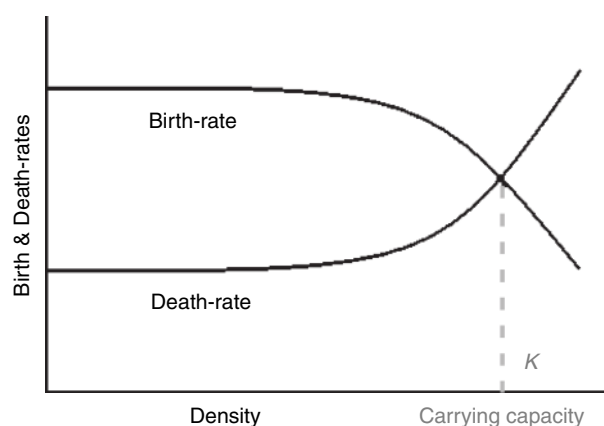


Figure 1.3 In the wild as population density increases, birth-rate decreases and death-rate increases. At the point at which the birth-rate and death-rates are equal, recruitment and death are equal and the population size may reach a stable equilibrium size. This is known as K , the carrying capacity.

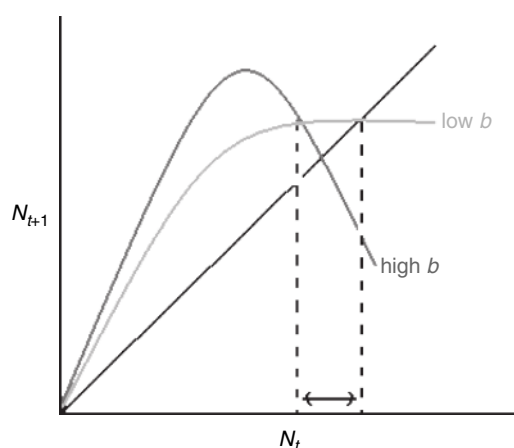


Figure 1.4 Variation in the value of parameter b affects the robustness of the predicted population size in the next time period (N_{t+1}). When b is low the predicted population curve cuts the 45° line close to the horizontal, so that a small amount of variation in the current population (N_t) has very little effect on the prediction of the subsequent population. However, when the value of b is large the predicted population curve cuts the 45° line in such a way that a small level of variation in the estimated population now makes a great difference to the predicted size of the next (future?) generation.

as oak trees or large mammals; those with high values of b and R , which are prone to dramatic changes in population size, are more likely to be associated with agriculture, such as locusts.

Species that are pests of agricultural systems tend to have the capacity to produce large numbers of offspring (they have large values of R) and therefore

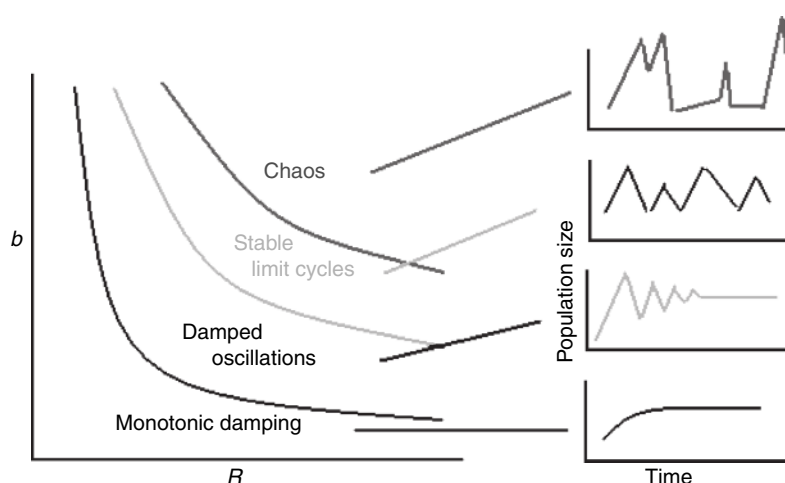


Figure 1.5 Knowing the parameters R and b allows long-term predictions to be made about the stability of population size. Species that are pests of agricultural systems tend to have populations that have chaotic dynamics and are prone to rapid increases and decreases that are difficult to predict.

their populations have the ability to increase very rapidly. When this is combined with high values of b , which make it difficult to make reliable predictions of the population from generation to generation, then the long-term population dynamics of agricultural pest species can be difficult to predict (see Figure 1.5). However, the chaotic population dynamics of many agricultural pests does not mean that their populations cannot be predicted, just that increasing amounts of data are required to successfully predict over reduced periods of time. Plus, given that many of the apparently random population crashes result from agricultural control measures, it is not true to say they are genuinely chaotic.

Two species interactions in agriculture

Much of the above discussion of the population dynamics of single species considered pest species, but of course these do not live as single species, and although intensive agriculture is often regarded as the management of monocultures, the reality is rarely so simple. In many farming systems managing different species together in the same space at the same time is the norm; therefore, if we are to successfully control pests or optimise yields over several species, we need to develop our understanding of the population ecology to more complex systems.

Two different experimental approaches have been developed by crop-ecologists to investigate the competitive interactions between two species. The two methods

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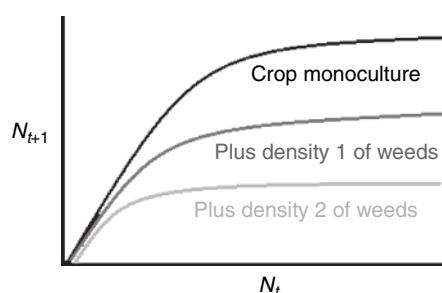


Figure 1.6 Additive experimental designs are useful for investigating the impact of the addition of different infestation rates of weeds on the yield of crops sown at a fixed density. Alternatively the experiment can be reversed and used to quantify the potential of the crop to reduce known weed populations. A similar experimental approach can be used to look at the suppression of weeds resulting from chemical control measures.

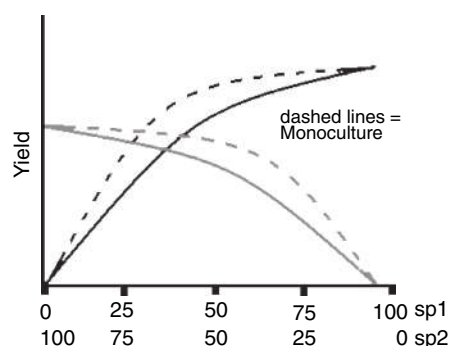


Figure 1.7 Replacement experimental designs have a fixed sowing density, but within a plot the ratio of two species varies from monoculture of one species through to the monoculture of the second.

relate to different applications. Firstly, additive experiments (see Figure 1.6) involve the addition of different levels of a second species to a fixed population of the first species. This can be used to represent the occurrence of a population of weeds or a second crop species in a fixed sown population of a crop. Secondly, there are replacement series experiments (sometimes called De Wit replacement experiments in honour of the Dutch ecologist who developed the approach), in which individuals of one species are replaced by individuals of a second, but with the overall population being kept constant (see Figure 1.7). This second approach is useful when trying to establish the optimal ratio of two species to use when bi-cropping.

Replacement experiments typically demonstrate a phenomenon of fundamental significance to agro-ecology. Competition between species is usually less intense than is competition within a species. This is because individuals of the

same species have the same environmental requirements, they compete for exactly the same resources. In contrast, different species will have different resource requirements, they will need different nutrients, or may root at different depths or grow at different times of the year, etc. Two very important facts result from this:

1. Overall yields (in terms of biomass production) tend to be higher with two species than in monoculture.
2. Such species have the ability to coexist by competing for different resources and so diversity is assembled.

Of course reality is more complex than this simple assertion, but it is an important factor that operates behind many agricultural processes. The first complication arises from the experiment's simple assumption of a fixed ratio of species. Just because two species are sown at a fixed ratio does not mean that they remain at that ratio; this is particularly true where there is differential growth or spread, such as with vegetative species. Secondly, in the artificial situation of a replacement experiment both species are usually established at exactly the same time. In the field, however, species may establish at different times or over a period of time. This can be important in further promoting diversity, because species that are competitively inferior (and over time would be lost due to competition) may not be excluded by competition if they have the opportunity to establish before the normally competitively dominant species. In addition, from an agricultural point of view the simple statement that overall yields are higher with two species than one may have little value, because the yield of total biomass may be less useable and there can be many practical problems in the management and harvesting of more than one species. Certain varieties of cereals and legumes can successfully be combined together and their grains separated mechanically, but other combinations with different maturation times can be more difficult to process.

An additional complication in the agricultural application of replacement experiments is that the outcome is often density dependent and such experiments are typically carried out at a single fixed sowing density. When a replacement experiment is performed at low density there is plenty of opportunity for the two species to exploit different resources (and therefore have higher yield in comparison to monoculture). However, when the same experiment is repeated at a higher overall sowing rate, the level of competition between individuals is more intense and the subtleties of between species differences are reduced as individuals struggle to survive, so that the increased yield potential of bi-cropping is reduced. Therefore, if replacement experiments are to be used to

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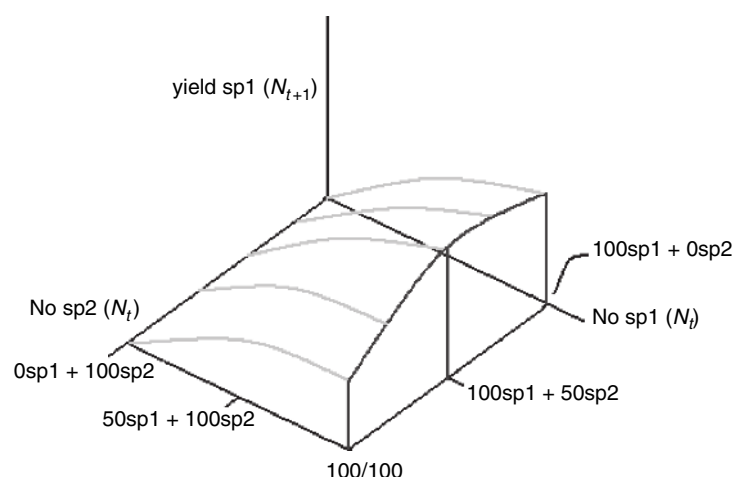


Figure 1.8 Response surface analysis of competition between two species over a range of ratios and overall sowing densities can be used to optimise bi-cropping systems or to identify optimal stocking rates and ratios of different livestock species such as cattle and sheep. In this figure the x and y axes are N_t and N_{t+1} as in Figure 1.4 while the z axis (N_{t2}) represents the size of the sown population of the second species at the time 0.

optimise ratios and sowing densities in bi-cropping systems, a series of experiments is needed, over a range of sowing densities (see Figure 1.8).

Parasites, pests and diseases

So far we have been considering the population dynamics of two competing species within agricultural systems such as weeds and crops, two species of grazing animals or combining two crops. This situation is different when one of the species is a domesticated species and the second is a direct predator, parasite or disease. Above we saw that many pests and diseases have the ability to rapidly increase in numbers to exploit available agricultural resources; their large reproductive potential allows them to generate lots of viable offspring, which are the raw material upon which natural selection acts in adaptive evolution. The rate of evolution of agricultural pests can be rapid for two reasons: firstly the large numbers of individuals involved, this does not just reflect the large numbers of progeny produced but also the vast areas of agricultural production over which they are produced; secondly the intensity of the selection applied by chemical, biological, genetic or physical means can be intense. It is no surprise, therefore, that when agriculturalists try to produce enough food to feed a global human population of six billion plus, other species adapt to exploit this vast potential food resource. Whatever control measures are applied, pests seem to