MODELS OF DISPERSAL AND DIVERSIFICATION

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There remain therefore algebra and arithmetic as the only sciences in which we can carry on a chain of reasoning to any degree of intricacy, and yet preserve exactness and certainty.

David Hume, *Treatise on human nature*

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I. Starrfelt, J. and Kokko, H. 2008. *Are the speeds of species invasions regulated? The importance of null models.* **Oikos** 117: 370-375

II. Starrfelt, J. and Kokko, H. 2010. *Parent-Offspring Conflict and the Evolution of Dispersal Distance.* **American Naturalist** 175: 38-49

III. Starrfelt, J. and Kokko, H. *The Multicausal Nature of Dispersal*. Manuscript invited to appear in *Dispersal and Spatial Evolutionary Ecology*, eds. Jean Clobert, Michel Baguette, Tim Benton and James Bullock. Oxford University Press.

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Contributions

	I	II	III	IV
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ABSTRACT

Ecology and evolutionary biology is the study of life on this planet. One of the many methods applied to answering the great diversity of questions regarding the lives and characteristics of individual organisms, is the utilization of mathematical models. Such models are used in a wide variety of ways. Some help us to reason, functioning as aids to, or substitutes for, our own fallible logic, thus making argumentation and thinking clearer. Models which help our reasoning can lead to conceptual clarification; by expressing ideas in algebraic terms, the relationship between different concepts become clearer. Other mathematical models are used to better understand yet more complicated models, or to develop mathematical tools for their analysis. Though helping us to reason and being used as tools in the craftmanship of science, many models do not tell us much about the real biological phenomena we are, at least initially, interested in. The main reason for this is that any mathematical model is a simplification of the real world, reducing the complexity and variety of interactions and idiosynchracies of individual organisms. What such models can tell us, however, both is and has been very valuable throughout the history of ecology and evolution. Minimally, a model simplifying the complex world can tell us that *in principle*, the patterns produced in a model *could also be produced in the real world*. We can never know how different a simplified mathematical representation is from the real world, but the similarity models do strive for, gives us confidence that their results could apply.

This thesis deals with a variety of different models, used for different purposes. One model deals with how one can measure and analyse invasions; the expanding phase of invasive species. Earlier analyses claims to have shown that such invasions can be a regulated phenomena, that higher invasion speeds at a given point in time will lead to a reduction in speed. Two simple mathematical models show that analysis on this particular measure of invasion speed need not be evidence of regulation.

In the context of dispersal evolution, two models acting as *proof-of-principle* are presented. Parent-offspring conflict emerges when there are different evolutionary optima for adaptive behavior for parents and offspring. We show that the evolution of dispersal distances can entail such a conflict, and that under parental control of dispersal (as, for example, in higher plants) wider dispersal kernels are optimal. We also show that dispersal homeostasis can be optimal; in a setting where dispersal decisions (to leave or stay in a natal patch) are made, strategies that divide their seeds or eggs into fractions that disperse or not, as opposed to randomized for each seed, can prevail.

We also present a model of the evolution of bet-hedging strategies; evolutionary adaptations that occur despite their fitness, on average, being lower than a competing strategy. Such strategies can win in the long run because they have a reduced variance in fitness coupled with a reduction in mean fitness, and fitness is of a multiplicative nature across generations, and therefore sensitive to variability. This model is used for conceptual clarification; by developing a population genetical model with uncertain fitness and expressing genotypic variance in fitness as a product between individual level variance and correlations between individuals of a genotype. We arrive at expressions that intuitively reflect two of the main categorizations of bet-hedging strategies; conservative vs diversifying and within- vs between-generation bet hedging. In addition, this model shows that these divisions in fact are false dichotomies.

INTRODUCTION AND SUMMARY

THEORY IN ECOLOGY AND EVOLUTION

As ecologists and evolutionary biologists we are interested in the living world, but why do we need mathematics? Surely Darwin did not use any in his *On the Origin*. And surely, algebra is not living organisms, interacting and eating, dispersing and diversifying, being born and giving birth. Still, any textbook of ecology or evolution will contain at fair share of mathematical treatments of a number of issues, at least population dynamics (with different interactions) in ecology, and at least some population genetics and possibly other frameworks for representing evolutionary change in the latter. Some philosophers of science see the presence of mathematically rigorous theory as a sign of a mature science (see e.g. Godfrey-Smith 2003), though some working scientists are not very happy with the presence of a lot of mathematics, particularly so in ecology (e.g. Simberloff 1981; Simberloff 1982; Peters 1991).

Regardless whether one sees the presence of mathematical treatments of particular phenomena or mechanisms as a sign of a mature science; mathematics is a pervasive part of evolution and ecology. By this I mean in addition to the calculations involved in statistics, which mainly deal with how to treat empirically collected data. Mathematical ecology and mathematical evolutionary biology is here, and it's most likely here to stay. Unfortunately, at least in my mind, theory and mathematics is often mixed up within evolutionary ecology; some of the journals where mathematical treatments of ecological and evolutionary issues are more common than others (like *Theoretical Population Biology* and *Journal of Theoretical Biology*) bare names which easily gives the impression that mathematical treatments is what constitutes theory. I started my PhD thinking I was a theorist or theoretician, but I end it thinking that I am a modeller. There is much

more to theory than just mathematical tinkering of models of interesting biological stuff. The best example of this is that natural selection (which in my perception is a theoretical concept) has several mathematical model formulations, but surely these mathematical formulations can not be considered the whole of natural selection, seeing as different models capture different aspects and that *all* models of evolutionary change make assumptions that are themselves subject to be altered by natural selection (but see Grafen 1999; Grafen 2007 and below). Theory also needs to give us interpretations of what these models and their constituent parts mean, and evolutionary ecology needs a philosophy that makes it clearer to both the interested common woman and the working scientist what these mathematical models actually contribute with. Theory is also often seen as much more than *one* model, but rather a family or cluster of models taken together (Levins 1966; Lloyd 1988; Thompson 1989). Some do not agree with me in this division of models and theory (e.g. Fagerström 1987), while others think that theory is distinct from, but qualitatively improved by the inclusion of mathematics (Caswell 1988). In many cases the division is not needed. In addition, within ecology and evolution theory and models are often used interchangeably, and what one sees as a model, another sees as a theory. For the purpose of this introduction, they will be used interchangeably, and in cases where the difference is of importance it will be pointed out.

Before we can get to what I see as *my* philosophy of mathematical models in evolutionary ecology, we need to spend some time on what models are.

WHAT ARE MODELS?

Usually mathematical treatments of anything that purports to be reasonably inspired by some real (or imagined) phenomena are called models, but these are not the only models science deals with. For instance, in atomic physics, the way most people (by that I mean most people but hard core

physicists perhaps) think about an atom is according to what is called the Rutherford-Bohr **model**. The modification of Rutherford's model of the atom was presented by Niels Bohr about a century ago, and is a way to represent how we think an atom looks at a smaller-than-microscopic level, with electrons circling a positively charged nucleus. An example from biology is the double-helix model of DNA. These are not purely mathematical (though there's a lot of mathematics in the Rutherford-Bohr model if you dig into it), but perhaps more graphical. In biology we also deal with a number of **model species**, species that have been studied more extensively than other ones. These species are often seen as a model for at least some similar species, where findings about how something work in the fruit fly *Drosophila melanogaster*, might have relevance for other insects, and possibly also a wider range of animals. Yet a different model is the deductive-nomological model of how it was once thought that proper science was to be done. So models are more than just mathematical models.

This is a list of some different kinds of models that Stanford Encyclopaedia of Philosophy mentions;

> Probing models, phenomenological models, computational models, developmental models, explanatory models, impoverished models, testing models, idealized models, theoretical models, scale models, heuristic models, caricature models, didactic models, fantasy models, toy models, imaginary models, mathematical models, substitute models, iconic models, formal models, analogue models and instrumental models are but **some** of the notions that are used to categorize models.

Note that they only list *some* of the notions used to categorize models (Frigg and Hartmann 2009).[1]

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[1] Spending ones time constructing mathematical models of some particular behavior of individuals or pattern of living organisms, one often start to wonder what this really means (or at least this author has); how are we better equipped to understand or predict what goes on in the natural world by me

Even if we are not willing to accept mathematically developed theory to be sign of a mature science, there is no doubt that mathematical models are prevalent within the fields of ecology and evolution, and that they have played an important part in the history of the fields. Within evolutionary biology R. A. Fisher, together with S. G. Wright and J. B. S. Haldane, working in the first half of the 20th century were instrumental, using mathematical models, in the development of the modern evolutionary synthesis that matured in the 1930-50's. The modern synthesis is still seen, at least by most people (Pigliucci 2007), as the current paradigm of evolutionary biology (Mayr and Provine 1980; Mayr 1982).

The models in this thesis are mathematical structures meant to have some similarity with the real world (Godfrey-Smith 2003). This similarity is hard to define in a more precise way; the chief reason for this is that they are not alike in the way they are similar to the real world. A second reason is that we can not possibly know everything about any real biological system, and therefore we can not easily judge how similar or how different a model is from it. I see the models in this thesis to be so similar to the real world that conclusions reached in the models *could in principle* hold for some or many biological systems. Whether these conclusions do hold or not is not for a model to answer to, only empirical studies can answer such questions.

The models in this thesis are not used to analyse or treat empirical data and, as most mathematical models, they are analysed by treating a set of assumptions as true. These assumptions are of course not true, in the sense that they hold for some, many or all real biological systems, but the output of these models come about with complete

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analysing this particular model? The most interesting part about the Stanford Encyclopedia of Philosophy entry on *Models in Science* is the end; "Models play an important role in science. But despite the fact that they have generated considerable interest among philosophers, there remain significant lacunas of our understanding of **what models are and how they work**." (my emphasis). My consolation therefore is that philosophers are also a bit unclear on these issues.

disregard for the truth-value of their assumptions. Mathematical models differ in the way they attempt to represent the world and both in *how similar they are* to the world and *how they are similar* to it. I find it therefore useful to attempt to make an overview of the value of mathematical models in ecology and evolution, without emphasis on their direct relation to the real world, but on how they are used by ecologists and evolutionary biologists, and more specifically how the use of models is legitimized by ecologists and evolutionary biologists. But before we delve into the different uses of models, we will look at one great optimist and a list of critics.

MATHEMATICAL MODELS

The fact that some mathematical models are often seen as important in the furthering of a field, have of course gathered a crowd of faithful believers in the prospects of mathematizing the fields of ecology and evolution. One extreme view is captured by a quote of L. B. Slobodkin;

> "We may reasonably expect to have eventually a complete theory for ecology that will not only provide a guide for the practical solution of land utilization, pest eradication, and exploitation problems but will also permit us to start with an initial set of conditions on the earth's surface (derived from geological data) and construct a **model** that will incorporate genetics and ecology in such a way as to explain the past and also predict the future of evolution on earth." (Slobodkin 1962, my emphasis)

In this quote, Slobodkin exhibits a wide range of commitments to different views of how the world works, how we do science and what models are, in particular that models can be used to *explain* and *predict* aspects (indeed, *all* aspects) of the living world. Slobodkin's belief, that with proper theory we could model and thus explain all past evolution and predict all future evolution and ecology on

earth, is perhaps a bit on the optimistic side. Half a century later we are nowhere near having anything in the vicinity of what Slobodkin hoped for. Stephen J. Gould (1989) has famously asked the question, and attempted to give an answer (that Slobodkin would have been disappointed with), in a similar way; what would happen if we 'replay the tape' of evolution? If the history of life on earth had been rewound and played all over again, how would the world then look? Gould holds that not at all the same thing would happen (Gould 1989). A more philosophically grounded version of this, which also would be a blow to Slobodkin's belief in perfect predictability of evolution, is John Beatty's contingency thesis (Beatty 1995), a proper elaboration inspired by Gould's rewound videotape. Contingency can be thought of as something that is, at least partially, dependent on chance and in the context of evolution that would include all coincidences through the history of life (just think of the dinosaurs). But Beatty's contingency thesis encompasses more than this; it holds that evolution, or more specifically natural selection, can in principle break down any pattern, mechanism or generality, and thus, we can not expect there to be any strong biological generalities that holds for evolving biological systems.

Though many a mathematically inclined ecologist or evolutionary biologist obviously sees some value in the use of mathematical models, I suspect that most practicing modellers and theoreticians these days are not as optimistic as Slobodkin was. But before we delve into the potential benefits mathematics can have in ecology and evolution, we will focus on those that are not so optimistic about the use of models.

CRITIQUE OF MATHEMATICAL MODELLING

EXPLICIT ARGUMENTS

Even if the past and future of evolution on earth is not entirely predictable or explainable, Slobodkin's quote indicates a strong optimism about the value and promise of mathematical models. It has to be recognized, however, that some ecologists and evolutionary biologists have been a bit sceptical of mathematical treatments. In fact more than some and more than a bit.

One of the contributors to the modern evolutionary synthesis, Ernst Mayr (1963), expressed his scepticism;

> "The Mendelian was apt to compare the genetic contents of a population to a bag full of coloured beans … To consider genes as independent units is meaningless from the physiological as well as the evolutionary viewpoint … These authors, although sometimes disagreeing with each other in detail or emphasis, have worked out an impressive mathematical theory of genetical variation and evolutionary change. But what, precisely, has been the contribution of this mathematical school to evolutionary theory, if I may be permitted to ask such a provocative question"[2] (as quoted in Crow 2008).

Mayr was obviously of the impression that the *assumptions* used in the early population genetical literature were highly unrealistic, and that such beanbag genetics had little scope for providing any valuable insight, since they were so far removed from the complex reality of the real world. Notable ecologists at the same time also expressed their scepticism;

> "The ecologist should be careful to avoid the *misuse* of mathematics. Ecologists, and especially mathematicians with a slight knowledge of biology, seem to be prone to the mistake of building a model with symbols which, they pretend, represent certain qualities of animals. The symbols are then manipulated according to the rules of mathematics and, finally, the conclusions are translated into words which purport to describe some law of biology." (Andrewartha and Birch 1954, p. 11)

Andrewartha and Birch (1954) were worried that mathematical models often give an impression of truth, or are often taken in favour of particular hypotheses, almost in the same way empirical data are. In ecology, the regulation of populations (i.e. how they change in numbers over time, and more importantly; what are the important factors that determine their change) has been an ongoing debate for close to a century (see Cooper 2003 for a nice history of the debates). Many of the proponents of the importance of density dependent factors (that e.g. birth rates decrease with high densities), have actually used mathematical models as arguments alone, such that the asserted importance of density dependent factors "… is not really a conclusion based on scientific experiment but rather that it has more of the status of dogma" (Andrewartha and Birch 1954). In the same vein, Hedgpeth (1977) noted that "Unfortunately […], many and for the most part those not directly concerned with modelling activity see in equations *facts* rather than ideas" (my emphasis). More recently the same is found of several of the classic mathematical models frequently referred to and introduced in most textbooks (e.g. the logistic model, the Lotka-Volterra models and Ricker models). They are in fact not supported by much evidence at all, particularly from natural systems (Hall and DeAngelis 1985; Hall 1988); and despite

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[2] It should be mentioned that even though Ernst Mayr wrote this in his Animal Species and Evolution (1963), in his later work on the history of evolutionary thought (Mayr 1982, p 555), he (rightfully) credited R. A. Fisher with contributing greatly to the reconciliation between geneticists and naturalists, particularly with his 1918 article (see section on Haldane's defence). For many readers it was obvious that "these authors" were referring to Haldane, Fisher and Wright.

this it is very common for these models to be presented "more or less as truth" or as a "basic law" (Hall 1988).

One of the reasons for why model results are sometimes (wrongfully) seen as evidence is that all models come with particular interpretations. Even in the simplest of models, far removed from the vicinity of being closely representative of any real biological systems, the particular aspects of a model are (usually) given biologically meaningful interpretations. Models have, for instance, parameters for mutation rates, clutch-sizes and longevity, concepts which refer to both meaningful and measurable quantities in real biological systems. Conclusions from a model, presented in a scientific article, will use the terminology and interpretation in a way that easily gives rise to the misunderstanding that they are stating facts. In Chapter II, for instance, we state that "…selection favours longer dispersal distances under maternal control of dispersal", which sounds like it applies in general. This is of course not the case. Minimally, it applies only to our model; whether selection would actually favour longer dispersal distances under maternal control in real biological systems is not to be judged by the output of our model. This misunderstanding of model interpretation is, as noted by Hedgpeth (1977), perhaps more common among those not particularly familiar with models. Examples of such misinterpretations are numerous, particularly in evolutionary biology where models predicting a particular evolutionary response or optima consistent with empirical observations are often interpreted as evidence of them being adaptive (Gould and Lewontin 1979) or at least the result of selection (see for example the discussion on fisheries induced evolution, Jørgensen, Enberg et al. 2007; Browman, Law et al. 2008; Kuparinen and Merilä 2008).

Others also contemplated on the dangers of too much mathematical modelling. This can be exemplified by Skellam (1972), who himself contributed with several mathematical treatments (e.g. Skellam 1951 is of relevance to this thesis);

"Without enlightenment and eternal vigilance on the part of both ecologists and mathematicians there always lurks the danger that mathematical ecology might enter a dark age of barren formalism fostered by an excessive faith in the magic of mathematics, blind acceptance of methodological dogma and worship of the new electronic gods." (Skellam 1972)

Perhaps the sharpest critic of the pervasive use of mathematical models in ecology was Robert H. Peters. In a range of different articles (Peters 1976; 1978; 1980) and in his book *A Critique for Ecology* (1991), he puts forward his strong criticism against construing mathematical models of ecology and evolution as being scientific at all;

"If scientific theories are characterized by predictive ability, the branches of science are distinguished by the objects of prediction. Ecology seeks to predict the abundances, distributions and other characteristics of organisms in nature.... This book contends that much of contemporary ecology predicts neither the characteristics of organisms nor much of anything else. Therefore it represents neither ecological nor more general scientific knowledge." (Peters 1991)

By 'much of contemporary ecology' Peters refers, among other things, to mathematical models, which according to him can not be considered theoretical at all. These models are but deductive games that provide some vague 'insight', and that they more often than not are entirely untestable. Peters suggests that ecology get rid of ideas of *explanation* (in the sense of understanding the causes of things) and just use mere predictions; if a curve-fitting produces a particular relationship between two variables in some mammals (say body size and densities), it predicts similar patterns in similar animals, and is therefore predictive, and therefore theoretical (Peters 1991). Any mathematical model that would attempt to include mechanisms that could produce such patterns (i.e. a model we investigate possible causal links

between size of individuals and densities) are not needed and non-scientific. They are only tautologies which "…are not subject to empirical falsification and are incapable of prediction" (Peters 1976 p. 2). The charge of tautology is perhaps most discussed in the evolutionary literature on whether or not natural selection is a tautology (Peters 1976). Peters thinks so, but there have been put forward quite a few arguments against him (see for instance Sober 1984).

Peters' view of tautologies is somewhat complex. In propositional logic, a tautology is a sentence that is of the form 'P or not P'; "It is raining, or it is not raining". Such statements are, according to Peters, completely devoid of empirical content, are always true and are therefore not very useful in science, (note that his argument is not only based on whether or not *mathematics itself* is tautologous). He argues that mathematical models in general can only show what is possible, and that models therefore, in effect, are tautologies. For instance, one of the conclusions of chapter II in this thesis is that in our model there is a parent-offspring conflict over dispersal distances. This means that mothers would 'prefer' that their offspring disperse more widely than the offspring 'prefer' themselves, hence there is a *conflict* over dispersal distances. This conflict is there *in our model*. But this model does not show anything else than the *possibility* of this conflict in real biological systems. The conflict might disappear for many reasons, through different mechanisms that we have excluded from the model (though one of them is analysed in the chapter). So the conclusion from the model is that 'there *can* be a conflict over dispersal distances'. The interpretation in terms of the real world would be "there is conflict over dispersal distance OR there is not conflict over dispersal distance", which is obviously of the form 'P or not P'. And Peters does not recognize tautologies as being particularly scientific.

Peters does not hold that mathematical models are completely useless for ecologists, but he is not willing to call them scientific; models can for instance be used to "…lessen our logical work load…" (Peters 1976), to clarify ideas and to perform other tasks in what he terms the 'subjective' part of a scientist's work (Peters 1991). This subjective part can be described as anything that helps us in forming ideas. But just as having a particular language (say Italian) with fairly clear definitions helps us form ideas and shaping hypotheses, this language is not science.

Other authors have also pointed to the fact that there is a dense jungle of models that do not even attempt to describe something that can possibly predict anything that can be held up against the natural world, and that the 'field' of theoretical ecology and evolution is close to being a field completely detached from empirical biology;

> "Models are being constructed, refined, elaborated, tinkered with, and displayed with little or no effort to link them with the real world." (Pielou 1981)

So not only do many mathematical models fit the world badly (Hall and DeAngelis 1985; Hall 1988), they are also less frequently challenged by empirical investigations. This is also due to a lack of communication between modellers and empiricists;

> "In the case of ecology, though, it seems as if many theoreticians are only able and willing to address other theoreticians, and as if a large portion of the theories are proposed only for their own sake." (Grimm 1994)

And it has been noted that such models seem to only pile up and become more and more distanced from empirical study of the biological world;

> "Ecology is awash in all manner of untested (and often untestable) models, most claiming to be heuristic, many simple elaborations of earlier untested models. Entire journals are devoted to such work, and are as remote from biological reality as are faith-healers" (Simberloff 1981).

Simberloff goes on to advice that mathematical or verbal theory "…without direct rigorous field testing no longer be recognized as a significant contribution" (Simberloff 1981).

These are but some of the criticisms voiced over the presence or excesses of mathematical ecology and evolution (see particularly Chapter 5 in Cooper 2003). There is a wide range of different problems highlighted, the most common ones being that there is a lot of mathematical models that either 1) are never (or can not) be properly tested and therefore say little about the real world, 2) have been tested and failed the test but are still in widespread use and 3) mislead scientific endeavours, and 4) are *de facto* tautologies and are therefore not scientific.

IMPLICIT ARGUMENTS

In addition to these explicit critiques, there are some more implicit arguments against the use of, at least some, models in ecology and evolution. Many of the familiar models (logistic growth, Lotka-Volterra, population genetics etc), purport to be general. Generality is a frequently used description of models, though it is sometimes unclear what this generality entails (Cooper 2003). Sometimes a model is referred to as being general because other more specific models can be either derived from it or at least put in the same 'framework' (see Chapter IV). Other times it seems like generality implies that a model attempts to describe general biological patterns or mechanisms, i.e. that the conclusions from a model should hold for many different taxonomic and ecological systems. In light of John Beatty's 'contingency thesis' (1995), it is not obvious that this can even possibly be achieved. It might be that, even though all biological populations undergo ecological fluctuations in size and distribution and evolutionary changes over long periods of time, there are very few such generalities to be found, since natural selection can break down any such pattern. The best example of this is that all models of evolutionary change make

assumptions that are themselves the result of natural selection (Ruse 1973; Thompson 1989; Beatty 1995).

Another implicit critique of the use of general models in ecology is based on a more practical view; the numerous challenges ecology needs to address and help society to deal with, that of environmental policy (Shrader-Frechette and McCoy 1993). Shrader-Frechette and McCoy (1993) argue that general ecological theory has rarely, if ever, contributed significantly to conservation and environmental problems, and that progress in conservation is usually based on *case studies*. That is, environmental problems are best tackled with in-depth, detailed knowledge of the particular system and not more general theories or models (see also Simberloff 1988). This can be seen as possibly giving rise to two fundamentally different ways of doing ecology (and evolutionary biology); top-down or bottom-up. Top-down ecology would be a scientific endeavour that starts with general models, based on idealized assumptions of how we think the world works (or at least could work). Then specific systems are compared to this idealized standard, and we learn perhaps something more about both the idealized standard and the specific population.

Bottom-up ecology would be the science of case studies; there are millions of different species, with different distributions, diets, life-histories, predators etc., and the science of ecology and evolution would perhaps not look for general patterns, but be composed of a collection of case-studies. Shrader-Frechette and McCoy are less sceptical of the use of more system-specific models (i.e. models tailored towards this particular fish in this particular pond) than they are of 'general' models, because specific models can be of help in understanding the specific systems under threat (Shrader-Frechette and McCoy 1993).

In their suggestions on how to strengthen ecology as a science Belovsky, Botkin et al. (2004) also recognized the problem of generalities; "We acknowledge that it may not be possible to pose universal statements that encompass all ecological scales of organization, space and time" (Belovsky,

Botkin et al. 2004). Such universal statements are often what are being made in the interpretation of general models.

RESPONSE TO THE CRITIQUE

There have been numerous explicit responses to the criticisms voiced in the last section, some refuting the assumptions about what is to be considered scientific (as in challenging Peters (1991) staunch instrumentalism (Cooper 2003)), others emphasizing ideas about what different *roles* models play in scientific reasoning (Odenbaugh 2005) or posing *legitimate* theoretical pursuits (Caswell 1988). Roles of models and legitimate pursuits include, for instance, models as tools to help our logic (Haldane 1964), models as conceptual frameworks on which to build ecological and evolutionary research programs (Odenbaugh 2005) and the value in proving that something is in fact possible (Haldane 1964; Caswell 1988; Odenbaugh 2005). Others have yet argued that keeping a theory or a model, in spite of negative evidence against it can be advisable (Wimsatt 1987) and that models should be (and are) judged on other criteria than only testability and 'passing' of tests against the real world (Fagerström 1987). In addition, some have turned the tables and laid out arguments against the automatic preference for empirical work and value of 'pure' data (Fagerström 1987; Haila 1988), and that the validity and value of 'testing' is perhaps not as simple as often portrayed, at least not in the sense of automatically giving it preference to models.

These were, at least partly, in defence of keeping the vast array and developments of mathematical models that are somewhat removed from the real world, and in some cases, demonstrably wrong. There has, nevertheless, also been a slight turn in the kind of models that are produced. Firstly, it is now more common with more system specific models, i.e. applying to only a particular species or population (Colwell 1984; Cooper 2003). Secondly, more models are tailored to be predictive, or have at least a tighter link with empirical data (see e.g. Clark and Gelfand 2006). Thirdly, there has also been a shift toward more mechanistic models, as an attempt to make them closer to the real biology than "faith-healers" (Cooper 2003), in addition to embracing a more pluralistic approach (McIntosh 1987). And lastly, the problems of generality and how general models relate to biological phenomena, have reached a debate on what generalities we can make, especially in ecology and whether or not there are *laws* in ecology (Lawton 1999). Some argue for some general law-like structures in ecology and evolution (Lawton 1999; Murray 2000; Turchin 2001; Colyvan and Ginzburg 2003) , while others argue that there are no laws in ecology and that we don't really need them (e.g. O'Hara 2005).

I will go through some of the more substantial contributions to the response to the critics of mathematical models. There are, of course, also other expositions on the utility of models that have been voiced, though not in direct response to the criticisms above. One highly cited article is Richard Levins' presentation on the strategies of model building (Levins 1966). Though not as a response to direct criticisms of the use of models, it serves as a nice starting point of our discussion of ways to legitimize model building in ecology and evolution. I also have to add that I do not claim that this is an exhaustive overview of all the responses that have been or could have been made against the charges above, only that it can be seen as a representative sample.

LEVINS' STRATEGY OF MODEL BUILDING

Richard Levins has made several substantial contributions to the development of the mathematical side of evolutionary biology (e.g. Levins 1968), in addition to his contributions on philosophy and the more political side of biology in society (Levins and Lewontin 1985; Lewontin and Levins 2007). In 1966 he published an article called *The strategy of model building in population*

biology, where he describes a trade-off between three potential goals of a model; realism, generality and precision (Levins 1966). One of his main arguments is that the real world is too complex to be accurately modelled in the sense of being realistic, general and giving precise outcome at the same time. He describes three strategies that have 'evolved', each of them sacrificing one of these to two others. Though some of his arguments are partly diminished by technology (particularly computers), these three different dimensions models can be compared in are, at least in my mind, still useful, at least in delimiting different directions a model could be extended; more (or less) realistic, general or precise.

Levins states that his favoured side of this trade-off is to sacrifice precision to realism and generality. By this he seems to intend that the models he deals with are realistic (i.e. they include a larger set of mechanisms that he/we believe to be important for any given problem) and general (they rarely make very specific assumptions that would make the models *apply* to or describe specific systems), but they are less precise (they often give qualitative answers). His approach can partly be contrasted with the earlier population genetical models that were already well developed in his days, which can be said to be general and precise, but perhaps not so realistic. It is, however, important to realize that Levins did not intend this 'trade-off' to be absolute, he merely pointed out some of the different directions models in population biology had taken at that time (Levins 1993). It might also be pointed out that for any given model, it might be changed to be both more realistic, more general and more precise, even though it might not be possible to *maximize* these at the same time (Levins 1993).

Levins also describes some of the pitfalls in using models;

> "There is always room for doubt as to whether a result depends on the essentials of a model or on the details of the simplifying assumptions. This problem does not arise in the more familiar models,

such as the geographic map, where we all know that contiguity on the map implies contiguity in reality, relative distances on the map correspond to relative distances in reality, but colour is arbitrary and a microscopic view of would only show the fibres of the paper on which it is printed. But, in the mathematical models of population biology, it is not always obvious when we are using too high a magnification" (Levins 1966)

By 'the essentials of a model', he most surely is referring to the parameters or relations in a model that purports to be a more accurate representation of a biological system, that there is some similarity to the real system. But before delving into how one can get at these essentials, I wish to follow his analogy of a mathematical model of ecological or evolutionary phenomena to that of a geographic map, since this analogy is often drawn (e.g. Kokko 2007; McElreath and Boyd 2007).

Levins underlines the problem of putting a map under the microscope; you will not see the street you live in and the neighbour's dog running in the yard[3]. The map is a representation of how the world looks from above, and is only useful at a particular scale of analysis and it's useless to zoom in too much. But the opposite is also true; the maps of the world that are present in most classrooms (or schoolbooks) are also a mere representation of the world. But in these maps, contiguity is not guaranteed; we know the world is round, but still Antarctica is at the bottom and it seems like the world ends to the west of the Americas and to the east of the pacific. Even worse, at such a scale, relative distances do no even hold (usually); in fact there is a wide range of different ways to project the world (a sphere) onto a two dimensional flat piece of paper. Some of these projections are used for navigation (like one of the most common, the Mercator projection), and actually keep angles more than relative distances (it seems as the distance around the world 5 kilometres south of the

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[3] At least for classic maps on paper, perhaps not so for Google Earth.

north pole is the same as around the equator and Greenland looks the size of Africa, which is about 15 times as large in km^2). So if the map is a good example of a model, there is the danger of both zooming in too much and *out* too much; any good model works only within a particular scale (in this case a spatial scale). It also shows that, to represent the globe on a plane, there is no right or wrong; it all depends on the purpose; right angles for navigation is perhaps a better one, but it is not a more correct representation of the world.

There is a second aspect that we can learn from thinking of maps as models; that they are fraught with conventions which have a more contingent historical basis than any basis in being a better representation. Some might argue that putting north up, using the Mercator projection, and putting Europe in the middle is a conventional remnant of the colonial past, but whether or not we choose to see this as a result of human history and politics, we surely recognize it as not being dependent on representing the world more accurately. This property is much the same in the mathematical models used in ecology and evolution; there are so many conventions on how to set them up, and this can be problematic; it makes it harder to think outside the box. If one searches the latest editions of any ecological or evolutionary journal, finds an article that uses mathematical models, I suspect that close to all of them will be models which are only slightly different compared to models presented before. When somebody suddenly does move outside these conventions, however, it can become a very fruitful avenue of new developments of models. One good example of this is in the simplicity of Price's publication of his now-famous equation (Price 1970). In his Nature article published in 1970 (without *any* references), George Price presented work that has been so successful as a description of natural selection and evolution (see for instance Frank 1995; Rice 2004; Gardner 2008) that it has lead well-regarded mathematical biologists to print T-shirt stating 'The Price is Right' in its honour. But there can be no doubt that most mathematical biologists work within a wide

set of conventions, and they can be just as misleading as thinking that Europe really is that big and in the middle of the world.

Levins also recognized the problem of conventions, or at least the problem of making some sort of assumption(s) which is not of importance for the problem at hand. His main response to this was to argue for making several (if not many) models of the same biological phenomena, but building them with the explicit intention of making different particular assumptions. The Mercator, Gall-Peters or Albers projection of the world onto a plane can not *individually* represent the world the way it properly looks; while together, a wide range of different projections might give a more proper view of the world. In the same vein, Levins emphasizes the importance of making several models; that making several different kinds of models of the same phenomena, if the results are similar they are more robust, and quips;

> "Hence our truth is the intersection of independent lies" (Levins 1966).

It is unclear, however, what Levins means by this "truth", if it is intended to be the truth about the real world, or if it's intended to be about the *possibility* of the particular pattern in the real world. The only way that more models of the same can make it more *likely* or *probable* that the modelled process is important in real natural systems (or "true"), is if we assume that there is a finite number of ways the world *could* work. One model shows that something is possible, and if there is only N number of ways the world could possibly work, the analysis of the model has increased the probability of it being "true" for natural systems by $1/N$. That there are only a finite ways of representing the world, however, is a highly contentious issue, and one that I am personally not convinced by.

A third aspect of the geographical map as a model is worth mentioning is that the map is meant to be purely descriptive. There is no inherent *explanation* in a map. The presence of a lake does not explain *why* there is a mountain four clicks to

the east. There is no way that we can manipulate parts of the map, and see what happens to some other aspect of it. In a mathematical model, we can often change the setting of one parameter (increasing competition, number of species or whatever is relevant in the model), and we investigate the consequences of this. A geographical map does not work in that way, but it is the way that we usually want mathematical models to work.

Levins' *Strategy of Model Building*, does not explicitly relate to the value of models, except for in the claim that our "truth is the intersection of our independent lies", but is more a description of how models are built in population biology.

HALDANE'S DEFENCE

The charge and question by Mayr (1963) of what population geneticists have contributed, was interpreted by J. B. S. Haldane to be directed at himself, R. A .Fisher and S. G. Wright, and he wrote a direct response in *A Defense of Beanbag Genetics* (Haldane 1964). In this polemic article he gives many examples of what he sees as the main values of population genetics models, and makes several points. First, he sees phrasing hypotheses or ideas in the form of algebra is of help, because compared to verbal arguments or lines of reasoning, they are *forced* to be entirely logical or rational. He mentions a few examples (of Mayr's own work of course), where the verbal reasoning seems insufficient and so complex that phrasing them in the form of a mathematical model would clarify the line of thought; "I hope I have given enough examples to justify my complete mistrust of verbal arguments, where algebraic arguments are possible…" (Haldane 1964). This is an explicit mention of the use of mathematical models as a way to *externalize our rational thinking*, they work as tools of logic that we can depend on when our internal logic seems insufficient. By putting our ideas and reasoning in mathematical form, concepts are clarified, relations are made explicit and often quantitative, and following the logic is

usually made easier. Note that this is regardless of whether the 'model' or reasoning will apply to any biological system. It is a methodological argument.

It is worth pointing out that models as an *externalization of our logic* can either be fully externalized or only partially. For instance, in chapter II we present fairly complex individual-based models where there are a number of assumptions that form the basis for the calculations performed in the model. The output of the model follows from our assumptions according to the 'rules' we have defined to be in the model (and the logic of mathematics). This is an example in which our logic can be seen as fully externalized, and even with analysing the output of the model it is perhaps difficult for us to *understand* everything that happens in the model. On the other hand, in chapter IV we present a general population genetic model. We posit two alleles that can differ in their mean and variance of fitness, and use the reproductive successes (R_i) of two genotypes as (see appendix of chapter IV for the details)

$$R_1 = \frac{1}{Nq_1} \sum_{j=1}^{Nq_1} (\mu_1 + \alpha_{1,j})$$
$$= \mu_1 + \bar{\alpha}_1$$

$$R_2 = \frac{1}{Nq_2} \sum_{j=1}^{Nq_2} (\mu_2 + \alpha_{2,j})$$
$$= \mu_2 + \bar{\alpha}_2$$

Using these fitnesses for the two alleles, we arrive at the following equation describing the change in the frequency of the first allele;

$$\mathbb{E}(\Delta q_1 | q_1) = q_1 q_2 \{ (\mu_1 - \mu_2) + (q_2 \rho_2 \sigma_2^2 - q_1 \rho_1 \sigma_1^2 + (q_1 - q_2) \rho_{12} \sigma_1 \sigma_2) \}$$

Now, for many (again, at least for this author), immediately understanding how equation (2) follows from equation (1) is hard. But by making the derivation explicit (as we do in the appendix to chapter IV), it is easier to follow the logic of every step taken, and in this case the model serves as a partial externalization of our logic. Instead of relying entirely on the mathematics to be logical while giving up full understanding of the model, we explicate the algebra and it functions more as an *aid to* our logic, than a *substitute for* our logic.

Haldane also mentions one of the most commonly presented virtues of biologically motivated models; "It is, in my opinion, worth while devoting some time to proving the obvious" (Haldane 1964). By this he is invoking the general use of model as *proof-of-principle*; by setting up a model where the assumptions are not too far from what *could* be a fairly realistic representation of a biological system, the outcome of a model must be seen as a *possibility*, even in real systems. We will return to this below. Haldane realized that possibility might be misinterpreted as actuality, as pointed out above (Andrewartha and Birch 1954; Skellam 1972; Hedgpeth 1977);

> "There is, however, a danger that when mathematical investigation shows a possible cause of a phenomenon, it is assumed that it is the only possible cause" (Haldane 1964).

The value of proving the possible has also been pointed out by several other biologists; according to Lewontin for instance, mathematical developments "… is the science of the possible" (Lewontin 1968, also see following sections). This was also recognized by Peters (1991), but he did not deem them to be legitimate pursuits of ecology, or that they were scientific due to their *de facto* tautologous nature.

Through the history of ecology and evolution, however, there are many such *proof-of-principle* contributions that have been of value. One thing to point out in this regard is that data or observations

are never theory-free, they are theory-laden; there is no such thing as observations that are completely devoid of some *mindset* or without any degree of expectation to it (also see the introduction of chapter I below). This can lead to two fallacies. Firstly it can lead to a conclusion based on empirical analysis that does not recognize the "theory" behind the analysis and the observations (again, see introduction of chapter I below). Secondly, and even worse, often data that don't fall into the current expectation of observations are often neglected or disregarded. One example from evolutionary biology is the presence of helpers at the nest of some birds (see Fagerström 1987). These helpers are individuals who aid other parents raise their chicks, and were once seen as unexplainable by evolutionary theory, and therefore "impermissible" observations. They were often termed abnormal and were likened to other irrelevant reproductive behaviour (like homosexuality). It was not until the theoretical development of kin selection, whereby individuals are expected to have an 'interest' in the survival and reproduction of other related individuals than their direct descendants (Hamilton 1964a; 1964b), that these observations were made *permissible* by rigorous mathematical models. Showing that something was possible from an evolutionary standpoint increased the recognition of such behaviour as not necessarily aberrant, but perhaps even adaptive (Fagerström 1987). Going even further back, R. A. Fishers demonstration that continuous variation was indeed *possible* with discrete Mendelian units of inheritance (Fisher 1918) was instrumental in settling a long dispute in early evolutionary biology, and indeed paving way for the modern evolutionary synthesis (Mayr 1982). So in many cases, just proving that something is possible is well worth the effort.

So models can help us in our rational thinking or our logic, and they can also be seen as *proof-of-principle* models; they can prove what is possible. Externalization of our logic does not necessarily entail any empirical implications, but proving what is possible can.

CASWELL'S DIFFERENT PERSPECTIVE

Hal Caswell is a well-renowned mathematical ecologist, particularly for his work on structured population models (Caswell 1989). As a reply to Simberloff's (1981) complaint about the presence of too many models in ecology, he published a small paper on theory and models in ecology (Caswell 1988). In his defence of the usefulness of models, he ends up with a "beginning of a list of types of theoretical problems" he thinks are valuable contributions to the furthering of ecology;

1. Exploring the consequences of theory.

2. Demonstrating the connection between apparently unrelated theories.

3. Evaluating the robustness of, or lack thereof, of theoretical results, by examining different models for the same phenomenon.

4. Developing mathematical methods for the analysis of theoretical models.

5. Finding the simplest possible model capable of generating an observed pattern.

6. Designing empirical and/or experimental tests of theory.

Caswell's main point was that there are many other virtues of theory or mathematical models besides developing explicit tests of them, thereby responding to the charge that these models are often not tested, and if they are they often fail.

The last point (6) is the one recognized by the critics as having scientific value. Models that generate clear predictions that can be held against the natural world are valuable. Caswell does not, however, explicitly point to how one should deal with models that are demonstrably wrong, or models which yield wrong predictions. By exploring the consequences he points to the same as Haldane (1964); showing that something is, indeed, possible. The purpose of developing different models for the same phenomena (3) has

also been proposed before, most notably by Levins (see above). Demonstrating the link between seemingly unrelated models/theories (2) and developing different models for the same phenomena (3) can be construed as somewhat of a contradiction; one goal is to link seemingly different models and the other is to explicitly develop different models. In a more dynamic scientific perspective, however, it makes sense. First we might show a particular pattern could arise from one kind of model, it acquires robustness from a different model showing the same, and over time some overarching general model can perhaps subsume all of the previous ones.

Alan Grafen's (e.g. 1999; 2006; 2007) *Formal Darwinism* project is a recent and good example of Caswell's point (2). Grafen laments that "... there are many mathematical models that show natural selection at work, but they are all examples" (Grafen 2007). The aim is to mathematically develop a theory that "captures Darwin's argument in its entirety" (Grafen 2007) and to clearly show the explicit relationships between these different mathematical versions of evolution and natural selection. This is clearly in line with demonstrating the link between models/theories.

Point (4) claims that it is a legitimate pursuit of ecological and evolutionary theory to develop mathematical methods for the analysis of theoretical models. Development of the basic tenets and general mathematics behind the framework of adaptive dynamics serve as a nice example of this (e.g. Geritz, Kisdi et al. 1998; Geritz, Gyllenberg et al. 2002; Geritz 2005; Kisdi and Geritz 2010), adaptive dynamics being one of several ways of modelling evolutionary changes. Much of this literature can be considered fairly distant from real biological systems, but nevertheless analysis of more specific models of biological problems are made easier with such theory. Some might argue that, though they are legitimate pursuits, they perhaps belong more to the area of mathematics proper, and perhaps not ecology or evolution.

Trying to find the simplest possible model that can produce an observed pattern (5), is a subset of point (1); proving what is indeed possible. The idea of Ockham's razor comes to mind; if there are two different models that both are plausible and both produce the same pattern, then the one that is 'simpler' should be given higher rank, due to its simplicity. We do not need to invoke more complex mechanics if it can be explained or produced by simpler means. This principle of *parsimony* is of widespread use in ecology and evolution, as well as science in a wider sense. As a guiding principle it can be seen as having scientific value, but for many practical purposes it can also be confusing; all models are often not plausible to the exact same extent. Even if simpler models can produce the same pattern as more complex models, these more complex models are often considered to be stronger in *realism*, in that they take more of the known mechanisms into account. The choice between a simple but unrealistic model and a complex, more realistic model will then not solely be guided by the principle of parsimony. Also, in many cases of evolutionary theory, we are not just interested in the *simplest* possible factor or explanation of a pattern, but to charter as many possibilities as possible. The favouring of dispersive traits through natural selection, for instance, can come about through spatio-temporal variability in availability of resources, avoidance of kin competition or avoidance of inbreeding (see below). If we were to explain the presence of dispersal in natural systems, deciding which of these models of dispersal evolution is *the* simplest is perhaps both difficult and not recommended. Is it *simpler* to assume that the population is structured in space (which makes you compete more with kin) or that the environment is variable in space and time (which would lead to variability in availability of resources)? We could also, for instance, be interested in *all* possible mechanisms that could lead to the evolution of dispersal, and not only the simplest one.

Regardless of the problems of parsimony and finding the simplest possible model that can produce an observed pattern, it does emphasize an important point in the evaluation of models; that models are evaluated, not only on their ability to predict and fit patterns in the real world, but also on other aspects, for instance their simplicity. Fagerström has also highlighted other aspects of a model.

FAGERSTRÖM'S CRITERIA FOR GOOD MODELS

Fagerström (1987) makes the case for models to be judged not solely by their ability to produce results consistent with data from real biological systems, and charters these other criteria in a pragmatic sense; by looking at how individual models or theories have been judged through the history of ecology and evolution.

He lists *simplicity* as one of the criteria of a good ecological theory; that it is possible to understand both the assumptions behind the model, and why the implications follow from the assumptions. He does not directly refer to the principle of parsimony, but that models are more easily accepted if they are easy to understand. They might not at all be better at predicting what happens in real biological systems, in fact, he uses the Lotka-Volterra equations as an example of models being kept despite negative evidence against them (Fagerström 1987). If we were to extend the Lotka-Volterra equations to include all possible more realistic aspects of a population, the model would become so complex that most people would not *feel* they understood the mechanics of it to the same extent as very simple models. In a way, the idea of simplicity can be seen as appealing to a *partial externalizing our logic*. If models are too simple, we might not need the mathematics to help us, and if they are too complicated, we might not feel that we understand the model at all, but somewhere in between, the mathematics is more of an aid in understanding. As noted above, there's a difference between mathematics as an *aid to* our logic and a *substitute for* our logic. (It could be pointed out that this

difference is perhaps not absolute, but will vary from person to person).

 A second criterion is that models need to be *consistent* with prevailing ideas in the scientific communities; the logistic equation describing population growth is consistent with the general idea that if some resource is limited, then there has to be some upper limit to how large populations can grow.

 A third reason why models, like the Lotka-Volterra equations again, have a predominant place in ecology is that they have been *productive*. Simple models that give rise to development of new concepts and ideas are often successful. The basic models of kin selection and community dynamics need only be mentioned, these have sparked off an immense literature of both theoretical and empirical value. It should be noted, however, that with this criteria Fagerström is getting quite close to measuring the success of models by the success of models, which is obviously not too informative.

 One of the last commonalities he finds among successful models is their *beauty*. Sometimes a model "... may evoke a feeling of having glimpsed truth like a crystal; clear, hard and pure" (Fagerström 1987). He claims that such beauty is often in a combination of generality and economy (simplicity), that a model is "... universal in content and pregnant in form", a feeling not unlike this author's when he first spelled out equation (8) in chapter IV. The recognition of such beauty is perhaps more common among mathematicians than ecologists, but it nevertheless has an impact on how successful a model becomes.

 The last point that Fagerström (1987) delves upon is the idea that all models need to be tested, or that they need to be challenged by the natural world, to see if they hold up to empirical scrutiny. He does recognize this as an important aspect of *some* models, and that testing as a way of "finding the truth", should perhaps be seen as an *ultimate* demand on well developed theories. This does, according to him, not mean that they are the only *proximate* purposes of models. So models should, in the long run, perhaps be held up against nature,

but in a shorter time-perspective, this need not be their main purpose.

ODENBAUGH'S BASIC PURPOSES OF MODELS

Jay Odenbaugh, a philosopher of science with emphasis on biology, has written several accounts on the use of models in ecology in particular (Odenbaugh 2001; Odenbaugh 2003; Odenbaugh 2005; Odenbaugh 2006). If Fagerström's (1987) inspection of what is common to many models being used or successful in ecology and evolution, Odenbaugh has gone into more depths as to *what* they are being used for. This can perhaps be more of help than Fagerström's (1987) since, for instance, it is hard to judge a model on its productivity the day it is presented. In one of Odenbaugh's expositions on models in ecology (Odenbaugh 2005), he charters for what different purposes models are used in theoretical biology[4];

1. Models are used to explore possibilities.
2. Models give scientists simplified means by which they can investigate more complex systems.
3. Models provide scientists with conceptual frameworks.
4. Models can be used to generate accurate predictions.
5. Models can be used to generate explanations.

He avoids elaborating on the last two points, and the first point here is already discussed, *proof-of-principle*.

 Odenbaugh uses the Lotka-Volterra predator-prey equations as an example of how simple models can be used to investigate more complex systems. He sees the Lotka-Volterra equations as a false model, with which we can use as a basis to

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[4] Odenbaugh is very explicit in that he does not mean that this list is exhaustive.

investigate what needs to be added to the models to better predict real systems. The rationale is that models do not just fail, but that they fail in particular ways and for reasons that can be informative. All predator-prey interactions do not consist of the perfect oscillations and limit cycles that appear in the Lotka-Volterra equations, and how we need to change these models to fit the world better can be informative (Odenbaugh 2005).

A concept is an abstract idea, and Odenbaugh argues that models can serve as conceptual frameworks. Odenbaugh puts forth the example of the quest for an old ecological proposition, first proposed by Elton (1958); that more complex ecosystems are more stable. This hypothesis was phrased as simply as that, but some years later mathematical models of the ideas were presented (May 1973; see also Pimm 1984). These models have helped develop the concepts of complexity and stability. As soon as Elton's idea was formulated in algebraic form in idealized communities it became apparent that both complexity and stability were not unambiguous concepts, there were different aspects of the model that would correspond to what we intuitively would see as both complexity and stability. So these models have functioned as *conceptual frameworks*, in that they, perhaps despite their "falsity" have helped as logical aids in developing more consistent and clearly defined concepts. This is related to Fagerström's (1987) notice that successful models are often productive and Haldane's (1964) externalization of logic as well as a general proving the possible perspective.

WIMSATT'S VALUABLE FALSE MODELS

William C. Wimsatt, a philosopher of science who also studied population biology under Lewontin and Levins, has presented a view that false models can in many cases have genuine scientific value, despite the fact that they are false (Wimsatt 1987). This also falls in line with the famous quote by R. A. Fisher's son-in-law, George E.P. Box;

"Remember that *all* models are wrong; the practical question is how wrong do they have to be to not be useful" (Box and Draper 1987).

Wimsatt first notes that models can be false or wrong in many different ways; for instance, they could have *local applicability*, in which case it is false if applied outside its domain; it could also be an *idealization*, which means that the conditions for the model to hold are never found in nature (for instance treating population sizes as continuous variables, with the possibility of 138.92 individuals). Thirdly a model can be *incomplete*, in that it leaves out one or more relevant variable. Models can be purely *phenomenological*; in that they are derived only to make predictions or descriptions, and that the parameters of the model are not given an explicit meaningful interpretation. One example of this would be classic models of allometric growth, the study of the how the rates of growth of different parts of the body relate to the body as a whole (Huxley 1932). This study includes a general model of allometric scaling, in which the interpretation of one of the parameters in the model "… is here of no particular biological significance,…" (Huxley 1932 p. 4), however see an attempt in White and Gould (1965).

Lastly, models can be false in the way that they give a "totally wrong-headed" picture of nature (where posited entities or properties do not exist) and, the classic; fail to *describe or predict data* correctly.

He then goes on to make a list of *functions* that false models can serve, "in the search for **better** ones*"* (Wimsatt 1987 p. 30, my emphasis), indicating that false models' highest virtue is in the search for better models. It is somewhat unclear what he deems to be better models, but the final test of predictability of data must surely be one of the standards 'better' models are held to. This list is too long for complete inclusion here (12 elaborated points), but a few notes on some of the merits of false models will be made. All of the merits of models already mentioned are in some form or another included in Wimsatt's list.

Wimsatt argues that, when it comes to arguments about optimization and adaptive design, an important aspect of evolutionary models, false models can be built with the explicit goal of being false. This is also noted by R. A. Fisher (1930; and others, e.g. Maynard-Smith 1982) who argued for, as an example, constructing models where species consist of three (or more) different sexes, to better understand why there are always two. Models like these are frequently made in studies of adaptation, where we need to consider why a particular attribute of an organism is adaptive by attempting to model a non-existent alternative, and show that they are likely to be maladaptive.

Another important role false models can play is to describe two ends at a continuum, where reality is supposedly somewhere in the middle, but also where this 'middle' becomes very complicated to both model and understand. One example related to this can be in our exposition in chapter IV (also in Levins 1968 use of an "adaptive function"), where the grain of the environment can be understood as being somewhere between the extremes of fine-grained and coarse-grained. Calculations and analysis of models where the 'grain' of the environment is somewhere in-between is slightly more complex, but there are some lessons to be learnt from just posing the two extremes, both of which are perhaps unlikely.

SELECTED TEXTBOOKS IN MATHEMATICAL EVOLUTION AND ECOLOGY

The utility of models in ecology and evolution is often mentioned in textbooks about modelling. How the use of models is legitimized in two books will be used as examples.

In John Maynard-Smith's now classic book on the use of game theory in evolution (Maynard-Smith 1982) he alludes to the different values of models. For instance about the Lotka-Volterra equations he states that, despite the fact that they "are manifestly false […] their merit is to show that even the simplest possible model of such an interaction leads to sustained oscillation." He here invokes the 'proving the possible' argument, in a mixture of Caswell's point 1 and 5 above. He also uses the same argument that Haldane uses, that mathematical models help us in our reasoning, because these sustained oscillations (i.e. cycles) of the Lotka-Volterra equations is a "… conclusion it would have been hard to reach by purely verbal reasoning" (Maynard-Smith 1982).

Maynard-Smith also notes on the Hawk-Dove game, a game that purports to be some representation of animal contests, that the game "… is not to represent any specific animal example, but to reveal **the logical possibilities** (for example, the likelihood of mixed strategies) inherent in all contest situations" (Maynard-Smith 1982, my emphasis). Here he is more ambiguous; he states that the models are not meant to represent any specific example, but still that they reveal *the* logical possibilities in *all* contest situations, which seems to imply that this model not only shows what is possible, but that it can map the space of the possible in its entirety for all contest situations. So this is a statement about both general models *and* the real world of contests.

He also talks about general theories ("evolution is the result of the natural selection of variations which in their origin are non-adaptive" (Maynard-Smith 1982, p. 8)) and specific theories ("theories which claim to identify the selective forces responsible for the evolution of particular traits or groups of traits."), and that general theories are not necessarily to be directly tested, but only tested through their relation to more specific theories or models. This is related to Fagerström's ideas on *proximate* and *ultimate* goals of models, but phrased in a sense that more general models have as a *proximate* goal to be used to develop more specific models, which can be directly tested, or at least give some predictions.

Mathematical Models of Social Evolution (McElreath and Boyd 2007) is a recent contribution to the growing textbook material for models of ecology and evolution. They start the book by stating that "simple mathematical models are experiments aimed at understanding the causal

relationships that drive important natural phenomena" (McElreath and Boyd 2007 p. 1), perhaps purposefully vague. But they continue to list four different ways simple models can "aid our understanding" of the world. One of them is of course to give rise to predictions, to be tested against the natural world. But the other three points are worthy of mentioning.

Models can provide existence proof. This is at first glance the same as Caswell's point (1) (exploring the consequences of theory) and Maynard-Smith's revealing of logical possibilities. They continue on these existence proofs that "they provide proof that some candidate set of processes *could* explain the observations of interest" but they go further than others by stating that existence proofs also "narrow down the fields of possibilities". It seems like models can not only prove the possible, but also proving the impossible. This is a conjecture I am not convinced by; a model can prove that something is in principle possible in the real world, but it can not prove that something is *not* possible in the natural world. It *can*, however, prove that something is not possible *in the model*.

One example from evolutionary biology that serves to illustrate that models should not be seen as delineating what is *impossible*, is the history of reinforcement in studies of speciation. Reinforcement is the idea that prezygotic isolation is enhanced by natural selection in sympatry (Coyne and Orr 2004). Put simply, imagine two seemingly different species where there is some level of hybridization, but these hybrid have a reduced fitness, will then natural selection lead to behaviour that reduces this hybridization? Decades ago, this was thought to be, not only possible, but also probable. In fact, Dobzhansky even thought that such selection against hybridization represented a nearly obligate step in speciation (Coyne and Orr 2004, p. 353), and its importance was also highlighted by others (e.g. Lewontin 1974). The acceptance of the theory of reinforcement fell dramatically in the late 1980's, not because of lack of empirical support, but because of an interpretation of models in which it

was unlikely to occur, as showing that the process was unlikely in the real world (e.g. Spencer, McArdle et al. 1986; see also Noor 1999; Marshall, Arnold et al. 2002). Again, as commented on by Andrewartha and Birch (1954), people mistook conclusions from models to apply directly as conclusions of the world. After the decline of the appreciation of the importance of reinforcement in speciation, it rose to prominence again in the 1990's and later, because of a combination of more models *and* data (Noor 1999; Marshall, Arnold et al. 2002; Coyne and Orr 2004).

McElreath and Boyd (2007) also list the concept of 'counterintuitive results' as a way that models can aid our understanding of the world. This can, just as Caswell's point 5, be seen as a subset of proving the possible, just that the possible was not really what we would have guessed before the model was built and analysed. Though counterintuitive results are often highlighted in the literature, it is important to remember that what was once considered counterintuitive can quickly become so obvious to scientists that this particular value is no longer seen. Again, Fisher's proof that continuous variation can come about through inheritance of discrete genetic elements (Fisher 1918), was by many seen as counterintuitive when it was published, but it has been accepted as both intuitive, expected and not particularly surprising since the modern evolutionary synthesis (Mayr 1982).

The last, and extremely important way models can help us to understand the natural world, has little to do with the natural world (except perhaps its complexity) and more to do with us; models are of great aid in communication. This is an extension of the 'models as externalized logic' argument; not only do models make logic easier because we can do it on a piece of paper or in a computer, but it can also make it a lot easier to communicate our logic to other scientists. As an example; in a quick survey on the use of the concept of stability in ecology Grimm, Schmidt et al. (1992), found more than 40 different uses of the word stability.

Though one might argue that we shouldn't need over 40 different uses of *one* word, it becomes much clearer within any given context, if the particular notion of stability one is referring to can be algebraically defined within a particular model.

THE MINIMAL VIEW OF MODELS

We have now chartered some of the ways to legitimize the pervasive role of theory or use of models in ecology. In doing so, we have covered some ideas on how models are built (Levins), what models can contribute with (Haldane), what are legitimate theoretical pursuits with models in ecology and evolution (Caswell), certain characteristics of successful theories/models (Fagerström), what are basic purposes of models (Odenbaugh), what is the use of false models (Wimsatt) and lighter versions of how model use is introduced in some textbooks.

The criticisms of the use of models in ecology and evolution presented, and their responses can be categorized according to how the charge was interpreted. I see the complaints of Simberloff (1981; 1982), Peters (1976; 1978; 1980; 1991), Andrewartha and Birch (1954) and others as being composed of *two* different claims. The first claim is that models tell us very little about the real world, and the other is such modelling activities are not legitimate parts of either ecology and evolution (Mayr 1963; Simberloff 1981) or science at large (Peters 1991). Most of the responses are methodological; i.e. they respond by claiming that models are legitimate *tools* we use to do science. Models can be used as conceptual frameworks (Odenbaugh), as ways externalize our logic (Haldane and others) or that general mathematical models can be used to analyse other models (Caswell). These are all arguments that are not directly related to telling us anything at all about the real world. Models as valuable tools (see particularly Cooper 2003), is a response to the charge that models are not legitimate parts of ecology and evolution. The perspective of models

as tools is, however, not responses to the charge that many models say very little about the real world.

That some models can be used to make predictions that can be tested is one response (which is often what the critics ask for), the second response that deals with what we can learn about the real world from our models is proving what is possible. This is, admittedly, a weak kind of prediction, and for some it is not to be considered a prediction at all (Peters 1991). However, we have also given quite a few examples where such *proof-of-principle* have been instrumental in the history of ecology and evolution (Fisher's continuous variation from discrete Mendelian genes, Hamilton's kin selection models), and there are numerous others.

My personal philosophy of models is based solely on this idea of proving what is possible, and I term this a Minimal View of Mathematical Models. In encountering any scientific (or unscientific for that matter) exposition where one uses *any* kind of mathematical model, I am not willing to interpret the model as 'putting probabilities' on the world at all.

This is in opposition to both of our textbook examples, where the authors seem to mean that some models can charter *all* possibilities in the real world (Maynard-Smith 1982) or be used to show *impossibilities* in real systems (McElreath and Boyd 2007). My view of mathematical models in ecology and evolution is that even though the structure of the model is *similar* to the real world, we can never know how similar it is, or in which exact way it is similar. This means that any conclusion from a model needs to be taken with more than a pinch of salt, and that, if the assumptions of a model are not extremely unreasonable (as in Wimsatt's "totally wrong-headed picture of the world"), the only conclusion we can draw is that the world *could* work the way our model does, and therefore the conclusions of the model *could* hold in real systems. If something is impossible in a model, it *could* be impossible in the real world, but this is, at least in my perception, a less useful conclusion.

The Minimal View of Models is a pragmatic perspective that attempts to draw lessons from the history of our field. It does not accept that *impossible* or *unlikely* in a model corresponds to *impossible* or *unlikely* in the world. How certain models of reinforcement led many to believe it was unlikely is an example of why; a premature dismissal of a particular mechanism as unlikely when it turn out to not be that impossible after all. The Minimal View is also consistent with the implications of Beatty's contingency thesis; by not posing statements pertaining to be generalizations that are expected to hold (i.e. putting probabilities on the world), but to keep such statements as possibilities, give room for the idea that natural selection can break down any generalization. Whether a mechanism, pattern or any other model output holds for a particular system is up to empirical investigation.

It is important to realize that such a view of models does not diminish most of the other purposes or legitimate pursuits explicated by the authors above. Haldane's idea of externalizing our logic, Caswell's ideas of demonstrating the link between apparently unrelated models and developing mathematical methods for the analysis of models, Odenbaugh's ideas of models as conceptual framework (and most of the other points raised above) are all compatible with the Minimal View. In fact, most of the points raised by the defenders of mathematical models rest on (minimally) such a Minimal View; that the similarity between a model and the real world is in such a way that a conclusion of a model *can possibly* hold for a real system. Levin's idea of robustness does *not* make the conclusions from these models more likely to hold for real systems, but they increase our certainty about the *possibility* of these conclusions to hold.

This Minimal View of mathematical models as *only* proving the possible is still subject to Peters' critique of them being *de facto* tautologies. Either predator-prey systems show oscillations OR they do not show oscillations. I am personally not so worried about this charge. From a historical perspective, we have seen that just proving the

possible can have a substantial effect on the development of a field. Others have also expressed similar attitudes and that the charge of tautology is perhaps over-emphasized (Sober 2008). Taking the tautology "It is raining, or it is not raining" as an example, if we initially had no idea that it actually could rain (and particularly if the common belief was that it was impossible), such statements are of immense value.

It should also be noted that the Minimal View does not mean that there are no ways to put probabilities on the world, i.e. to argue for a process, mechanism or pattern to be probable. It only states that a model alone can not do this.

In summary: Mathematical models provide ecologists and evolutionary biologists with *proof* of the possible, and any conclusion about the real world over and above this must be based on empirical studies. Models do, however, serve important functions as *tools* for ecologists and evolutionary biologists which are legitimate parts of the fields, even without directly making predictions.

THESIS OVERVIEW

The models in this thesis deal with dispersal and diversification. Dispersal is often defined as 'movement that potentially leads to gene flow' (e.g. Ronce 2007), i.e. movement of any kind of individual (adult, young, seeds or gametes) that can change the spatial structure of genes in a population. In many ecological studies, however, the emphasis will not be on the distribution of genes or alleles, but focus more on the moving individuals themselves. The first chapter deals with dispersal in a more ecological sense, by focusing on the presence and absence of individuals, without incorporating genetics. The second and third chapters deal with the evolution of dispersal and are more in line with the definition above.

By diversification I intend that genotypes, in one way or another, diversify the phenotypic

expressions (i.e. that the genotype-phenotype map is 1 to many). For instance, in the models in chapter II and III, a particular genotype can be seen as giving rise to individuals that differ in the phenotype relevant to movement. In chapter II we explicitly vary the way this diversification is achieved; if dispersal is under maternal control her genotype will 'diversify' her offspring with regard to how far they disperse. If, on the other hand, dispersal is under offspring control, this diversification is achieved as a randomization within the individuals themselves, with two individuals of the same genotype potentially dispersing different distances. Chapter III concludes with a simple model in which dispersal is modelled as a tendency to leave a natal patch; dispersal decisions can either be randomized individually among offspring, or a mother can opt to encase a certain fraction of her offspring with dispersive traits, with such 'homeostatic' dispersal strategies often being adaptive. In chapter IV we develop a general population genetic model in which a particular kind of diversification is investigated; diversification that is selected for by virtue of reducing the correlations between individuals of the same genotype (bet-hedging).

REGULATION OF INVASIVE SPEEDS

Invasive or exotic species are organisms that, for some reason, have managed to arrive at, establish and spread in areas outside their 'natural' range. Such species are in many cases seen as unwanted, often due to their potential of having a negative effect, particularly reducing local biodiversity (Clavero and Garcia-Berthou 2005) and having severe economic impacts. Ecological studies of invasive species have risen remarkably the last decades (Puth and Post 2005), no doubt because of a combination of ecology's recognition of having to solve environmental problems and the fact that more and more such species have a detrimental effect on the natural world.

Despite a general increase in research on invasive species, it has proven difficult to come up with generalities that can be used to predict success of invaders or susceptibility of communities to invaders (Ehler 1998). Recently, Arim, Abades et al. (2006) presented an empirical investigation of invasive species that showed a remarkably consistent pattern of invasions across a wide range of different taxa of invaders and communities invaded. The idea was that species invasion can be characterized by a particular speed or rate of invasion and, they argued, this rate was a regulated process. Regulation in this context is akin to the regulation of a thermostat; if there is too much of something it will decrease and if there is too little it will increase. So the regulation of invasion speeds would be the case if too speedy invasions were slowed down and too slow invasions were speeded up. The implications of this pattern could have a direct effect on what appropriate measures one should use to avoid the further invasion of an unwanted species; if we attempt to slow down an invasion, the species might just respond by increasing the speed of invasion.

This was in fact what Arim, Abader et al. (2006) found for 30 distinct invasive species, ranging from mute swans, through water hyacinths to foot-and-mouth disease. They claimed that this evidence showed that invasions are a regulated process and that they had manage to show a general pattern of invasions, in contrast to the view of invasion as idiosyncratic phenomena (Shrader-Frechette and McCoy 1993; Ehler 1998).

We took notice of this article and were interested in finding out how this regulation at the level of the invading front of the population could actually work, i.e. we had plans for making mechanistic models focusing on the individuals that an invasion consists of, and perhaps figuring out what were some of the possible processes or mechanisms that could bring such a regulation of invasion speeds about. One prominent alternative to explain the pattern would be Allee effects, that small populations (i.e. recently invaded areas) can have a tendency to exhibit slow or even negative growth. However, we noticed something very different.

As pointed out by both Caswell and Odenbaugh above, we started our search for how this regulation could come about through making the simplest of models, in the hope that we could extend these to more complex models in which some mechanism would create regulation of the speed. We developed two simple models of species invasions to simulate data to be analysed in the same way as Arim, Abades et al. (2006). The classic argument of robustness (Levins 1966; Wimsatt 1987; Caswell 1988) was the main reason for making two models with different assumptions. Both of these models were run to create patterns of the invasions, analysed in the same way as Arim, Abades et al. (2006), where there were no mechanisms in the model that could be said to plausibly create regulation of the invasion speed. And in fact, both of our models show patterns that would be interpreted as regulation using the measure of speed defined as in Arim, Abades et al. (2006), without any plausible mechanism generating regulation. Similar results have also been found by De Valpine, Cuddington et al. (2008). The main conclusions from this article is that more thought needs to be put either into the development of *proper* measures of invasion speed where regulation might be detected or other ways of analysing the invasion speed (as defined in Arim, Abades et al. 2006) to detect regulation.

Since it is hard to think about speed (as defined) in even with the simplest of invasions, our models can serve as an *externalization of our logic*. Where my abilities to reason stop, a mathematical model can help, and in this case it has helped us to realize that with this particular measure of invasion speed, detection of regulation is not as easy as presumed in Arim, Abades et al. (2006). By using these models as an aid in our reasoning, we showed that the patterns discovered *could* actually be explained by *how* the measure of speed was defined, instead of indicating regulation of any sort. Note that our findings do not mean that species invasions *are not* regulated, but that the analysis of Arim, Abades et al. (2006) is not sufficient to detect it.

CONFLICT OVER DISPERSAL DISTANCES

Dispersal is often defined as 'movement that leads to gene flow', i.e. movement of individual adults, juveniles, eggs, seeds etc. that affect the spatial structure of the genetic composition of a population (see for instance Ronce 2007). Often such movement is seen as risky; by moving out of the habitat one is born in, the probability of surviving decreases and the fitness of the moving individual is believed to be reduced, hence adaptations for such movement should be selected against (note that this verbal reasoning can also be considered a model). One of the major contributions from mathematical models of dispersal has been to show that there are a number of mechanisms (or factors) that *can* lead to such adaptations, despite the fact that such movement is risky (see Clobert, Danchin et al. 2001 for an introduction). This is yet another example of models proving the possible; by showing that certain plausible mechanisms *can in principle* lead to the evolution of seemingly costly traits.

The factors that have been proposed as selecting for dispersal are kin competition, inbreeding, resource competition and environmental variability (for a review see Bowler and Benton 2005). Some level of dispersal is favoured over complete philopatry if competition between kin is local; by dispersing the negative impact of one individual's presence on related individuals with whom it shares some genes will be diminished (see e.g. Hamilton and May 1977; Frank 1986; Frank 1998). Dispersing away from natal patches can also be favoured to decrease the chance of mating with related individuals which leads to inbreeding (e.g. Perrin and Mazalov 1999), often thought to have negative fitness consequences.

In kin selection theory, one often imagines individuals maximizing inclusive fitness (Hamilton 1964a; Hamilton 1964b; Frank 1998; McElreath and Boyd 2007), where an individual's inclusive fitness will be its own regular fitness, plus the fitness of related individuals, weighted by their relatedness. In other words, my inclusive fitness

does not only include my own offspring, but also my brother's offspring discounted by our degree of relatedness (Hamilton 1964a; Hamilton 1964b; Grafen 1985; McElreath and Boyd 2007). In such a perspective, which individual mechanistically controls the development of these dispersive traits is of importance. When investigating the evolution of dispersal in higher plants, adaptations for dispersal occurs through the development of the maternal tissue surrounding the fertilized egg, which is determined by the genome of the mother plant. However, in most mobile animals, it is more likely that dispersal strategies are primarily determined by the genotype of the dispersing animal itself. The inclusive fitness calculations will in models of dispersal differ between these two perspectives (Grafen 1985; Frank 1998); in the perspective of the mother, all seeds have the potential to contribute equally to her inclusive fitness, whereas if individuals control their own dispersal, their siblings (indirect fitness) are not weighed as much as their own (direct) fitness.

Considerations of the relatedness structure have led earlier models of dispersal evolution to show that there can be a parent-offspring conflict over dispersive traits (Motro 1983; or a 'battleground', Godfray 1990). It is termed a conflict since the optimal dispersal behaviour differs between a maternal and an offspring perspective; in general dispersal by individuals determined by their parents (as in plants) favour higher rates of dispersal, compared to similar circumstances where the individuals determine their own propensity to disperse (as expected in most animals). These models investigate the evolution of dispersal rates, where the spatial structure of the population is *implicit*, i.e. that the population is modelled as consisting of a large number of patches, and that dispersal occurs through leaving a focal patch and potentially land in *any* other patch (e.g. Motro 1982a; 1982b; 1983). Such a scenario is often construed as unrealistic and that we should also model dispersal in a spatially *explicit* context, where all patches are not equally 'connected' (Travis and French 2000; Ronce 2007). In such contexts, dispersal

propensities are usually modelled as dispersal kernels, which are distributions that determine the probability of an individual moving a particular distance (Travis and French 2000; Rousset and Gandon 2002; Ronce 2007).

In the models presented in chapter II we investigate the potential for a parent-offspring conflict over dispersal distances, using different dispersal kernels. Again, robustness arguments led us to develop two models that differ in how the distribution of dispersal distances is implemented. In the simplest case, an individual's probability of moving a particular distance is controlled by a single diploid locus, determining the mean value of an exponential distribution. In the more complex model, we introduce 10 loci each determining an (unscaled) probability of moving a particular distance. Both models yield the same conclusion; there *can* be a conflict over dispersal behaviour, when dispersal is modelled in a spatially explicit context. Again, arriving at such a conclusion without the use of a mathematical model in our reasoning would be quite the challenge.

THE MULTICAUSAL NATURE OF DISPERSAL

The multicausal theory of dispersal is a semantic view of the theory of dispersal (Lloyd 1988; Thompson 1989), where *the* theory of dispersal is considered the collection or family of models that deal with the phenomena of dispersal and the interpretations of these models. The relation between these models is not *axiomatic*, i.e. they can not all be derived from a common set of true assumptions, but they are related semantically; what we intend by dispersal as defined verbally can be put into models in different ways. In some models dispersal is formalized as a rate of leaving a patch, in other models it can be seen as a dispersal kernel (as in chapter II) and in yet different models, dispersal can be used to denote the strategies by which individuals decide to stay or leave a particular patch. This manuscript charters some of these models, and focuses particularly on how ideas of causality are used in

dispersal theory. In addition we highlight that, even though models come with interpretations, for some models several different interpretations are valid.

In evolutionary thinking causes are usually categorized into *proximate* and *ultimate* (Tinbergen 1963; Mayr 1988). An individual might move out of a particular area because of the sudden appearence of a threatening predator, and the presence of this predator can be seen as a proximate cause of this movement. On the other (ultimate) hand, if such predators become more common over a long enough period of time, it can also be seen as an ultimate cause of the evolutionary changes in how these prey individuals respond to the presence of predators.

In addition to the ultimate/proximate distinction, causes can also be said to be either deterministic or probabilistic. The sight of a predator can either *always* make an individual move (deterministic) or it can *increase the probability* that it moves. All of these notions of causality are invoked in models of dispersal. As an example Travis, Murrell et al. (1999) construct an evolutionary model (*ultimate* causation) where individuals have a particular probability of dispersing (*probabilistic* causation) depending on the density in the patch they are born in (*proximate* causation).

We also emphasize that models are more than just the mathematics; models come with interpretations as well, and that in many models dispersal is implemented in ways that can be interpreted in more than one way. For instance, in some evolutionary models of dispersal rates, these rates are often interpreted as the fraction of individuals dispersing from a single patch, the fraction of offspring of an individual that disperses or the probability of a given individual to disperse (e.g. Hamilton and May 1977; Frank 1986; Frank 1998). A small simulation model is constructed to show that, while these different interpretations are valid for some models, they can be teased apart in other models. This model also functions as a *proof-of-principle* of the idea of dispersal homeostasis, where selection favours that offspring

are divided into fractions that disperse or stay philopatric, instead of letting dispersal propensities be probabilistic for all these offspring. Thus the causality of dispersal itself (probabilistic or deterministic) is considered to be under evolutionary change. In addition to proving that dispersal homeostasis can work, the model also serves as a robustness check (see Levins section, and Caswell's (4)) on earlier models predicting rates of dispersal (Hamilton and May 1977; Motro 1982a; Frank 1986; Frank 1998).

BET-HEDGING; MEANS, VARIANCES AND CORRELATIONS

When the returns of an investment are uncertain, putting all your money in one single stock is unwise; instead diversifying the investment is recommended to minimize risk of losses. For instance, a classic recommendation in the financial literature is to diversify one's investments in assets whose expected returns are negatively correlated, e.g. buying stocks in an company selling umbrellas and one selling ice-cream (e.g. Brealey, Myers et al. 2001 p 272ff; Penman 2003 p 649-650). The main effect of this is to reduce the variability of the total profit; the variance in the payoff of your investment will decrease, since periods when one stock does badly the second one goes up. In other words, it's not always wise to put all your eggs in one basket.

Similar mechanisms can be at work in evolutionary thinking; just as variance in financial investments is unwanted, so can variance of fitness be detrimental for the success of a genotype. These ideas have lead to the concept of bet-hedging (Slatkin 1974; Seger and Brockmann 1987; Philippi and Seger 1989); that strategies with a reduced variance in fitness can invade a population consisting of individuals that *on average* do better. One way to achieve this is through phenotypic diversification. In the same way as investments in different stocks reduces variance in total financial payoff, a genotype that gives rise to different

phenotypes which have uncorrelated fitnesses also achieves a lower variance in genotypic fitness.

In this conceptual review we use a population genetic model to show how variability in fitness at the level of the genotype can be broken down into variance at the level of the individual, and correlations among individual fitnesses. We highlight that variance in fitness has effects both for short-term and long-term evolutionary changes, and that bet-hedging theory can more easily be understood when the variance in *genotypic* fitness is separated into variance of fitness at the level of individuals and the correlation among these individuals.

The general model can be seen as a *conceptual framework* (in the sense of Odenbaugh), whereby the breakdown of genotypic variance into a product of correlation and variance among individuals gives a clearer mathematical underpinning of two classic ways to categorize (i.e. conceptualize) bet-hedging strategies (conservative vs. diversified, and within-generation vs. between-generation). The general model is also used to show that both of these categorizations are in fact false dichotomies and are better viewed as ends at two continua along which bet-hedging strategies can be placed. As such the model also suggests that this separation of correlation and individual level variance can be used as a way to better understand, if not analyse other more specific models of bet-hedging (for instance models that are developed to investigate the potential for bet-hedging in dormancy, ovipositioning or dispersal), in line with the comments made by (Maynard-Smith 1982) of a division between general and more specific theories.

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