BUTTERFLY METAPOPULATIONS IN DYNAMIC HABITATS

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Abstract

Many species require habitats that are naturally patchily-distributed and ephemeral, but human activities fundamentally alter the rate and scale of habitat change. This thesis describes the development of a new metapopulation simulation model applicable to a broad range of species that depend on dynamic habitat. I apply the model to two case studies, both involving butterfly species that use early-successional habitats and that are UK Biodiversity Action Plan priority species. I describe two methods for parameterising the model for a particular metapopulation in a particular landscape. One method uses parallel disturbance and population presence data for a few consecutive years; the other derives population parameters and landscape parameters from separate data sources.

In the first case study, I found that the BAP target for Heath Fritillary (*Melitaea athalia*) populations in the Blean Woods, Kent, could either be met by approximately doubling the coppicing effort, or by concentrating the existing effort into one of the larger woodland blocks. In the second case study, I found that the rate of heathland burning in the South Stack area of Anglesey was not enough by itself to sustain the metapopulation of Silver-studded Blues (*Plebejus argus*). However, the metapopulation is probably saved from extinction by the existence of permanently-suitable habitat close to the coast.

I have also elucidated an important phenomenon in metapopulations with dynamic habitat: the relationship between patch occupancy and patch connectivity can be obscured by the temporal changes in habitat. This has important implications for the debate about whether many real populations actually fit the metapopulation paradigm because the existence of metapopulation dynamics is often determined by testing the connectivity-occupancy relationship.

The simulation model, "MANAGE", is an important new tool for integrating landscape-scale information, and answering conservation questions, in a field which is relatively new and unexplored.

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Declaration

The material in this thesis is my own work except where specific references have been given to the work of others. Where data have been obtained from external sources this is specified in the text and in the acknowledgements.

The simulation model MANAGE was designed jointly by me, Chris D. Thomas (University of York) and Atte Moilanen (University of Helsinki), based on an original idea by CDT. AM wrote the model in C++. I then tested the model extensively, which led to successive rounds of editing by AM and later by me. I re-wrote a large proportion of the code controlling habitat dynamics.

1 General introduction

1.1 Rationale

An organism's habitat is rarely completely stable over time. Monophagous herbivores, parasites, mutualists, epiphytes and commensals, as well as species adapted to a narrow successional stage, can be faced with habitat that is never in the same place for more than a few generations at a time. Invertebrates associated with very early and very late successional stages appear to be over-represented among declining and threatened species in Britain, and their declines are often associated with changes in human land-use and land management (Thomas *et al.* 1994). The survival of a species on a dynamic landscape is not a simple function of the amount of habitat available – the rates of habitat creation and destruction, variability in these rates, and aggregation of habitat in space are also key variables. This generates difficulties in understanding the dynamics of such species and complications in the development of conservation management plans. Dynamic simulation models can help us to understand such complex systems. In many cases, habitat creation and/or destruction will occur as discrete patches, and so it seems natural to use a metapopulation framework for modelling. If they are on an appropriate temporal and spatial scale, and use informative parameters, these models can be employed in planning management for conservation. Although some dynamic landscape metapopulation models have already been published, there is a noticeable gulf between heuritsic models that are not applicable to any particular species or landscape, and highly specific models that require a huge amount of species- and landscape-specific data. I have attempted to bridge the gap between these models by designing a model which is as simple as possible while still having the potential to answer the questions that conservation managers are most interested in.

1.2 Metapopulations

A metapopulation is a collection of local breeding populations of one species separated by space but linked by dispersal (Hanski & Simberloff 1997). Although each of the subpopulations may be vulnerable to extinction, the chance of re-colonisation can give the whole metapopulation stability and a low extinction risk (Levins 1969, 1970).

To study metapopulations is to study the importance of space, and spatial heterogeneity, to populations. Natural ecosystems are strikingly patchy, and this can have implications in all aspects of ecology, an idea which was by no means new when metapopulation theory was first developed. Evolutionary ecology was perhaps the first discipline to formalise spatial heterogeneity; such formalisation was necessary to explain for example the maintenance of clines in allele frequency and the genetic isolation that leads to speciation (Fisher 1930). At the other end of the temporal and spatial scales, behavioural ecology developed theory for optimal foraging, recognising that almost everything animals search for is patchily distributed (MacArthur & Pianka 1966; Wiens, J. A. 1976). Then Island Biogeography Theory (MacArthur & Wilson 1967) paved the way for a generation of research with its very simple model of a balance between extinctions and colonisations that determines the composition of a community. The first studies of metapopulation-like systems concerned the factors that contribute to the stability of natural enemy interactions. Huffaker's (1958) study of predator and prey mites in a universe of oranges showed that extinction could be avoided by restricting dispersal so that populations on different oranges peaked at different times. Monro (1967, cited in Wiens, J. A. 1976) documented the unsteady equilibrium between introduced *Opuntia* cactus and *Cactoblastis* moths introduced to control them in Australia: some isolated stands of cactus always manage to 'keep ahead' of moth outbreaks. The latter study reveals an early recognition that the distribution of habitat can change with time – a possibility that subsequent metapopulation models have tended to ignore (but see later).

Metapopulation biology has been a fertile area of research in the last two decades: Hanski and Simberloff (1997: their figure 1) showed the boom in publications from 1990 to 1995, and this growth has continued (there were 73 publications in 2006 that cited Levins' (1969; 1970) original metapopulation model, and 286 publications in 2006 with the topic "metapopulation" on the ISI science citation index). The simple (deterministic and continuous) mathematical approach of Levins (1969; 1970) has proved amenable to numerous variations that make it more biologically realistic (e.g. Hastings 1991; Tilman *et al.* 1997; Sjögren-Gulve & Hanski 2000). One adaptation that has been studied extensively is the incidence function model (Hanski 1994). The incidence function model (or IFM) is a spatially explicit metapopulation model where one summarises the habitat as a number of discrete patches, specifying their centre points and their areas. It then assumes that:

- population size in a patch is a simple function of the patch area;
- emigration rate from a patch is a power function of area (the surrogate for population size), but otherwise emigration doesn't affect the home patch dynamics;

- the frequency of dispersal declines exponentially with distance away from the home patch;
- therefore the number of immigrants to a patch can be calculated from the size of all the other patches and their proximity, and number of immigrants to an empty patch determines colonisation probability;
- extinction probability of a patch depends on population size, and, if there is a rescue effect, on number of immigrants, but otherwise immigration doesn't affect the recipient patch dynamics.

A major advantage of the IFM is that it is to some extent analytically tractable: one can calculate the invasibility and equilibrium occupancy of a patch network (Hanski & Ovaskainen 2000; Ovaskainen & Hanski 2001), the relative value of each patch (Ovaskainen & Hanski 2003) and the time scale of recovery from perturbation (Ovaskainen & Hanski 2002).

Although numerous species experience naturally fragmented, patchy habitat (Dobson 2003), metapopulation theory has frequently been discussed in relation to the conservation of species in habitats fragmented by human land use change. It has given new insights to conservation scientists, who are now concentrating more on the whole landscape scale and the linkages between populations (Harrison 1993; Sutherland 2000). There are a number of examples of the IFM and similar models being used to aid conservation decisions (Hanski & Thomas 1994; Gutierrez *et al.* 1999; Gutierrez 2005; Hoyle & James 2005; Schtickzelle *et al.* 2005).

A patch occupancy metapopulation model such as the IFM (which only sees patches as either full or empty) offers an attractive, solid and simple way of thinking about spatial relationships between populations. But it also offers some immediate puzzles to an ecologist wanting to test the theory's relevance to real populations. Firstly, the theory demands that we define the habitat of our organism of interest; we must know its biology well enough to tell the quality of habitat even when the organism in question is not present (a key prediction of metapopulation theory is that some suitable habitat will always be unpopulated). The most famous examples of metapopulations are backed up by considerable natural history knowledge of the study species (Baguette & Mennechez 2004). Secondly the theory demands a way of linking an observed pattern of presence and absence to the processes of colonisation and extinction. (For example is high occupancy due to high colonisation or low extinction? Is there a rescue effect? Is the metapopulation far from equilibrium?) Hanski (1994) recommends that a metapopulation be characterised by at least 2 time points of presence-absence (i.e. a chance of observing colonisations and extinctions) and also some mark-release-recapture data on the extent of dispersal between patches. Moilanen (2002) shows by simulation experiments that different kinds of data inaccuracy can have different implications in terms of (mis)understanding metapopulation persistence. The most misleading kind of data inaccuracy seems to be undetected presences of the species (Moilanen 2002). Knowledge of the species' history in the study area will help to decide whether metapopulations are likely to be at equilibrium (e.g. Has it recently been introduced? Has there been recent severe habitat loss?), and therefore whether the colonisation and extinction parameters can be estimated from the patch occupancy (Moilanen 2000).

There has been considerable debate about the risks of applying metapopulation models in situations where they are not relevant (Harrison 1993; Baguette 2004; Hanski 2004). The assumptions of patch occupancy models are most applicable to species with fast population growth rates and simple behaviour. Accordingly they have been applied mostly to insect populations, and also to amphibians (Tscharntke & Brandl 2004; Cushman 2006). Plants, which seem obvious candidates, tend more often to be modelled with the view that one patch is space for only one adult individual. Much debate has focussed on the simplifying assumptions that metapopulation models make about dispersal (Ims & Yoccoz 1997; Van Dyck & Baguette 2005). Different dispersal kernels (functions describing the distribution of dispersal distances from the natal patch) are advocated by different authors, but the choice of the dispersal kernel probably makes only minor differences to model predictions in most cases (Moilanen & Nieminen 2002). Much more damaging to the reliability of metapopulation model predictions would be the existence of absolute dispersal barriers in the landscape, or certain kinds of complex dispersal behaviour (e.g. dispersal only in response to overcrowding or environmental conditions, Bowler & Benton 2005). Patch area is not always a good correlate of population size if there are large differences in habitat quality between patches, but actually it is straightforward to include habitat quality in metapopulation models, and this can lead to better predictions (Thomas *et al.* 2001; Franken & Hik 2004).

The validity of the assumptions of metapopulation models also depend on the spatial distribution of habitat: they work best if habitat is a small proportion of the landscape, and quite fragmented (Hanski 2004). The reason for this goes to the heart of the metapopulation approach: the separation of scale between the local and regional population processes. When applying metapopulation models to real landscapes, one is sometimes faced with a large, heterogeneous patch that could be considered as several smaller patches. If it is modelled as several patches, one ignores the fact that density-dependence might synchronise the population fluctuations, making the whole complex more likely to go extinct at once. On the other hand, if it is modelled as one patch, one ignores all the dispersal that goes on between the sub-patches (Cizek & Konvicka 2005). It is often left to "biological expertise" to determine the suitable spatial scale at which to study a population, but the same population viewed at different scales can fit different theories (Menendez & Thomas 2000). If the spatial scale of interactions that affect individuals' mortality and fecundity largely overlaps with the spatial scale of inter-patch distances, then a patch occupancy metapopulation model is not really appropriate, and one may need a model that considers continuous space (Thomas & Kunin 1999).

It has been suggested that a "classical" metapopulation model tends to work best for populations occupying early-successional habitats (Harrison 1993). Species adapted to early successional habitats should be adapted to a high likelihood of population extinction, and to having to colonise new habitat as it appears. Arguably it would be better to model such populations including the landscape dynamic processes that must interact with them, and this adds another level of complexity to theory and models. 'Landscape dynamics' covers a broad range of phenomena: events that make patches of habitat more or less suitable for a species could be very stochastic (e.g. landslides) or almost deterministic (e.g. depletion of nutrients), sudden or gradual, manmade (e.g. coppicing), biotic (e.g. disease outbreaks, shading by trees), or environmental (e.g. flooding), or a combination of these. In the next chapter I provide a thorough review of dynamic landscape metapopulation models that have been published so far, before introducing the new model developed as part of my research, which can be used to investigate the effects of different disturbance regimes on population persistence in a landscape of interest.

1.2 Habitat quality

In the previous section I have mentioned habitat patches, and habitat quality in the context of metapopulation models. However, it is not a trivial question to ask what defines habitat (Morrison & Hall 2002), and how habitat quality can be measured, in theory and in practice. Most metapopulation models consider space with a binary distinction between habitat and non-habitat (Hanski & Simberloff 1997). Designating somewhere as a habitat patch for the purposes of a patch occupancy model only makes sense if the patch contains all of the resources necessary to support a local breeding population (otherwise the concept of having an extinction probability and a colonisation probability associated with the patch does not make sense). This means that defining habitat patches for a species can become a complex, multivariate problem: What factors does the species really respond to? How close do different habitat elements have to be to each other? How small does a patch have to be before it cannot support a population? Some of these questions can only ever have approximate answers. In practice habitat is usually defined by choosing variables that are likely to be important based on the species' natural history, then making numerous observations of how well these variables correlate with the species' presence in sites (O'Connor 2002). For variables that have a correlation with presence but no clear threshold, a threshold must be imposed in order to define discrete patches of habitat.

Using a continuous measure of habitat quality removes some of the problems inherent in the binary approach, but introduces others. For a patch occupancy metapopulation model, quality should be a measure of the average population density of a site, given that it is occupied. Then, the smallest possible patch becomes one whose quality multiplied by its area (average population size) is less than 2 (or some other sensible extinction threshold). Note that for some of the analyses in this thesis, I refer to the patch quality multiplied by the patch area as the "carrying capacity". This is not conceptually the same as the carrying capacity parameter in a model of population numbers – my "carrying capacity" is simply the size of the population when it is present, and this size may fluctuate randomly but reproduction and death are not modelled.

Measuring population density is generally more difficult and time consuming than measuring occurrence. Population densities can fluctuate enormously from year to year, so several years of measurements may be needed. It is necessary to identify variables that are predictive of the average population density in order to impute the quality of unoccupied sites. Also, if habitat variables fluctuate less than the population density, then one may be able to filter out the noise of unpredictable population fluctuations by basing the measure of habitat quality on the habitat variables. Recall that in a patch occupancy model, quality only matters insofar as it affects the average extinction risk of a population, and the average number of emigrants from it. For some species and some landscapes of habitat, this will be an unreasonable simplification, and the exercise of trying to measure habitat quality may reveal where this is the case. For example, if there is a strong element of source-sink dynamics (Pulliam 1988), the quality of habitat will appear to change depending on the quality of neighbouring habitat. It might still be possible to model this system by treating a source and its adjacent sinks as a single patch with intermediate quality, but if not, a more complex model will be needed.

For successional species, we expect the quality of a habitat patch to change over time, so it becomes very important to quantify habitat quality in order to model the metapopulation dynamics. Unfortunately, there is an extra hurdle to measuring habitat quality in a dynamic system: the population density is likely to be affected by the quality in previous years as well as the present quality. One way around this is to fit extinction, colonisation and quality parameters in a single analysis (see chapter 3): effectively asking what quality values would be capable of giving the observed extinction rates at different successional stages.

1.3 Conserving habitats by managing succession

The aims of conservation management are often expressed in terms of maintaining habitats and/or improving their quality for various species (Morris 1991). There has been a long-standing recognition (e.g. Westhoff 1970), but perhaps less quantification, of the benefit of habitat diversity: a variety of habitat types in a patchwork fine-grained enough that organisms can easily disperse across the boundaries. In Britain (and other European countries) conservation management often equates to halting succession or creating certain kinds of successional cycle (Morris 1991), and the proximate reason for this is that it mimics pre-industrial land management practices, to which our native species became adapted, sometimes over thousands of years. Invertebrates associated with very early and very late successional stages appear to be over-represented among declining and threatened species in Britain (Thomas *et al.* 1994). The late successional species, for example those depend on dead wood, are the more poorly understood group, and, certainly in historic times, their habitat has continuously been rare in the British landscape (restricted to forest set aside for game, old pollards in wood pasture, churchyards, etc.). The early-successional species, including those of calcareous grassland, heathland, woodland floor and reed beds (Thomas 1991b) have experienced dramatic declines in the availability of habitat at the right successional stage, since humans no longer exploit the landscape in the way they used to.

Lowland heathland is largely a manmade community – initiated by forest clearances starting in Neolithic times, and maintained by grazing and probably burning (Webb 1986). Heathland developed on land that was either intrinsically very nutrient poor, or had been exhausted of nutrients by cultivation, and was then left to go to "waste". Grazing animals on the heath by day, and keeping them enclosed at night, represented a way of concentrating nutrients in the enclosures (as dung), which could then be used to grow crops, and this perpetuated the low nutrient status of the heaths. The heath was also exploited by cutting peat/turf and gorse for fuel. Such systems of land use were already established by Norman times, and continued to be very widespread until the 17th century (Webb 1986). An increase in controlled burning probably resulted from a decrease in stocking densities on heaths during the 18th and 19th centuries, because the grazing was no longer enough to keep the heathland from reverting to scrub (Webb 1986). The dominant ericaceous shrubs of heathland are to some extent adapted to fire, and they will readily re-grow from ground level after the shoots have been burnt. After about 10 years post-fire, the growth rate and forage quality of the heathers decline, and their flammability increases, making fires difficult to control; hence, it is normal to have a burning rotation of around 10 years (Webb 1986). A variety of species of plants, invertebrates and reptiles benefit from the warm microclimatic conditions of early-successional heathland, including the Silver-studded Blue butterfly (*Plebejus argus*).

Starting around the 18th century, the area of lowland heathland in Britain declined and it became increasingly fragmented: some was improved for agriculture, and increasingly it was claimed by urban expansion (Webb 1986). During the 20th century, the decline in area continued, and most of the heathland that remained was left completely unmanaged (Webb 1986). This was disastrous for the early-successional species. Now the conservation of heathland is recognised as a national priority in the UK, and there are numerous heathland nature reserves. Management by burning or grazing has been re-instated on many heathland reserves for the specific purpose of benefiting wildlife (Webb 1986). Burning can be less labour-intensive than keeping grazing animals, but both are very difficult to manage on small, isolated fragments so here mechanical cutting or rotavating may be used (Webb 1986). Although there may be cultural reasons for re-instating whatever pattern of management was 'traditional' on a particular heath, managers may also want to use improved knowledge of the ecology of heathland to design a grazing, fire or other disturbance regime that maximises the populations of rare species given the reserve's budget.

Coppicing is a traditional form of woodland management which yielded fast-growing wood for fuel and long, straight poles for construction. Only certain tree species can be coppiced (notably hazel, Harmer 2004, and introduced sweet chestnut): it depends on their ability to produce multiple trunks from a single root stock, and to re-sprout from the base once they have been cut. There are good historical records of the extent of coppiced woodlands in Britain since the Domesday Book, which is an indication of their high economic importance (Rackham 1970). After coppice cutting, insolation of the forest floor is at a maximum, and it gradually declines over 5-15 years (depending on the tree species and soil quality, etc.). The clearings are colonised by a diverse ground flora, numerous invertebrates and birds.

The decline in coppicing began around the late 18th century (Rackham 1970). As the coppice products were no longer needed, coppice stands were abandoned; many were converted to conifer plantations in the early 20th century (Peterken 1991; Thomas 1991b). As this has happened, many woodland gap-dependent species have declined (Thomas 1991b). The decline of the Heath Fritillary (*Melitaea athalia*) and the *Viola*-feeding fritillaries have been particularly well documented (Thomas 1991b). Re-instatement of coppicing has been started on some woodland nature reserves (Peterken 1991; Thomas 1991b), but it is expensive (especially the initial effort to clear a long-abandoned coppice stand, Harmer 2004). For some species, establishing permanently open glades and rides can provide the habitat they need, but these are often taken over by competitive species like bramble, and the open ground is lost. It is an intriguing possibility that these threatened species could be given a major boost by humans' adaptation to climate change, if we start major afforestation and use more wood as fuel.

1.4 Study species

My study species are the butterflies *Melitaea athalia* Rott. (Nymphalidae) and *Plebejus argus* L. (Lycaenidae). As explained in the last section they are both early-successional species. Both have suffered large declines in range and numbers in the last century, mainly due to loss of suitable habitat. *M. athalia* occupies 11 of the 10km squares of Britain at present (Fox *et al.* 2006, figure 1), and this is less than 1/5 of its original distribution (Asher *et al.* 2001). *P. argus* currently occupies 80 10k squares (Fox *et al.* 2006, figure 2), and this is less than a quarter of the squares it has occupied in the past (according to data supplied to me by Butterfly Conservation). As a result of their declines, both species are the subject of Biodiversity Action Plans (Barnett & Warren 1995; Ravenscroft & Warren 1996).

P. argus and *M. athalia* have both been studied previously with respect to their habitat requirements, and their dispersal abilities (Warren 1987a, 1987b, 1987c, and see below). Both have relatively limited dispersal: most individuals do not move further than 300 m or even 100 m in their lives. The types of habitat they are found in are quite different, especially with respect to the processes of patch creation (see previous section and individual chapter introductions for more details). The fact that these species have fairly well-defined habitat requirements, limited dispersal, one generation per year and a fairly short flight season makes them relatively easy to survey. However, a dedicated search strategy is needed: monitoring by permanent transects (which are established in many reserves) does not work very well because the patches of suitable habitat are so dynamic (T. Brereton, Personal Communication).

The *Plebejus argus* populations in North Wales are also the subject of one of the longest-running metapopulation studies in the literature. Thanks to previous studies there is a wealth of data that is relevant to parameterising a metapopulation model.

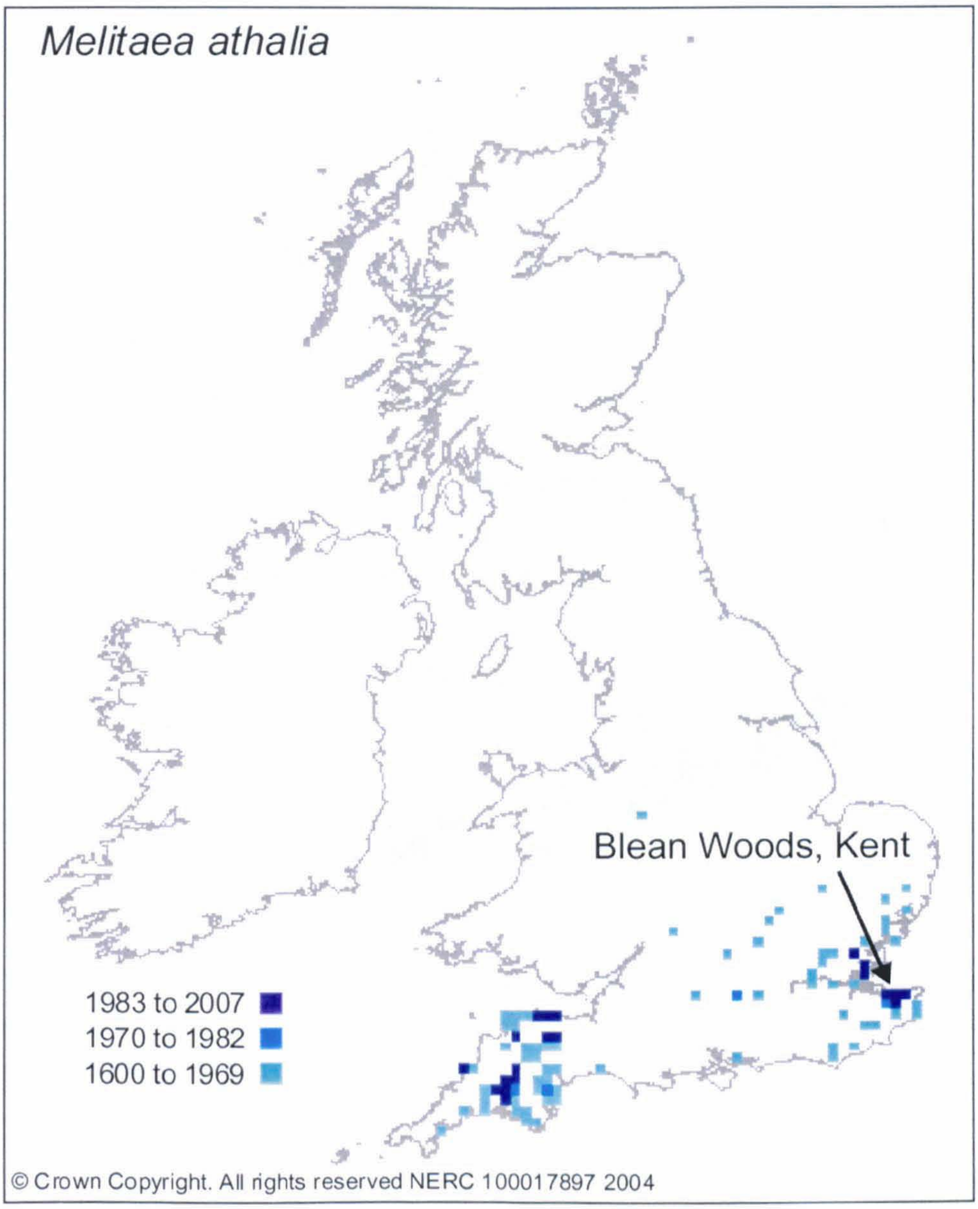

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Figure 1: Decline in distribution of *M. athalia* in Britain over the last century, according to national records database. Study site for work in chapter 3 is labelled. Records obtained from NBN gateway (www.searchnbn.net).

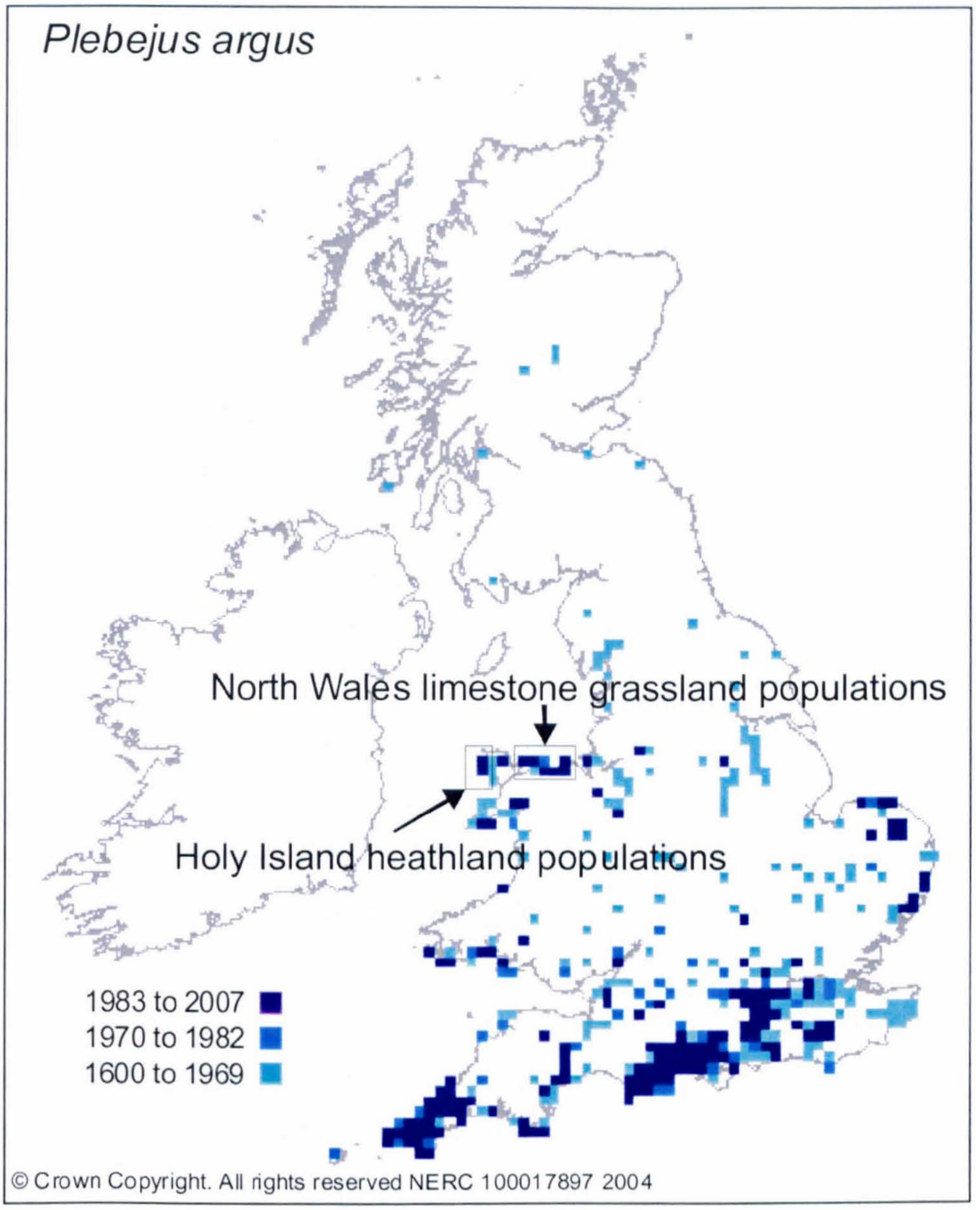


Figure 2: Decline in distribution of *P. argus* in Britain over the last century, according to national records database. Study sites for work in chapters 4-6 are labelled. Records obtained from NBN gateway (www.searchnbn.net).

The ecological requirements of *P. argus* are quite specialised: they require sunny and sheltered microclimates, and a high density of ants of the genus *Lasius*, which tend the caterpillars in a mutualistic relationship (Jordano *et al.* 1992; Jordano & Thomas 1992). The caterpillars feed on a variety of plants, but select the meristematic tissue, and across Britain they can be found on heathland, chalk/limestone grassland, mossland and even sand dunes (Thomas 1983). In North Wales there are some populations on heathland, similar to those elsewhere in Britain, and a separate race which evolved on the Great Orme – a large promontory of limestone. This race *P. argus caernensis* uses a novel food plant (*Helianthemum*) and a different host ant species to the nearest heathland populations (*Lasius alienus* rather than *L. niger*). The race is also characterised by smaller body size and earlier emergence dates. The early work of Thomas

(1983; 1985a) aimed to establish the habitat requirements of both these races in terms of vegetation, aspect, exposure and the ant interaction, providing a good basis for defining patch networks later (Thomas & Harrison 1992; Thomas *et al.* 2002).

Observing the spread of *P. argus* to new areas over a number of years has provided information on its colonisation abilities, another essential component of metapopulation dynamics. The limestone race was introduced to one site in the Dulas Valley, about 15km from the Great Orme, in 1942 (Marchant 1956), and by the late 1950s had spread to occupy most limestone outcrops in that area (Dennis 1977). Since 1983 CD Thomas has made 3 further introductions of the race to new sites (only 1 of these still survives). Mark-release-recapture studies were done during one introduction and in an established metapopulation in the Dulas Valley (Lewis 1997; Lewis *et al.* 1997).

In 1972-3 Dennis (1977) recorded the distribution of the species by sampling every 100m square of the Dulas Valley and the Great Orme. There have also been 3 surveys of the entire North Wales distribution by the research group of C.D. Thomas: in 1983, 1990 and 1997 (Thomas 1985a; Thomas & Harrison 1992; Thomas *et al.* 2002). These surveys recorded the patch outlines, approximate population densities (except in 1990) and some aspects of habitat quality. In 2004, I undertook another survey of the entire North Wales distribution of the Silver-studded Blue, and I digitised the maps of the colonies/habitat patches from 1997, 1990 and 1983, and organised all the results into a common framework (the results are given in appendix 1, and they contribute to the work in chapters 5-6).

A high proportion of the patches included in the North Wales surveys underwent extinction or colonisation at some time, but the overall occupied area has not consistently increased or decreased. It was shown that heathland metapopulations experience higher turnover than limestone grassland ones (Thomas & Harrison 1992), and that the estimated turnover rates for limestone increase as more years' data are added to the dataset (Thomas *et al.* 2002). Both of these observations may be partially explained by the action of succession in the habitat patches. Succession (from bare soil to a continuous canopy of heather and gorse shrubs) happens relatively fast in heathland patches (Thomas 1991a; Webb & Thomas 1993), so the 'extra' extinctions might be due to habitat becoming unsuitable, rather than the processes traditionally considered in metapopulation models: demographic and environmental stochasticity. Succession is usually kept at bay in the limestone patches by grazing, but some changes might occur on a timescale of decades that make extinction or colonisation more likely (for example scrub can encroach, myxomatosis outbreaks can remove rabbits, and farmers can move sheep). Therefore, the P. argus metapopulations of North Wales provide a convenient testing ground to explore the interaction between metapopulation dynamics and successional dynamics, with a combination of modelling and field observations.

2 Technical introduction

2.1 Review of dynamic landscape metapopulation models

Dynamic landscape metapopulation models are extensions of metapopulation theory (Hanski & Simberloff 1997, see also section 1.2) to account for temporal changes in the availability or arrangement of habitat. They have been analysed by a number of authors, and constitute a sub-field of research that has grown remarkably in the last 5 years (figure 3).

It aids the understanding of dynamic landscape metapopulation models to realise that their intellectual roots are not just in metapopulation biology. Theoretically, the models are very similar to some predator-prey and host-parasite models (e.g. Hastings 1977; Caughley & Lawton 1981), if the resource/habitat is thought of as analogous to the prey/host. Indeed, I have considered Hastings (1977) as the first dynamic landscape metapopulation model, although it is couched in terms of predator and prey, and it was not until 2000 (Johnson 2000b) that the same model was analysed with successional habitat in mind. Also, these models have roots in the theory of vegetation disturbance-succession dynamics (e.g. Horn 1981), a field which has generated many bottom-up mechanistic models, for example models of forest growth (reviewed by Mladenoff 2004) and models of fire (reviewed by Keane *et al.* 2004). These different strands have been brought together, especially in the last 10-20 years, by the umbrella field of landscape ecology, with its focus on the roles of space and dispersal in species interactions (Tscharntke & Brandl 2004). I have attempted a comprehensive review of published dynamic landscape metapopulation models, because they have not been reviewed before and the recent growth of the field makes it timely (figure 3). The models I have reviewed are summarised in table 1. Unfortunately, empirical work on dynamic habitat metapopulations lags behind the development of models and simulations, but recently there have been a few very interesting statistical analyses of the spatio-temporal relationships within real metapopulations with dynamic patches (Snall *et al.* 2003; Verheyen *et al.* 2004; Biedermann 2005; Laine & Hanski 2006).

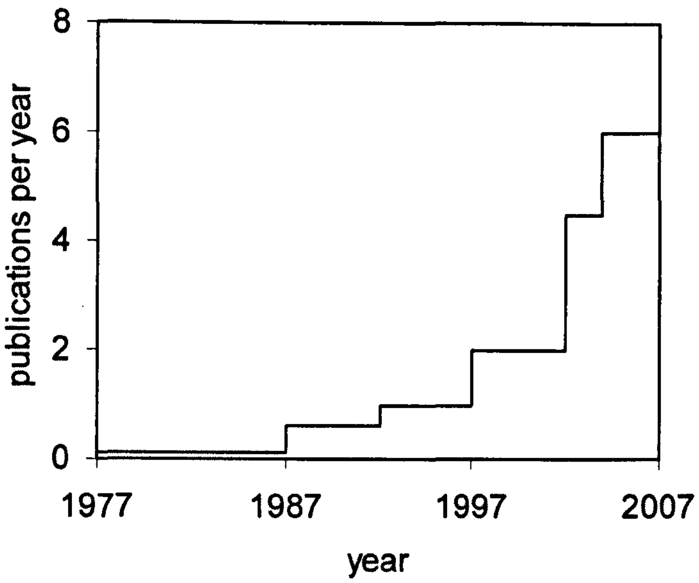


Figure 3: Rate of publication of papers that include dynamic landscape metapopulation models. Papers were found using a variety of search methods, but I cannot guarantee that I have found all those that are potentially relevant. There are 43 papers in total contributing to this figure and to table 1.

Two factors generally distinguish the theoretical case of a landscape of dynamic habitat from that of a predator prey or epidemic model. Firstly, the species of interest usually doesn't affect its habitat by its presence. Obviously there are important cases where species do affect the succession in their habitat, and this is treated in some of the models I have reviewed (table 1, "landscape depends on species" column), but more often tends to be included in the realm of community models (e.g. Moloney & Levin 1996). Secondly, one is often interested in the case of a fixed patch lifetime, perhaps with deterministic changes in habitat quality throughout (table 1, "disturbance" and "recovery" columns). This creates different dynamics from models with constant probabilities of transition between the suitable and unsuitable states. Notably, the extinction threshold can be higher (Johnson 2000b), because older patches will on average have higher occupancy. If both suitable and unsuitable phases are a fixed duration, population cycles can result (Ellner & Fussmann 2003), which further increases the likelihood of extinction. On the other hand, a few simulation studies have found that the best outcome for the metapopulation occurs when disturbances happen at regular intervals (Liu *et al.* 1995; Stelter *et al.* 1997; Menges *et al.* 2006); this deviation from the simple theory is probably accounted for by the fact that habitat quality decreases with age in these models.

Table 1: Summary of publications on dynamic landscape metapopulation models, ordered by complexity of the model.

Model type ("sim" = simulation)	Treatment of space ("Levins" means assuming an infinite number of patches, spatially implicit; "patch ≠ disturbance" means the populations and disturbance events are on different spatial scales)	Disturbance (how do patches become unsuitable? "1 rate" means all patches have same rate, or probability in discrete time, of being disturbed)	Recovery (how do patches become suitable? "quality profile" means that patch quality changes, usually deterministically, with time since disturbance)	Aggregation of patches/ disturbances ("corr"= correlated; "het"= heterogeneous in size or quality)	Landscape depends on species?	Dispersal depends on distance? ("nn"= nearest neighbour", "window"= neighbours within a fixed distance)	Within-patch pop dynamics?	For a particular species?	For a particular landscape?	References
analytical	Levins	1 rate	1 rate	0	n	global	n	n	n	Amarasekare & Possingham 2001
analytical	Levins	1 rate	quality profile	0	n	global	n	n	n	Gyllenberg & Hanski 1997
analytical	Levins	age-dependent	instantaneous	0	n	global	n	n	n	Johnson 2000b, 2000a; Hastings 2003
analytical	Levins	age-dependent	instantaneous	0	y	global	n	n	n	Hastings 1977
analytical	Levins	age-dependent	instantaneous	0	y	global	y	n	n	Hastings & Wolin 1989; Brachet *et al.* 1999
analytical	finite patches	1 rate	1 rate	disturbance corr in time	n	global	n	n	n	Wilcox *et al.* 2006
analytical	finite patches	size-dependent	size-dependent	het patches	n	$e^{-\text{distance}}$	n	n	n	DeWoody *et al.* 2005
analytical + sim	finite patches	1 rate	1 rate	0	n	global	n	n	n	Ross 2006
analytical + sim	finite patches	age-dependent	1 rate	het patches, and disturbance corr in time	n	global	y	n	n	Boughton & Malvadkar 2002
analytical + sim	finite patches	age-dependent	instantaneous	het patches	n	global	n	y	y	Hill & Caswell 2001
sim	non-spatial	1 rate	quality profile	0	n	global	n	y	y	Menges *et al.* 2006
sim	finite patches	1 rate	instantaneous	het patches	n	$e^{-\text{distance}}$	n	y	y	Verheyen *et al.* 2004
sim	finite patches	1 rate	quality profile	0	n	$e^{-\text{distance}}$	y	n	n	Bossuyt & Honnay 2006
sim	finite patches	1 rate	quality profile	disturbance corr in time	n	nn	y	y	y	Stelter *et al.* 1997
sim	finite patches	1 rate	quality profile	het patches	n	$e^{-\text{distance}}$	n	y	y	Wahlberg *et al.* 2002
sim	finite patches	1 rate	quality profile	het patches, and disturbance corr in time	n	complex	y	y	y	Lindenmayer & Possingham 1995
sim	finite patches	1 rate	variable	het patches and disturbance corr in space	n	$e^{-\text{distance}}$	n	y	y	Biedermann 2004

Table 1, continued

Model type ("sim" = simulation)	**Treatment of space** ("Levins" means assuming an infinite number of patches, spatially implicit; "patch ≠ disturbance" means the populations and disturbance events are on different spatial scales)	**Disturbance** (how do patches become unsuitable? "1 rate" means all patches have same rate, or probability in discrete time, of being disturbed)	**Recovery** (how do patches become suitable? "quality profile" means that patch quality changes, usually deterministically, with time since disturbance)	**Aggregation of patches/ disturbances** ("corr"= correlated; "het"= heterogeneous in size or quality)	**Landscape depends on species?**	**Dispersal depends on distance? ("nn"= nearest neighbour", "window"= neighbours within a fixed distance)**	**Within-patch pop dynamics?**	**For a particular species?**	**For a particular landscape?**	**References**
sim	finite patches	age-dependent	quality profile	het patches	n	$e^{-\text{distance}}$	n	y	y	Schroeder *et al.* 2007
sim	finite patches	size-dependent	variable	disturbance corr in space	n	$e^{-\text{distance}}$	n	y	y	Snall *et al.* 2005a
sim	finite patches, grid	1 rate	1 rate	0	n	nn	n	n	n	Keymer *et al.* 2000; Matlack & Monde 2004
sim	finite patches, grid	1 rate	1 rate	disturbance corr in time	n	window	n	n	n	Vuilleumier *et al.* 2007
sim	finite patches, grid	1 rate	quality profile	0	n	$e^{-\text{distance}}$	y	n	n	Johst *et al.* 2002
sim	finite patches, grid	1 rate	quality profile	disturbance corr in space	n	global	n	n	y	Leroux *et al.* 2007
sim	finite patches, grid	1 rate	quality profile	disturbance corr in space	n	complex	n	n	n	Wimberly 2006
sim	finite patches, grid	age-dependent	instantaneous after refractory period	0	y	$e^{-\text{distance}}$	n	n	n	Ellner & Fussmann 2003
sim	finite patches, grid	age-dependent	quality profile	0	n	$e^{-\text{distance}}$	n	n	y	Ranius & Kindvall 2006
sim	finite patches, grid	age-dependent	quality profile	disturbance corr in space	n	$e^{-\text{distance}}$	y	n	n	Johst & Drechsler 2003
sim	finite patches, grid	age-dependent	variable	disturbance corr in space	n	window	n	y	y	Mladenoff 2004
sim	finite patches, grid	complex	complex	disturbance corr in space	n	$e^{-\text{distance}}$	n	y	y	Snall *et al.* 2005b
sim	finite patches, grid	complex	complex	unknown	n	$e^{-\text{distance}}$	n	n	y	Gu *et al.* 2002
sim	patch ≠ disturbance	1 rate	quality profile	0	n	nn	y	y	n	Moloney & Levin 1996
sim	patch ≠ disturbance	1 rate	none	disturbance corr in space	n	global	y	n	n	Schrott *et al.* 2005
sim	patch ≠ disturbance	age-dependent	1 rate	0	n	$e^{-\text{distance}}$	y	n	n	Fahrig 1992
sim	patch ≠ disturbance	age-dependent	quality profile	0	n	complex	y	y	n	Pulliam *et al.* 1992
sim	patch ≠ disturbance	age-dependent	quality profile	het patches	n	complex	y	y	y	Liu *et al.* 1995
sim	patch ≠ disturbance	complex	complex	unknown	n	$e^{-\text{distance}}$	y	y	y	Akçakaya *et al.* 2004; Akçakaya *et al.* 2005; Wintle *et al.* 2005
sim	patch ≠ disturbance	complex	complex	unknown	n	global	y	y	y	Larson *et al.* 2004

Many studies have shown that the faster the rate of habitat change, the higher the risk of metapopulation extinction and the lower the (quasi)equilibrium population size even if the population is persistent. In the simplest deterministic models, this can be explained by the way that the parameter for habitat destruction rate enters into the solutions for persistent threshold and stable internal equilibrium point (Brachet *et al.* 1999; Keymer *et al.* 2000; Amarasekare & Possingham 2001; DeWoody *et al.* 2005). This simple situation can be modified if patch lifetimes are not exponentially distributed (as they are with constant creation and destruction rates): the best situation in terms of persistence is if the probability of patch destruction decreases with patch age (Johst & Drechsler 2003; DeWoody *et al.* 2005). This situation is not unreasonable if the habitat patches themselves form a metapopulation (e.g. a metapopulation of host plants that grow over time and are most susceptible to disturbance when small, Biedermann 2004). If the probability of patch destruction does decrease with patch age, this leads to a situation where a minority of long-lived patches contribute disproportionately to the metapopulation persistence. Hastings (2003) recognised that this could be the case and suggested it would be important for conservation to recognise where these systems occur in nature: they could be especially vulnerable because quite a subtle change in habitat dynamics, which did not change the mean patch age but altered the tail of the age distribution, could suddenly turn a persistent metapopulation into one doomed to extinction.

Several studies have examined the impact of temporal autocorrelation in disturbances (table 1 "aggregation" column). It seems that temporally correlated disturbances always have a negative impact on the metapopulation, and this can be understood in terms of a decrease in the minimum metapopulation size, and an increasing probability of a "gap" when no habitat is available (Boughton & Malvadkar 2002; Wilcox *et al.* 2006).

Many of the models in my review considered only global dispersal (as in the original Levin's model, table 1 "treatment of space" and "dispersal" columns). When dispersal is restricted by the distance between patches, it makes metapopulation extinction more likely - but there is no clear evidence that this effect is relatively worse for dynamic landscapes than it is for static ones (Johst *et al.* 2002). However, when disturbances (and disturbance caused extinctions) are spatially aggregated and the species has limited dispersal distance, this can be especially bad for metapopulation size and persistence (Johst & Drechsler 2003; Vuilleumier *et al.* 2007, note that these studies do not give adequate consideration to different strengths and scales of spatial autocorrelation: more research is needed on this point). There are certain special cases where, for a species with limited dispersal distance, an intermediate level of habitat turnover can lead to a higher metapopulation size than a static landscape. This has only been shown to happen in a grid with nearest neighbour dispersal, or where the species cannot cross non-habitat cells (Keymer *et al.* 2000; Wimberly 2006). In this case, populations may only be able to colonise part of a static landscape, but if disturbances caused shifting of the suitable habitat they will eventually be "bridges" to the whole landscape (Keymer *et al.* 2000; Wimberly 2006).

Since landscape dynamics are likely to restrict rather than enhance the persistence of metapopulations, it becomes crucial to take these dynamics into account in population viability analyses, and there have already been a number of attempts to do this for different species (table 1, "for particular species" column). Attempting to simulate a realistic, spatially explicit dynamic landscape can quickly become a very complex problem. Disturbances may be heterogeneous in size (producing different sized patches which we know will have an important effect on metapopulation dynamics), and may be correlated in space and/or in time. Disturbances often will have different effects in different parts of the landscape, dependent on the land cover and other environmental variables. There is also an argument that, with dynamic patches, it becomes more important to model the populations within the patches explicitly (rather than just modelling presence/absence). This is because the period between colonisation of the patch and its population growing to carrying capacity may be a significant proportion of the patch's lifetime (models such as the incidence function model, Hanski 1994, assume that this period is short enough to be ignored). One way around this problem without over-complicating the model is to assume that there is a time lag between patch colonisation and the patch becoming a source of colonists itself (Snall *et al.* 2005b use a 10 year lag).

Most of the dynamic landscape metapopulation models that have so far been used for conservation case studies have incorporated very complex population dynamics. For example, ALEX (Lindenmayer & Possingham 1995) and BACHMAP/ECOLOCON (Pulliam *et al.* 1992; Liu *et al.* 1995) use the individual or the breeding pair as the unit of simulation and RAMAS-Landscape (Akçakaya *et al.* 2004) uses a stage-structured matrix model which can be different for different patches. These models also include rather complex submodels for the different disturbance types (fire, logging, wind, etc) and succession. For ALEX and RAMAS-Landscape, there is not even a complete enumeration of the landscape parameters used (Lindenmayer & Possingham 1995; Akçakaya *et al.* 2004).

The advantages of these models for population viability analysis are flexibility, the ability to incorporate many aspects of the species' life history and the ability to avoid obviously unlikely situations which would damage the credibility of the model in the eyes of land managers. For example, BACHMAP's individual based dispersal function takes into account that birds can be expected to remember where they have come from (Pulliam *et al.* 1992) and LANDIS (the forest simulation module included in RAMAS-Landscape, Mladenoff 2004), in modelling fire ignition and spread explicitly, allows certain vegetation types to act as fire breaks if they are not flammable.

The disadvantages of such complex models are, firstly, that the data to parameterise them are unlikely to be available for most species of conservation concern. Even in the population viability analyses that have already been published, some parameters had to be guessed or extrapolated from other species. Secondly, the model becomes nearly impossible to validate. Perhaps it is not surprising that the only studies that have actually validated model output against the observed data used a patch occupancy model (the IFM) and a landscape where the successional history was known in great detail (Gu *et al.* 2002; Schroeder *et al.* 2007). Snall *et al.* 2005b attempt to validate their model against real data for a single year. The landscape dynamics are simulated by FIN-LANDIS (a modification of LANDIS) and the metapopulation model used is a grid based SPOM. They conclude that full parameterisation is impossible with one data snapshot, because as the fire frequency is increased, the model can be made to fit the data by increasing the colonisation rate. Thirdly, using a complex model when a simpler model would lead to the same management recommendations means that analysis time and effort has been wasted. For example in the population viability analyses that use RAMAS-Landscape, most of the information generated about tree species composition is discarded at the stage of defining suitable habitat patches for the animal species. The only information used is the height of the tallest trees and/or the identity of the dominant plant species (Akçakaya *et al.* 2004; Larson *et al.* 2004; Akçakaya *et al.* 2005; Wintle *et al.* 2005). Also, RAMAS-Landscape has the potential to generate very interesting information about how populations vary across the landscape but the viability analysis (except in Akçakaya *et al.* 2005) is always summarised based on the overall population size and patch occupancy, and spatially explicit data is not shown.

Against this background, Atte Moilanen, Chris Thomas and I designed and built the MANAGE model, which is intermediate in complexity between models such as RAMAS-Landscape, and the simplest patch occupancy models. Since MANAGE is new, and it forms an important part of all the studies in this thesis, I will introduce it in detail in the following section.

2.2 The dynamic landscape metapopulation model MANAGE

2.2.1 Model formulation

This population model simulates colonisations and extinctions of a species inhabiting small habitat patches. The habitat patches may appear in new locations, change in quality due to succession, and subsequently disappear. The population dynamics (colonisations and extinctions) are stochastic, and the habitat dynamics have both stochastic and deterministic elements. The model has discrete time steps that may be thought of as generations for the organism modelled. At each time step the habitat dynamics are updated first, followed by the population dynamics, but for reasons of clarity here I describe the population dynamic step first.

2.2.2 Population dynamics

The species may colonise any extant, empty patch in any time step. Any occupied patch has a chance of going extinct in every time step. Occupancy at time (t+1) is updated based on the occupancy, area, location and quality of patches at time t (after any deterministic extinctions caused by patches disappearing, see next section). The transition probabilities are given by the following extinction and colonisation equations:

$$\mathrm{p}[Extinction]_{i,t} = \min\{1, (1-\mathrm{p}[Colonisation]_{i,t})^{R} \cdot \frac{\mu}{(A_iQ_i)^{x}}\} \qquad (1)$$

for an occupied patch i at time t;

$$\mathrm{p}[Colonisation]_{i,t} = 1\text{-}e^{-y \cdot S_{i,t}} \qquad (2)$$

for an empty patch i at time t where

$$S_{i,t} = A_i^{c} \sum_{j \neq i} z_{j,t} \cdot e^{-\alpha \cdot d_{ij}^{\gamma}} \cdot (A_jQ_j)^{b} \qquad (3),$$

where i and j index the number of patches, A is patch area, Q is patch quality, z is patch occupancy state (0 or 1), d is distance between a pair of patches and R, μ, x, y, b, c, α and γ are parameters. Optionally, A_i^c in equation 3 can be replaced by $(A_iQ_i)^c$, which implies that colonists are less likely to settle in a low quality patch. Regionally correlated stochasticity can be considered by entering a parameter *s*. With regional stochasticity, the quality of all patches is multiplied by a log-normally distributed 'regional effect' for each time step, so that

$$Q_{effective_{i,t}} = Q_i \cdot 10^{r_t}; r \sim N(0,s) \quad (4).$$

2.2.3 Habitat patch dynamics

Table 2 summarises the features of habitat patch dynamics in MANAGE, and the number of variables involved. A disturbance event creates a patch of a certain size at a certain location, which increases from quality *Qmin* to quality *Qmax* linearly taking *t1* time steps (generations), then stays at *Qmax* until *t2*, then declines to *Qmin* linearly by *t3*. The patch can either be transitory, in which case it disappears at *t3*, or cyclical, in which case it remains at zero quality until *t4*, when disturbance is triggered again. Disturbances can be killer, in which case they "kill" any existing patches that they overlap, or non-killer, in which case they are not allowed to overlap any existing patches (for a description of the patch "killing" routine, see section 6.2).

There can be a number of disturbance types in the same simulation – a disturbance type being characterised by its values of *Qmin*, *Qmax*, *t1*, *t2*, *t3*, and *t4*, whether it is cyclical or killer, and also its distribution of patch areas (table 2, row 4). A "dummy" disturbance type can be used to denote permanent patches (whose *Q* does not change by succession, but it can change by regional stochasticity – see above). The initial conditions - patches present at *t*=0, and their occupancy - must be specified. These could be just the permanent patches, or all permanent plus some successional patches.

Table 2: Summary of habitat dynamic options in MANAGE

Feature		Variables
for each disturbance type	quality profile	*Qmin*, *Qmax*, *t1*, *t2*, *t3*,
	cyclical	(TRUE or FALSE) and *t4*
	killer	(TRUE or FALSE)
	area distribution	array of area values for natural and manmade disturbances, with probability for each
for each management unit	disturbance rates	per-time step average and, if applicable, standard deviation for each disturbance type for natural and for manmade disturbances
	disturbance costs	creation cost per patch, creation cost per ha, creation cost per patch perimeter length, maintenance cost per ha per-time step, and maintenance cost per patch perimeter length per-time step, for each disturbance type
	management rule	maximum distance or minimum colonisation probability
	map	2D grid of cells, defines which management unit each potential habitat cell belongs to (management units must be mutually exclusive)
global options	potential habitat map	2D grid of cells, defines where disturbances can happen
	disturbance rules	area target or patch number target; action when patch too big for potential habitat (fit or cut); management criterion; failure method (skip to next disturbance type or skip to next run)
	starting conditions	a list of patches, each with x-y co-ordinates, area, quality, maintenance cost per-time step, disturbance type and whether manmade, age, permanence and occupancy

Disturbances can only happen in potential habitat within the landscape, which is defined by a habitat map (see table 2, row 9). The resolution of this map can be arbitrarily high, and the sizes of patches are completely independent of the sizes of the cells. Disturbances can be natural (in which case they occur at random locations throughout the habitat space) or manmade (in which case they can be placed according to nearest neighbour criteria). Some disturbance types may only ever be manmade, or only natural; others may be manmade and natural in different proportions.

The landscape is divided up into a number of mutually exclusive management units, and rates of disturbance (i.e. patch creation) are set independently for each management unit (table 2, row 5). The geographical location of management units is set by a management unit map (table 2, row 8). To avoid ambiguity, the cells of the management unit map should be the same size as, or a multiple of the size of the habitat map cells. The ability to specify different management units gives MANAGE great flexibility: they can be used, as the name suggests, for parts of the landscape under different ownership and management, but also for regions where the disturbance regime is different for any reason (e.g. vegetation types, geology, etc.).

The amount of habitat created in each time step in each management unit by each disturbance type can be specified in terms of area or in terms of number of patches. The area criterion and using the patch number criterion cannot both be used in the same simulation. If the area criterion is used, an average ($A_{m,ds}$) and a standard deviation ($s_{m,ds}$) must be specified for each management unit m and disturbance type ds. The 'target' area T for each time step is then obtained by sampling from the following log-Normal distribution:

$$T = A_{m,ds} \cdot 10^{r}; r \sim N(0, s_{m,ds}) \quad (5).$$

Note that $A_{m,ds}$ is the median of the distribution, which is not the same as the mean unless $s_{m,ds}= 0$. If $s_{m,ds}= 0$, there will be no variation through time in the area target, but if $s_{m,ds}> 0$, the mean area target will be larger than the median, in fact the mean or expectation of T:

$$\int_0^{\infty} [T \cdot \mathrm{p}(T)] \mathrm{d}T = A_{m,ds} \cdot 10^{\frac{s_{m,ds}^{2} \cdot \ln(10)}{2}} \quad (6),$$

where p(T) is the probability density of T (equation derived by S.J. Cornell, personal communication).

Patches are added to the landscape one by one (according to a routine which is described below) until the target T has been met or exceeded. If, as is likely, the final patch to be added exceeds the target, it is removed again with a probability equal to the proportion of its area which is beyond the target. Therefore, even if there is no variation through time in T, there may be slight variation in the area of habitat actually created, depending on the size distribution of the individual patches.

If the patch number criterion is used, it is necessary to specify the average number of patches $P_{m,ds}$, and whether Poisson or minimal variance is required. If Poisson variance is chosen, then the actual number of patches created in each time step follows a Poisson distribution with mean $P_{m,ds}$. If minimal variance is chosen, $P_{m,ds}$ patches are created each time step, unless $P_{m,ds}$ is not an integer, in which case floor($P_{m,ds}$) are created with probability 1-($P_{m,ds}$ - floor($P_{m,ds}$)), and otherwise ceiling ($P_{m,ds}$) are created.

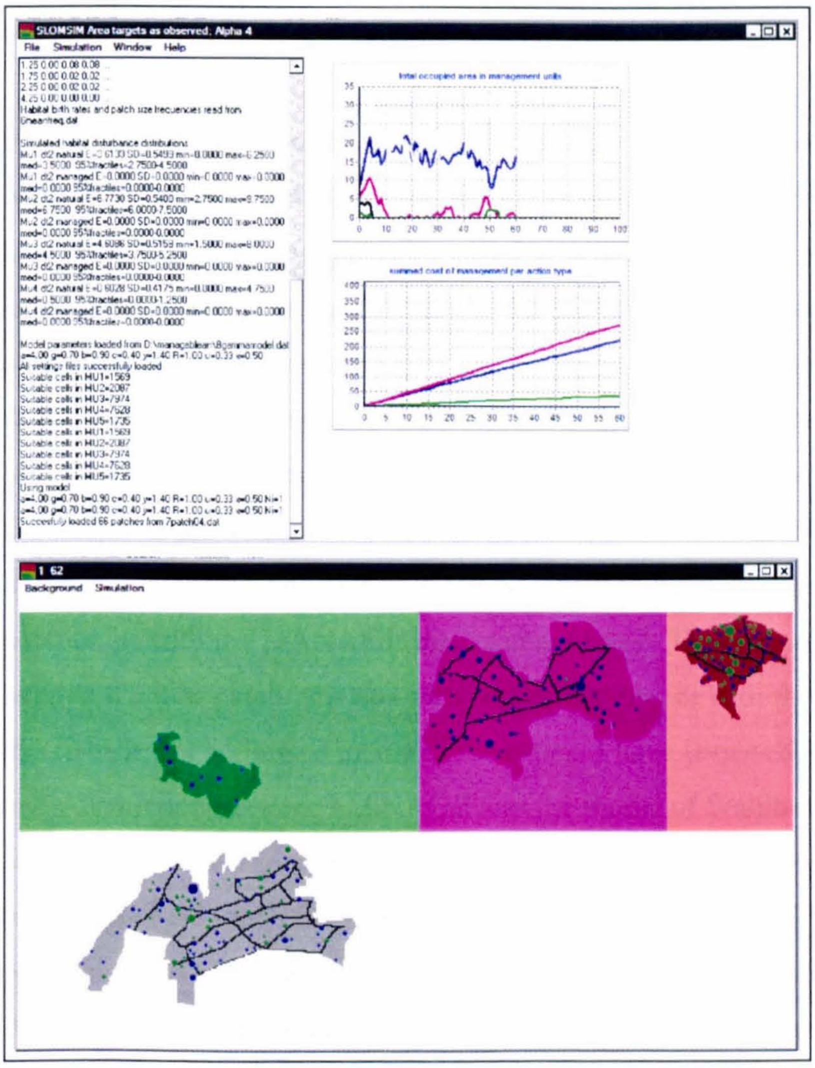
The location of a patch is decided by

1. picking a centre point randomly within potential habitat within the management unit.
2. if the disturbance type is non-killer, checking whether it overlaps with any existing patches, and if so, rejecting the location
3. checking whether there is enough potential habitat area to accommodate the patch (its centre is always within a potential habitat cell, but parts of its area may not be). If it does not fit, there are two possible actions: (1) reject the location, or (2) truncate patch area (A_i for the purposes of the population dynamics – see equations 1 and 3) to the habitat available within the patch circumference (the original radius is still saved for the purpose of calculating overlap with other patches). I have called these options "fit" and "cut" for short, and only one option can be used in each simulation (see table 2, row 10).
4. if it is a manmade patch, checking if it obeys the management rule, and if not, rejecting the location. The management rule sets either a maximum distance (to any existing patch, to an occupied existing patch or to an existing patch of a certain age) or a minimum colonisation probability for new manmade patches.

If a random location is rejected on any grounds, a new location is chosen and the process is repeated. It is quite feasible to enter patch areas and disturbance rates that are impossible to achieve in the landscape available (especially if patches are non-killer and so cannot overlap). To avoid the program 'hanging' I have built in a maximum number of locations to try for each patch (1 million if there is any management rule and 1000 if not). If the maximum is reached without any location being accepted, a warning is printed and the simulation skips, either to the next disturbance type, or to the next simulation run (see table 2, row 10).

2.2.4 Output

There are four types of model output from MANAGE. Firstly, there is a message window that informs the user on the progress of data loading and simulation (figure 4, top left hand side). Secondly, there is graphical output in the form of a colour-coded map and graphs of the population in and cost of each management unit (figure 4). These are updated each time step as the simulation runs. Thirdly, there is a text file summarising the amounts of available and occupied, manmade and natural habitat in each management unit in each time step, and summarising the management costs. Fourthly, there is the option to output a text file with landscape "snapshots" at defined time intervals. A 'snapshot' consists of a complete list of extant patches, each with its location, area, age, quality, occupancy, management unit, disturbance type and whether it is manmade.



```
1.25 0.00 0.08 0.08
1.75 0.00 0.02 0.02
2.25 0.00 0.02 0.02
4.25 0.00 0.00 0.00
Habitat birth rates and patch size frequencies read from
Gmeanfreq.dat

Simulated habitat disturbance distributions
Mu1 dt2 natural E=3.6133 SD=0.5493 min=0.0000 max=6.2500
med=3.5000 95%fractiles=2.7500-4.5000
Mu1 dt2 managed E=0.0000 SD=0.0000 min=0.0000 max=0.0000
med=0.0000 95%fractiles=0.0000-0.0000
Mu2 dt2 natural E=6.7730 SD=0.5400 min=2.7500 max=9.7500
med=6.7500 95%fractiles=6.0000-7.5000
Mu2 dt2 managed E=0.0000 SD=0.0000 min=0.0000 max=0.0000
med=0.0000 95%fractiles=0.0000-0.0000
Mu3 dt2 natural E=4.6086 SD=0.5159 min=1.5000 max=8.0000
med=4.5000 95%fractiles=3.7500-5.2500
Mu3 dt2 managed E=0.0000 SD=0.0000 min=0.0000 max=0.0000
med=0.0000 95%fractiles=0.0000-0.0000
Mu4 dt2 natural E=0.6028 SD=0.4175 min=0.0000 max=4.7500
med=0.5000 95%fractiles=0.0000-1.2500
Mu4 dt2 managed E=0.0000 SD=0.0000 min=0.0000 max=0.0000
med=0.0000 95%fractiles=0.0000-0.0000

Model parameters loaded from D:\manageblear\Bgammamodel.dat
a=4.00 g=0.70 b=0.90 c=0.40 y=1.40 R=1.00 u=0.33 w=0.50
All settings files successfully loaded
Suitable cells in HU1=1569
Suitable cells in HU2=2087
Suitable cells in HU3=7974
Suitable cells in HU4=7628
Suitable cells in HU5=1735
Suitable cells in HU1=1569
Suitable cells in HU2=2087
Suitable cells in HU3=7974
Suitable cells in HU4=7628
Suitable cells in HU5=1735
Using model
a=4.00 g=0.70 b=0.90 c=0.40 y=1.40 R=1.00 u=0.33 w=0.50 Ni=1
a=4.00 g=0.70 b=0.90 c=0.40 y=1.40 R=1.00 u=0.33 w=0.50 Ni=1
Succesfully loaded 66 patches from 7patch04.dat
```

Figure 4: Graphical output of the MANAGE model. The primary window (above) contains the message feed and the graphs of population size and management cost. The map window (below) shows the location of management units (different coloured rectangles), potential habitat (darker coloured areas within these) and suitable habitat patches (circles which are green if occupied, blue if unoccupied). This example is taken from the study described in chapter 3.

2.2.5 On the differences between MANAGE and closely related models

The population dynamic step in MANAGE is the same as is simulated in the program SPOMSIM (Moilanen 1999, 2004), which is based on the IFM (Hanski 1994). SPOMSIM has some features beyond simple simulation (e.g. parameter estimation, hierarchic cluster analysis) that MANAGE does not have. SPOMSIM also has several options for the functional forms of colonisation probability and extinction probability equations (Moilanen 2004), whereas

MANAGE has only one option for each, but MANAGE has extra flexibility in the connectivity equation (equation 3), provided by the parameter γ, (if $\gamma < 1$, the dispersal kernel is "fat-tailed"; if $\gamma = 1$ dispersal is exactly as in the IFM; if $\gamma = 2$, the dispersal kernel has the same shape as half a Normal distribution).

Among the already-published dynamic landscape metapopulation models (see table 1), MANAGE seems most closely related to the model described by Wahlberg *et al.* 2002. Unfortunately, this paper provides very few details of how the patch creation process was implemented, except to say that new patch creation was assumed to be normally distributed with mean 6 patches/year and standard deviation 4 (what happens in the portion of this distribution that is <0 is not explained), and succession was modelled by reductions in patch area over time. Wahlberg *et al.* 2002 also state that the areas of new patches are a sample from the observed distribution of patch areas, as I have used in MANAGE simulations (see chapters 3, 5 and 6), and that they can be forced to be within a certain distance of other patches (as with the MANAGE management rules). There is no indication of what might happen if a new patch overlaps with an existing one, or with the edge of the landscape (indeed this issue is not addressed in any of the papers I have reviewed, except for Fahrig 1992). The main distinction between MANAGE and the model of Wahlberg *et al.* 2002 seems to be that MANAGE was designed to be adaptable to a range of situations rather than being designed for a single case study. Other models which are based on the IFM, and provide an interesting comparison to MANAGE, are used by Gu *et al.* 2002; Snall *et al.* 2005b, and Schroeder *et al.* 2007, but in these the metapopulation dynamics are not simulated at the same time as the lanscape dynamics – landscape snapshots must be obtained from real data or from another model.

3 Viability of the Heath Fritillary populations in the Blean Woods depends on the spatial distribution of coppicing.

3.1 Introduction

British ecosystems all have a long history of anthropogenic modification and management. Against a background of widespread deforestation, humans manipulated the woodland that remained to maximise their economic utility (Rackham 1986). This resulted in woods with a different tree species composition and a quite different age structure, in which the natural processes of gap creation and succession were largely replaced by humans' planned disturbances (Peterken 1991). The Heath Fritillary butterfly (*Melitaea athalia*) is a good example of a species that now seems dependent on traditional forestry practices - it thrives in coppiced and recently felled areas, and at ride edges (Warren *et al.* 1984). This species' decline in range in the last century has been associated with the abandonment of coppice rotation. The area of woods in England with actively managed coppice fell by 90% between 1905 and 2000 (Asher *et al.* 2001). Half of the remaining coppiced areas are in Kent, and this is where the last surviving woodland metapopulation of Heath fritillaries is found (although there have been re-introductions to woodland in Essex, and there is a concentration of populations in South West England that use different habitat types (Warren *et al.* 1984)).

We can imagine that *M. athalia*'s habitat before human settlement was natural treefall, storm or fire - created gaps in forests, but obviously this is difficult to substantiate. One approach to the conservation of species like *M. athalia* would be "re-wilding": the creation of extensive reserves where natural successional dynamics can re-establish themselves without human intervention. Such a reserve would need to be substantially bigger than the largest natural disturbance size (Pickett & Thompson 1978), but in the case of storm and fire disturbance in forests this could be an impractically large size (Schwartz 1999). A further consideration is that it could take more than a century for today's forests to regain the kind of age structure where there is always a peppering of small natural treefall gaps. During the transition period from the managed to the "wild" state, there would be a very high risk that the *M. athalia* metapopulation would go extinct due to a bottleneck in habitat availability. Each cleared patch is only suitable for *M. athalia* for between 3 and 10 years, depending on the type of trees and their growth rate (Warren *et al.* 1984; Warren 1987c), and the need for new disturbances to replace overgrown patches makes the population very vulnerable. Indeed the metapopulation in Kent was brought to the brink of extinction by a lull in coppicing in the1980s (Barnett & Warren 1995). So, even though the Blean Woods complex in Kent is a large area with substantial amounts of ancient woodland, and the market for coppice products is weak, the re-wilding strategy does not seem appropriate for the short to medium term. Instead, the conservation strategy that has been adopted, and has been successful in expanding the Blean Woods metapopulation in the last 20 years, is to maintain and increase the rate of coppicing and ride widening using conservation funds and/or conservation volunteers (Warren 1991).

The Blean Woods complex, north of Canterbury (figures 1 and 5) includes 30 square kilometres of woodland, most areas of which have statutory protection (SAC, SSSI and/or NNR) and are managed by conservation charities. *M. athalia* is one of the species with highest priority for the managers of the Blean Woods: it is the subject of a specific biodiversity action plan (BAP, Barnett & Warren 1995). The Blean Woods has the highest concentration of populations in the country, and the BAP specifies a target to restore the 1980 population level of 28 hectares occupied (Wigglesworth et al 2004). The managers and Natural England, the body responsible for allocating a large proportion of the funding for conservation management, need to decide when, where and how much coppicing is enough to meet their target. As a starting point, they need to know whether their current management strategy is a reasonable one. They would also like to know what is the minimum amount of coppicing needed to sustain a population, and what are the pros and cons of trying to expand the metapopulation to other, outlying woods, or concentrating the metapopulation in a small core area (D. Rogers Pers. Comm.).

In this study I try to answer the above management planning questions, using simulations in the newly developed programme MANAGE (see section 2.2), taking parameters from data collected in the last few years as part of the conservation effort in the Blean Woods. In doing so, I demonstrate some key advantages of the MANAGE model:

- It can integrate large amounts of data from several sources, to take account of habitat dynamics and population dynamics in one framework;
- It predicts the most likely population size and the probability of regional extinction in the long-term, and also the uncertainty in these predictions due to stochasticity;
- It models the fact that management actions vary between management units (e.g. land with different owners), but that the species is not limited by legal boundaries, and the whole region can function as one metapopulation.

3.2 Methods

3.2.1 Data collection and digitising

The *M. athalia* populations in the Blean Woods occur in several woodland blocks with different owners and managers, see figure 5. The charity Butterfly Conservation have conducted timed count surveys of colonies in all the woods, and the Forestry Commission collated management data for all the woods in 2005 and 2006, but most of the data sets I was provided with covered no more than one wood. A summary of the data sets used in this chapter, and their coverage, is given in table 3.

Table 3: Coverage and sources of data used in this study. Management consists of all kinds of coppicing. Populations are populations of *M. athalia* recorded by timed counts or "sweep counts" of adults.

Wood	**Management data**		**Population data**	
	Years	**Source***	**Years**	**Source**
Church Woods	1998-2005	RSPB	2000-2005	RSPB
	2005	FC		
West Blean and Thornden Wood	1993-2001	Tilhill	2003-2005	BC
	2005	FC		
East Blean Woods	1999-2003	KWT	1999-2001+2003	KWT
	2005	FC	2004	BC
Ellenden Wood	2005	FC	2004-2005	BC

*RSPB=Michael Walter at RSPB; FC=Forestry Commission; Tilhill=Tilhill Forestry Plc. BC=Butterfly Conservation; KWT=John Wilson at Kent Wildlife Trust

Maps provided on paper were scanned to jpeg format. Using ArcMap (ESRI, Redlands, CA), jpeg files were georeferenced, and then each individual shape (representing a colony or a managed area) was traced on screen and saved in a shapefile. For each management record (a shape with a year of cutting), I calculated its area, centroid point and whether or not it was occupied by *M. athalia* in each of the years 2000-2005 (but not counting years before the year of cutting). The occupancy was determined in two alternative ways: whether any part of the shape overlapped with the *M. athalia* shapefile, and whether the centroid of the shape overlapped with the *M. athalia* shapefile (more stringent). I also calculated, for each management record, whether it overlapped with any more recent management. For each mapped *M. athalia* colony, I calculated its area and centroid point. All the shapefile records were then exported to R (R Development Core Team 2005) for statistical analysis.

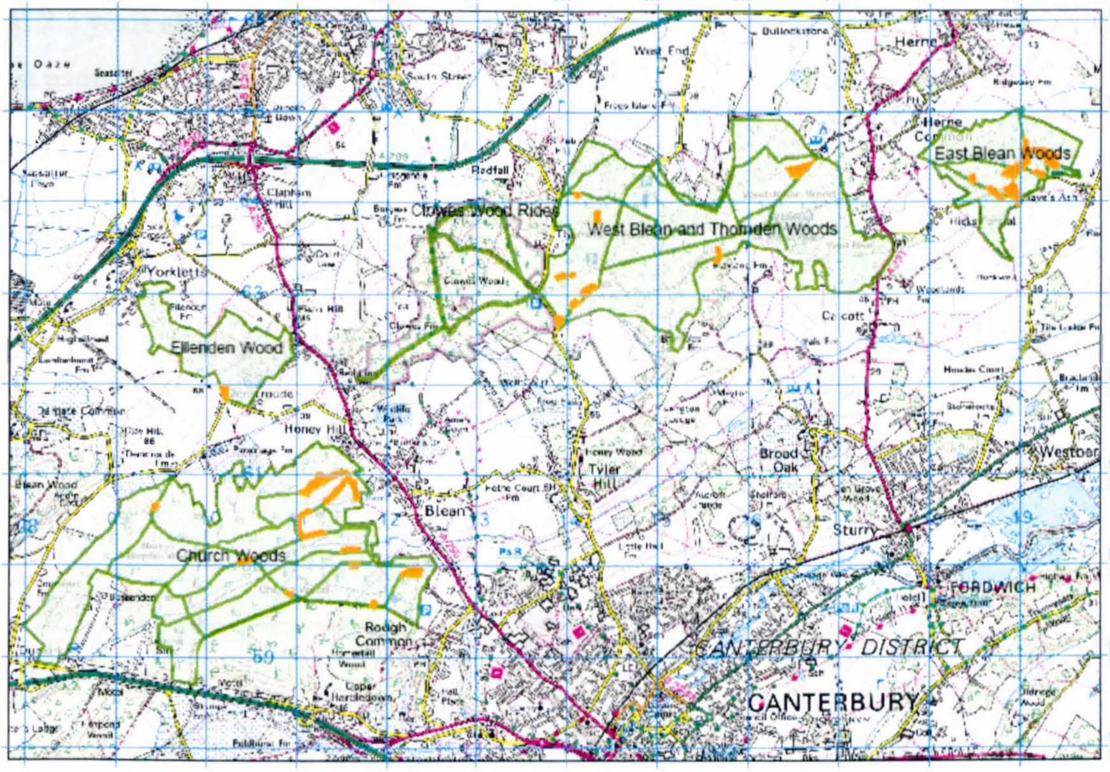


Figure 5: Map of the Blean Woods in Kent, UK and the *M. athalia* populations in 2004. Dark green lines show boundaries of woods used in the current study and location of wide rides. Orange polygons are sites of populations in 2004. Ordnance Survey 1:25000 raster tiles used with permission from Edina Digimap service. For sources of other data see table 3.

In order to define the management unit and potential habitat maps for simulating the populations with MANAGE (see section 2.2.3), the borders of the woods under different managers were digitised (see figure 5), then this layer was converted to a raster with 25m resolution. For simplicity in modelling, the whole of each wood was considered potentially suitable, but in reality some stands do not contain coppicing species. The wide rides were digitised and considered a separate management unit. Clearing the ride edges creates suitable *M. athalia* habitat but re-growth is quicker than for coppiced stands. Also, few data were available on the locations and rates of ride-widening, so this type of management was not included in the statistical analysis.

3.2.2 Statistical analysis of colonisation and extinction

Initial perusal of the data imported from the management shapefile showed that coppiced patches are most likely to be occupied in the year after coppicing (figure 6), and that many are even colonised in the year of coppicing (in the summer following coppicing in the winter). This accords with previous observations that *M. athalia* population densities are highest in the first 2-5 years after coppicing, and decline afterwards due to declining habitat quality (lack of host pants and/or warm microclimate)(Warren 1987c; N. Bourn Pers. Comm.).

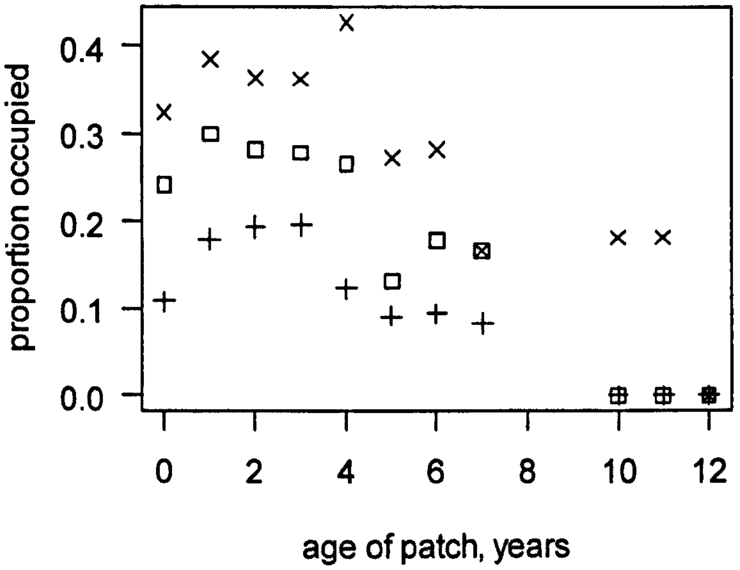


Figure 6: Occurrence of *M. athalia* in coppiced patches of different ages. Occurrence is determined in three different ways: whether the coppiced patch overlaps with a colony (crosses), whether the centre of the coppiced patch overlaps with a colony (pluses), and whether the coppiced patch overlaps with a colony and doesn't overlap with any more recent coppicing (squares).

Given this, I decided to fit metapopulation colonisation parameters for *M. athalia* based on each coppiced patch when it was aged 0 (if it was colonised in year 0) or 1 (if it was not colonised in year 0). Assuming that any differences in quality between the patches at this stage will not be serious enough to bias the results, I fit the model:

$$C_i(t) = 1 - e^{-y \cdot A_i^c \cdot \sum_j e^{-\alpha \cdot d_{ij}^{\gamma}} \cdot A_j^b}$$

where C_i is the probability of colonisation of an empty coppiced patch i between time t and time $t+1$, the patches j are the *M. athalia* colonies recorded at time t (if patch i is in a management unit where *M. athalia* data are not available at time t, it is excluded), A is patch area in ha, d is the distance between patches (edge-to-edge, assuming circular shapes as in MANAGE) in km, and y, c, α, γ and b are positive parameters. I use the generalised function "optim" in R (based on Nash 1990) to find parameters that maximised the likelihood of the occupancies observed at time $t+1$. Two alternative computation methods (BFGS and Nelder-

Mead) both converged successfully and gave the same results to 3d.p.. The best fitting parameters are shown in table 4. The parameter α was unexpectedly large (12), suggesting that the dispersal of this species is extremely limited. This could be biased by the fact that no very long distances are represented in the dataset used (no colonised patches were more than 300m from their nearest occupied neigbour and no patches at all were more than 1.1km from their nearest occupied neigbour.) A mark-release-recapture study by Warren (1987b) found that 1.4% of marked individuals moved from one colony to another over a distance of approx 1km, suggesting an α value of 4 would be more appropriate. Fitting all the other parameters with "optim" assuming α= 4 gives an alternative set of parameters (see table 4), and I decided it would be sensible to run simulations trying both alternatives to see how the results differed.

Table 4: Colonisation parameter values found by numerical optimisation

Parameter	Value when α is not constrained	Value when α is constrained
α	12	4
γ	0.65	0.7
b	1	0.9
y	25	1.4
c	0.8	0.4

Fitting extinction parameters for *M. athalia* was more problematic than fitting the colonisation parameters, as extinction probability depends mainly on population size, and I had no reliable way of calculating the population sizes in the coppiced patches. To solve this problem I used data provided by Butterfly Conservation on *M. athalia* colony survival in Exmoor between 1989 and 1999 (Stewart *et al.* 2001). There were 20 colonies recorded in 1989, with population sizes ranging over 4 orders of magnitude. The habitat here is moorland "coombes" that are mainly managed by grazing and do not show such extreme successional cycles as coppiced woodland. I excluded those that were less than 0.75km from their nearest neighbour, to minimise the influence of the rescue effect, and then fitted the model

$$Surv_i = (1 - \frac{\mu}{N_i^x})^{10},$$

where *Surv* is the probability of surviving between 1989 and 1999, *N* is the population size in 1989 and μ and x are positive parameters, using the "optim" function as described above. The maximum likelihood parameters were $\mu = 2.4$ and $x = 0.5$.

Finally, to find out how quality (proportional to population size) declines with age in the coppiced patches in the Blean Woods I used the data for all managed patches for any years where the patch was occupied at time t and the occupancy at time $t+1$ was known (provided that the patch was not overlapped by any more recent coppicing). For each patch i and time t I calculated $C_i(t)$ using both parameter sets in table 4, in order to factor in the rescue effect. Then I fitted the model

$$E_i(t) = (1 - C_i(t)) \cdot \frac{\mu}{(A_i \cdot Q_{age(i)})^x},$$

where μ and x take the values given above for the Exmoor data, and Q varies between $Qmax$ (at ages 0 and 1) and $Qmin$ (assumed to be 0.5, a value where even the largest patch (4 ha) will have extinction probability 1), taking t^* years. I used "optim" again to find maximum likelihood values of $Qmax$ and t^*, which were found to be 50.3 and 5 respectively. Interestingly, using $C_i(t)$ calculated using the second parameter set (where $\alpha = 4$, see table 4) gave the same $Qmax$ and t^* estimates but the maximum log-likelihood was much higher. The log-likelihood could be further improved by modifying $C_i(t)$ according to the relative quality of patches (so that low quality patches were less likely to be colonised as well as more likely to go extinct). This was achieved by replacing A_i^c with $(A_i Q_{age(i)}/Qmax)^c$.

So that MANAGE could use the same Q values in colonisation and extinction formulas, I normalised Q to $Q/Qmax$ and μ to $\mu/Qmax^x$, making μ 0.33.

3.2.3 Simulations of management and metapopulations

The modelling scenarios that I chose to use were targeted towards answering four key questions facing managers in the Blean Woods:

- Are current coppicing rates enough to sustain the population in the long term, and specifically are they enough to meet or exceed the BAP target area occupied?
- Is the existing distribution of coppicing effort (e.g. particularly high in East Blean, particularly low in West Blean and Thornden wood) better or worse than an even, or random distribution of effort?
- Do the management units bolster each other or are their populations independent?
- What is the minimum coppicing effort required to sustain the population in the worst case scenario?

To answer these questions I ran two related sets of simulations in MANAGE. (For detailed explanation of how MANAGE works see section 2.2.) Firstly, I ran "baseline" scenarios where the overall mean amount coppiced per year accords with the management data as in table 3, and looked at how the outcome was affected by the spatial distribution of management effort and the parameter uncertainty. Secondly, I ran simulations of "worst case scenarios" where I combined all the most pessimistic assumptions in the baseline scenarios, and varied the management effort step-by-step to estimate the persistence threshold. I found the thresholds both for the landscape as a whole and for the smallest (Ellenden Wood) and largest (Church Woods) management units in isolation. I judged that the minimum effort managers should use would be that which produced no more than one extinct run out of 100. This corresponds to having at least 95% confidence that the real extinction probability is less than 5% over the time period of the simulation (100 years).

Both sets of simulations were used to investigate whether the managements units bolstered each other's populations. I examined the data from the baseline simulations to determine whether it was possible for each management unit to be recolonised if it ever went extinct. I then examined the differences between the Ellenden Woods, Church Woods and whole landscape worst case scenarios to quantify what management units gain from being embedded in a wider occupied landscape.

Wherever possible I used the management data I had been given (table 3) to inform modelling variables. Sizes of coppiced patches were taken from the distribution of areas of coppiced patches with all years and management units pooled. (Ride-widening, as mentioned above, was difficult to parameterise and so was not included in these simulations.). Area coppiced per year was taken from the mean area coppiced per year (each year when data was available) for each management unit (table 5).

Table 5: Areas and management efforts of the Blean Woods management units.

Management unit	Total area, ha	Observed area coppiced per year, ha	Evened area coppiced per year, ha
Church Woods	498	6.8	6.4
West Blean and Thornden Wood	477	4.6	6.13
East Blean Woods	130	3.6	1.68
Ellenden Wood	108	0.6	1.4
Total	1214	15.6	15.6

The baseline scenarios differed with respect to:

- the colonisation parameters, using either of the two columns in table 4.

- the variability of area coppiced per year, using no variability or the observed variability. MANAGE samples from a log-normal distribution to introduce variability into the amount of management per year. Therefore, in scenarios with variability I used the geometric mean of the observed area coppiced per year, and the standard deviation of $\log_{10}$ area coppiced per year (see equation 5). The standard deviation turned out to be similar for all management units, so I used the same value (0.2) for all. To put this value into context, it means that in 87% of years, the amount coppiced will be between half and double the geometric mean.
- the distribution of management effort between management units, using either the observed distribution, a strictly even distribution (proportional to the management unit area) or treating the whole landscape as a single management unit so patches are placed randomly anywhere. An interesting effect of this latter option is that, when there is variability in the area coppiced per year, bad and good years are synchronised across the whole landscape, and this is potentially worse for the population than having independent variation in each management unit (see section 2.1).
- the starting quality of patches. The metapopulation parameters that I estimated (see previous section) assumed implicitly that all coppiced patches have the same quality when first created, but this is unlikely to be the case. For example it has been estimated that only 1/3 of coupes produce high quality habitat (Wigglesworth *et al.* 2004). I tried to account for this by simulating scenarios where Qmax is 2.5 (instead of 1) for a randomly assigned 1/3 of patches and 0.25 for the rest.

All simulation scenarios were run for 100 years and repeated 100 times. I used the population data of 2004 and the empty patches created in winter 2004-5 as a starting condition for the baseline scenarios, and also for the worst case scenarios with the whole landscape. For assessing the minimum effort needed in single management units I used a starting condition with 112 ha of randomly-placed patches which were all occupied. This was in order that extinction, especially in the smallest management unit, would not be biased by the 2004 conditions.

3.3 Results

3.3.1 Baseline simulations

The different baseline scenarios have quite different outcomes, even though the average coppiced area available is the same in each case (table 6, figure 7a). The most dramatic differences are caused by the two different options for colonisation parameters: when α is 12 (meaning dispersal is very short range) the BAP target of 28 ha occupied habitat is never met at the end of the 100 year simulation, but when α is 4 the target is usually met (table 6).

Table 6: Baseline simulations ranked in order of favourability for *M. athalia*. Scenarios are sorted first by the median area occupied in year 100, then by the median time to extinction if there is more than 50% extinction.

Scenario shorthand	Shorter-distance dispersal	Variable patch quality	Variable management rate	Evenly-distributed effort	All m-units vary together	Median occupied area in year 100	Percentage extinction by year 100	Time to 50% extinction	Percentage meeting BAP target: 28 ha occupied
sim4						38.8	0	~	96
sim4var			X			34.0	1	~	65
simeven4				X		33.5	0	~	66
sim4mono				X	X	31.7	3	~	59
sim4dud		X				25.3	0	~	34
simeven4var			X	X		18.6	21	~	25
sim4monovar			X	X	X	14.0	28	~	25
sim12	X					13.8	1	~	0
sim12var	X		X			10.5	25	~	0
sim12dud	X	X				0.0	53	96	0
sim12mono	X			X	X	0.0	100	28	0
simeven12	X			X		0.0	100	26	0
simeven12var	X		X	X		0.0	100	24	0
sim12monovar	X		X	X	X	0.0	100	22	0

Variation in patch quality (scenario shorthand "dud") has a negative influence on the occupied area and population persistence (table 6, figure 7a), and the reduction in occupied area (14 ha) is very similar whichever colonisation parameters are used. Recall that in the "dud" scenarios

2/3 of patches have low quality, but the average quality is not changed, so for some reason the butterflies are less able to exploit the available habitat. Variation in management effort from year to year (scenario shorthand "var") also has a negative influence on the occupied area and population persistence (table 6, figure 7a) – the extent of variation in the area of available habitat is shown in figure 7b. When all management units vary synchronously as opposed to independently (scenario shorthand "mono" compared to "even"), year to year variation in the available habitat is higher and, correspondingly, occupied area and population persistence are lower (table 6, figure 7a-b).

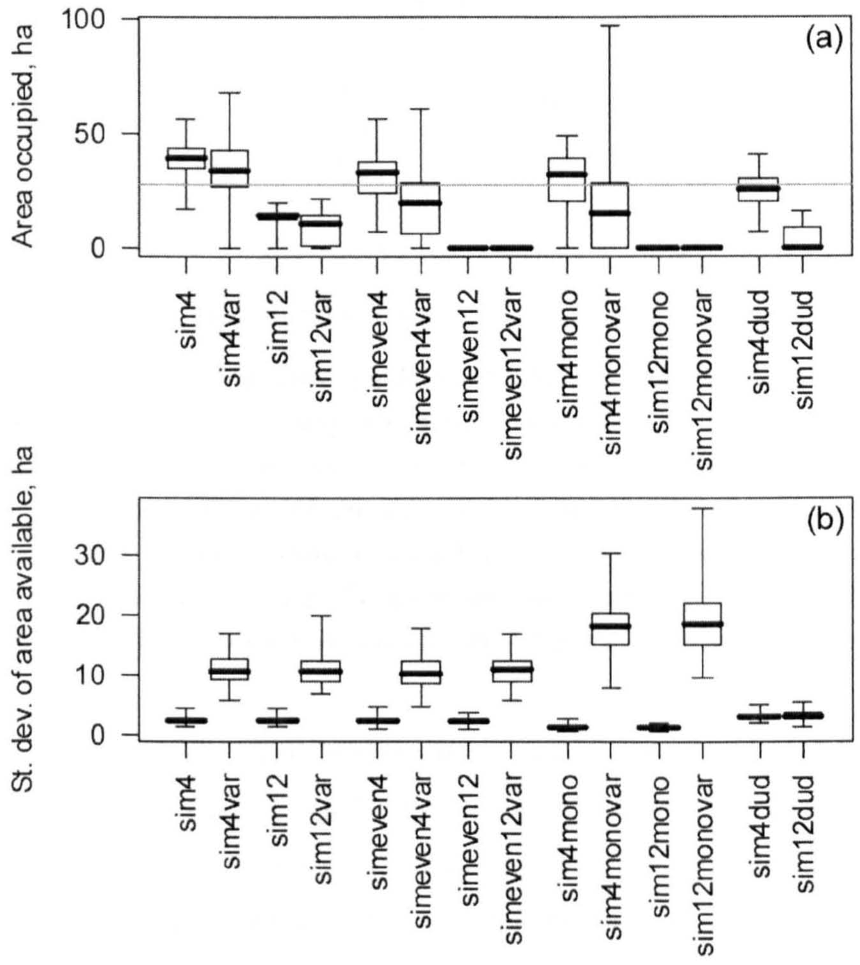


Figure 7: Differences in outcome between the baseline simulation scenarios. (a) Area occupied by *M. athalia* – the average of simulation years 96-100. Boxplots show the distribution over the 100 simulation runs; whiskers extend to the maximum and minimum. Grey horizontal line shows the BAP target amount of 28 ha. For explanation of the scenarios see methods and table 6. (b) Standard deviation of the overall area of habitat available between years 51 and 100 of the simulation, i.e. year-to-year variability. Boxplots show the distribution over the 100 simulation runs; whiskers extend to the maximum and minimum and staples show the 2.5 and 97.5 percentiles.

The observed distribution of management effort (see table 5) between management units seems to be better for the population than a more even distribution (note that in all these simulations, the spatial distribution of patches *within* management units is random). This is especially true if dispersal is assumed to be very short range (table 6). This can be explained by examining how management effort and the overall size of the management unit interact to influence the population size (figure 8).

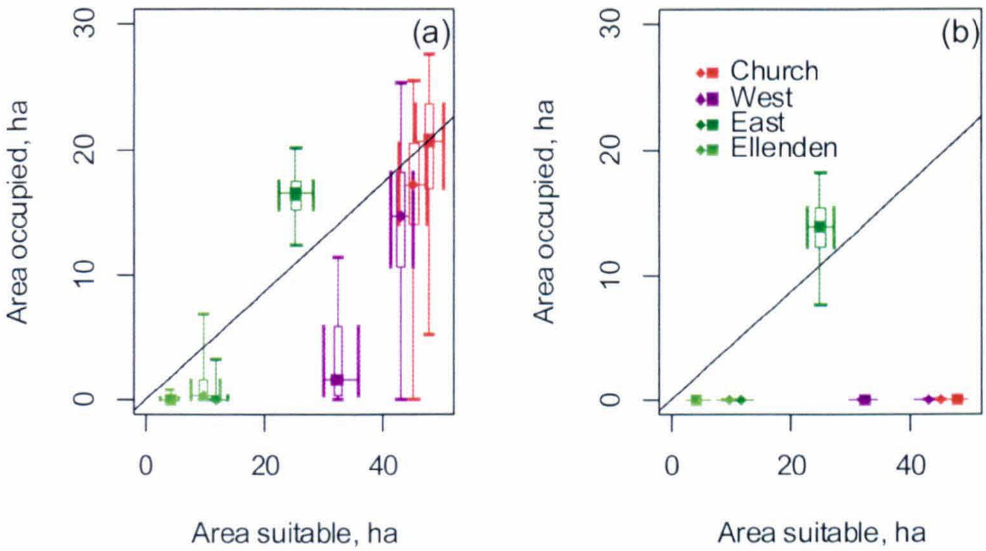


Figure 8: Suitable and occupied areas broken down by management unit for four different baseline scenarios, (a) sim4 and simeven4, (b) sim12 and simeven12. Filled symbols show the median of simulation runs; squares for the observed distribution of habitat and diamonds for the even distribution of habitat (see table 5 for more details). Boxes show the inter-quartile range and whiskers extend to the 2.5 and 97.5 percentiles. Colours are on a spectrum to represent the overall size of each management unit (see also table 5). The black line goes from the origin to the highest median for the largest management unit, in order to aid comparison.

With the observed management efforts, and assuming $\alpha=4$, both Church Woods and East Blean Woods have enough habitat to support a stable population (figure 8a, square symbols). West Blean and Thornden Wood does not have enough habitat to support a stable population, because although the effort is higher than for East Blean Woods, it is distributed over a larger area (almost as large as Church Woods). However, probably due to its location in-between Church Woods and East Blean Woods, West Blean and Thornden Wood is frequently re-colonised when the population goes extinct (99% of runs show at least one extinction-recolonisation cycle, and most show at least 5 re-colonisations in 100 years). Ellenden Woods has the smallest area and the smallest observed effort-to-area ratio, so contributes hardly anything to the overall area occupied, but it is worth noting that this management unit can also be re-colonised when it has gone extinct (100% of runs show at least one extinction-recolonisation cycle, and most show at least 7 re-colonisations in 100 years).

With the evened management efforts, and assuming $\alpha=4$, (figure 8a, diamond symbols), the two larger management units (Church Woods and West Blean and Thornden Wood) have enough habitat to support a stable population most of the time (respectively, 92% and 84% of runs show no extinction events in 100 years), but the two smaller management units do not. The reduction in overall population size in this scenario relative to that with uneven management effort (see previous paragraph and figure 8a, square symbols) seems to be mainly due to the change in status of the East Blean management unit: it changes from a stable population with the highest effort-to-area ratio, to an unstable population where management effort is effectively wasted. Probably because of its location at one end of the landscape, East Blean Woods is less likely to be re-colonised than the similarly-sized Ellenden Woods (median 4 and 8 re-colonisation events in 100 years, respectively).

When I assume $\alpha=12$ (figure 8b), the only management unit that supports a population is East Blean Woods, and only if the management effort is uneven (when this management unit has the highest effort-to-area ratio). In other management units and scenarios, the habitat is clearly too widely spaced to support populations with such restricted dispersal range.

3.3.2 Worst case scenarios

Given the results in the previous section, the worst case scenario would occur using the parameter set with $\alpha=12$, year-to-year variation in management effort with all management units varying together, and variation in patch quality. All the following results use these "worst case" parameters and vary the overall management effort and the landscape size (Ellenden Woods alone, Church Woods alone or the whole landscape).

For each landscape size, there is a similarly-shaped relationship between the proportion of suitable habitat and the probability of extinction in 100 years (figure 9). In a stochastic model, the probability of extinction is never zero, but it is possible to identify a point where it is low enough to be acceptable as a conservation strategy, and I have chosen the threshold of 5% extinction in 100 years. This threshold is met with 95% certainty if at least 19% of the entire landscape is suitable (figure 9, solid squares). Patches last 7 years, so this means that on average 2.3% of the landscape must be coppiced each year. When the landscape is smaller, the threshold is higher, so for Church Woods in isolation, at least 20% of the landscape must be suitable, and for Ellenden Wood in isolation, at least 29% of the landscape must be suitable (figure 9, open squares and diamonds, respectively). I could not achieve a large enough suitable area in Ellenden Woods so that no simulation runs went extinct, but this is partly due to a limitation of the MANAGE model: when around 30% of the landscape is covered with patches, since patches are not allowed to overlap, MANAGE often fails to find places for new patches, and so the habitat creation rate unavoidably slows (see section 2.2.3).

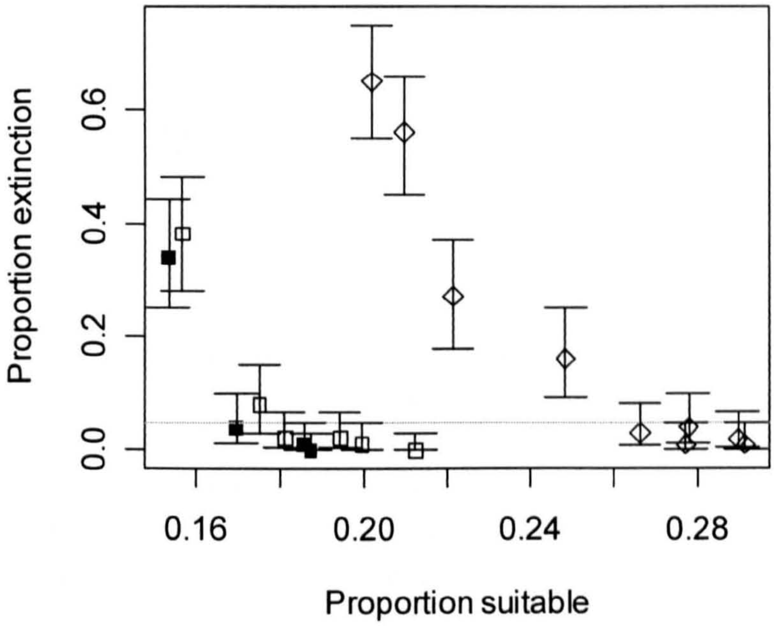


Figure 9: The extinction threshold for *M. athalia* populations in the worst case scenario given different landscape sizes – the whole landscape as in the baseline scenarios (solid squares), Church Woods alone (open squares) or Ellenden Woods alone (open diamonds). The grey horizontal line is at 0.05. The bars show probabilities of extinction that give a greater than 5% probability of observing the data (the number of extinctions observed out of 100 runs).

Although the threshold proportion of suitable habitat is higher for smaller management units, the absolute amount of habitat needed is lower (figure 10). The advantage of a small management unit in supporting a small population is that the patches are forced to be close together, but there may be practical limitations or conflict with other conservation objectives if coppicing is done very intensively in too small an area. The results of simulations like these can show how conservation targets can be reached within a given budget. For example, if it was not possible to do more than the observed amount of coppicing of 15.6 ha/year, figure 10 suggests that even in the worst case scenario the BAP target could still be reached by concentrating the effort in an area the size of Church Woods or a little smaller.

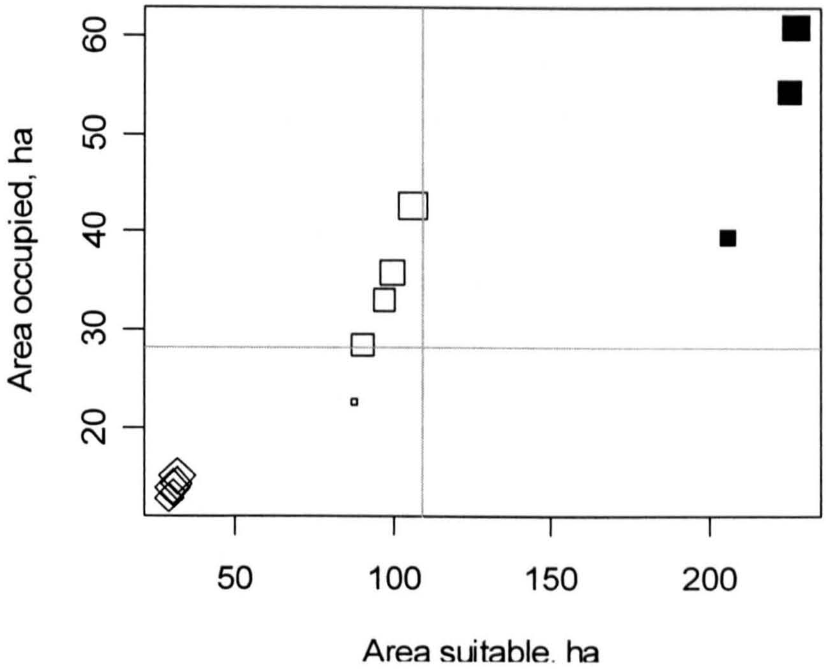


Figure 10: How equilibrium occupied area relates to managed area for landscapes of different sizes -- the whole landscape as in the baseline scenarios (solid squares), Church Woods alone (open squares) or Ellenden Woods alone (open diamonds). The median over 100 replicates of the value at year 100 is plotted. Symbol size shows the stability of the population – largest symbols for scenarios with no extinction, scenarios with more than 10% extinction are not shown. The grey horizontal line shows the BAP target amount of 28 ha occupied. The grey vertical line shows the observed effort of 15.6 ha per year (each patch lasts 7 years).

3.4 Discussion

With these simulations I have shown that, in a number of plausible scenarios, the Biodiversity Action Plan target for *M. athalia* in the Blean Woods is unlikely to be met. In order to meet the target in the worst case scenario, one could approximately double the coppicing effort in the entire landscape, or one could concentrate the existing effort into a much smaller area (smaller than the area of Church Woods). (With the former option of double coppicing effort, I predict that there would actually be 50-60 hectares occupied (figure 10), but that a population any smaller would be at risk of extinction.)

In a metapopulation model like this, one can always maximise the population size for a given management effort by having the patches as close together as possible, but for other reasons not included in the model this might not be practical or desirable. Firstly, the number of patches that can be fitted into an area is limited by the timespan of the coppice cycle. If the cycle is too short, the understorey may become crowded with grasses, brambles, and other species that might compete with *Melampyrum pratense*, the host plant of *M. athalia*; also, the coppice products will not be so useful. Secondly, a metapopulation spread across a wide area may be less vulnerable to extinction by catastrophic events. Thirdly, concentrating the population into just one management unit may fulfil the letter of the biodiversity action plan, but I do not believe that the managers would be content with this. No individual manager wants to lose *M. athalia* from their wood, in fact the long-term objective is for *M. athalia* to recover more and more of its natural range, and a strategy of maintaining a population in every management unit would mean that the minimum effort for each individual management unit would be lower than if it had to survive in isolation (figure 9).

The observed distribution of coppicing effort between management units is better for the population than an even distribution, but this is not to say that the observed distribution is the best that could be achieved. For example, there is disproportionately high effort in East Blean Woods, but this is not very well connected to the other management units. It might be better to transfer that effort to West Blean and Thornden Woods which is more central. It would be interesting to extend this study in future by running more simulations with alternative scenarios such as this, perhaps reflecting alternative plans proposed by the managers.

Two lines of evidence suggests that the management units support each other: the fact that all management units could be recolonised during simulations if they went extinct, and the fact that proportionally less effort is needed to sustain a metapopulation in a larger landscape (figure 9). Given this, it is worth considering stepping up management in Ellenden Wood and bringing other peripheral woods into management agreements. The worst case scenario simulations for Ellenden Wood suggest that a stable metapopulation can be maintained in a small management unit with as little as 4 hectares of coppicing per year, and less than that will be needed if there is a large core population to supply colonists.

The simulations show that in general, variation in patch quality and year-to-year variation in the amount of coppicing act to reduce population size and stability. These results accord with previous theoretical studies: temporal heterogeneity in habitat availability is always negative (Boughton & Malvadkar 2002; Wilcox *et al.* 2006), and heterogeneity in quality tends to have a negative influence in stochastic systems (Frank 2005). The levels of variation used in the simulations were quite realistic, and it would be difficult for managers to reduce this variation, but these results should be a warning to try and prevent variation increasing.

By far the greatest uncertainty in my predictions arises from uncertainty about the colonisation parameters. I am confident that either of the parameter sets in table 4 will predict short distance colonisations well, but the data I was using did not contain any really isolated patches, and a lot of data is always needed to estimate the probability of a very rare event. The mark release recapture study used to estimate that α equals 4 (Warren 1987b) was carried out on three populations in the Blean Woods, separated by no more than one kilometre, and such studies are also likely to underestimate the probability of long-distance colonisation (Schneider 2003). Therefore, my estimates of the extinction risk are likely to be quite conservative. The fact that the parameter γ was estimated to be less than 1 implies that the dispersal distance distribution is more 'fat-tailed' than a simple negative exponential. More information on *M. athalia* dispersal, especially the tail of the dispersal distribution, would be really valuable for making recommendations in the future.

3.5 Summary

- Simulations predict that the observed rates of coppicing will not be enough to meet the BAP target, except when the most generous modelling assumptions are made.
- The greatest uncertainty in the model outcome arises from uncertainty in the colonisation parameters.
- In the worst case scenario, a population could be sustained in the whole of the Blean Woods by coppicing 2.3% of the landscape each year, which is c. 30ha.
- The four woodland blocks are not independent – they support each other's populations.
- To sustain a population in a smaller landscape would require less habitat overall, but more as a proportion of the landscape.

4 Vegetation and microclimate variables affecting occurrence and abundance of *Lasius niger* on heathland.

4.1 Introduction

Plebejus argus inhabits a number of habitat types and uses several host plants across its geographic range (Thomas 1985a, 1985b; Ravenscroft 1990), but the most consistent feature of its preferred habitat is a high density of the ants *Lasius niger* and/or *Lasius alienus* (Ravenscroft 1990; Jordano *et al.* 1992; Gutierrez *et al.* 2005). Larvae of *P. argus* seem to have a mutualistic association with *Lasius* ant species (Jordano *et al.* 1992; Jordano & Thomas 1992), (similar relationships have been observed between many butterflies of this family, the Lycaenidae, and different ant species (Hölldobler & Wilson 1990)). While feeding, the larvae are tended and apparently protected by ant workers, and secrete a sugary liquid that the ants drink (Mendel & Parsons 1987; Jordano & Thomas 1992). While not feeding the larvae hide inside the ant nest (Ravenscroft 1990; Jordano *et al.* 1992). The larvae seem to be able to produce a chemical signal, highly specific to the species of ant that is their usual host (Jordano & Thomas 1992), that triggers 'adoption' behaviour in the workers (workers pick up the *P. argus* larva and carry it to their nest without harming it). On heathland habitats in the UK, *Lasius niger* is usually the host species for *P. argus* (Jordano *et al.* 1992). However, *P. argus* seems to occupy only a small proportion of the heathland area, and a small proportion of the sites occupied by *L. niger* (Ravenscroft 1990). It seems to be that *L. niger* is necessary but not sufficient to provide habitat for *P. argus.*

It has also been reported that patches of heathland where *P. argus* colonies are found are almost always recently disturbed by fire or physical disturbance (Thomas 1985a, 1985b; Ravenscroft 1990). However, *P.argus* seems to persist in later stages of heathland succession in the south of England than in North Wales (Thomas *et al.* 1999). These differences could be because of the thermal environments offered by early successional heathland: where there is less vegetation, the ground temperature can be boosted higher above the air temperature. This may lead simultaneously to:

- higher activity levels of the ants that protect the caterpillars while they are foraging,
- activity of ants and caterpillars earlier in the spring, and
- faster development of the caterpillars.

Further south, where all temperatures are higher, equivalent thermal environments may be found with greater vegetation coverage. It is not clear whether the early-successional vegetation favours *P. argus* directly, or favours the ant-caterpillar interaction (Jordano *et al.* 1992). Clarification of these causal relationships would help to parameterise simulations of *P. argus* populations on dynamic heathland landscapes with a range of disturbance regimes (to be described in chapters 5-6)

A couple of previous studies have measured temperatures in heathland at ground-level. Delaney (1953) studied microclimate at a heathland in Cornwall, and found that daytime summer ground temperatures were frequently 5 degrees, and up to 10 degrees higher on bare ground than under *Calluna vulgaris* 20 cm high. A similar pattern was observed in winter, but the differences in temperature were less extreme. Barclay-Estrup (1971) studied microclimate at a heathland in south-east Scotland and found that ground-level daytime temperatures between may and november averaged 17°C on bare ground, 14°C under heather 20cm high, and 11-13°C under mature and building phase heather 30-50cm high. The same study showed that the lowest maximum temperatures and the highest minimum temperatures in nearly all months of the year were under building and mature phase heath, (between 7 and 28 years old). Temperatures in the last, 'degenerate' phase of succession, when gaps start to appear in the heath canopy, could be almost as high as temperatures in pioneer the phase or on bare ground. The maximum ground level temperatures reported for the two studies were quite similar, 30-35°C, despite the difference in latitude between the study sites.

The physiology of all insects is affected by their body temperature. It is commonly found that ant foraging activity increases with temperature, up to a limit, above which the ants will suffer from over-heating and drying out (Brian 1977; Hölldobler & Wilson 1990). The temperatures that can be tolerated vary widely between species (Hölldobler & Wilson 1990). *Lasius niger* is distributed as far north as the Scottish Highlands in the UK, but in choice chamber experiments it has been shown to prefer a temperature of 18-20°C (Brian 1977).

The growth rate of butterfly larvae in a controlled environment is usually positively related to temperature (e.g. Bryant *et al.* 1997). One interesting study has shown that growth rate and development time in the field are linearly related to the available solar radiation (Weiss *et al.* 1993). The *P. argus* populations in North Wales are the most northerly extant populations in the UK, and they are probably near the edge of this species' natural northern range boundary (there were previously populations in Cumbria, and unconfirmed historical records from Southern Scotland, see figure 2).

The aim of this study was to find out which environmental factors drive the relationship between heathland succession and *Plebejus argus* abundance. I hypothesised that thermal constraints on ant activity during the spring, when the caterpillars are developing, would have a significant effect on the butterfly population. Therefore I hypothesised that ant activity could be predicted by the temperature at ground level, which in turn could be predicted by the ambient temperature and the vegetation height or the percentage of bare ground.

A second, related aim of this study was to obtain parameter estimates for the MANAGE model that define how habitat quality for *P. argus* changes with time after a fire on the heathland of Holy Island. My method of parameterisation was informed by the results of the data analysis, and therefore I have separated the methods and results of this study into part 1 – the field study on *L. niger*'s relationship to habitat, temperature and *P. argus* density, and part 2 – parameterisation of habitat quality for *P. argus* during succession.

4.2 Methods part 1: Field study

4.2.1 Ant transect

The ant community of Penrhosfeilw Common (figure 11) was sampled using a baited transect method in April 2005, a time when Silver-studded Blues would have been in the early instar larval stages, and presumably foraging with ants in attendance (Ravenscroft 1990). Tuna fish baits were placed every 10m along the route of the transect that the land managers use to record adult butterflies in summer. The route is 2.2km long, and describes an arc across the common (figure 11). Because of the length of the transect, and the unpredictable spring weather, baits were placed under a 'tent' made from two flat stones, which would not blow away and could be left for several days. Baits were checked when it was not raining and not less than 5°C, whenever possible between 3 and 24 hours after bait laying. Each bait station was checked for ants and refreshed with food at least twice, in order that differences between days could be controlled for.

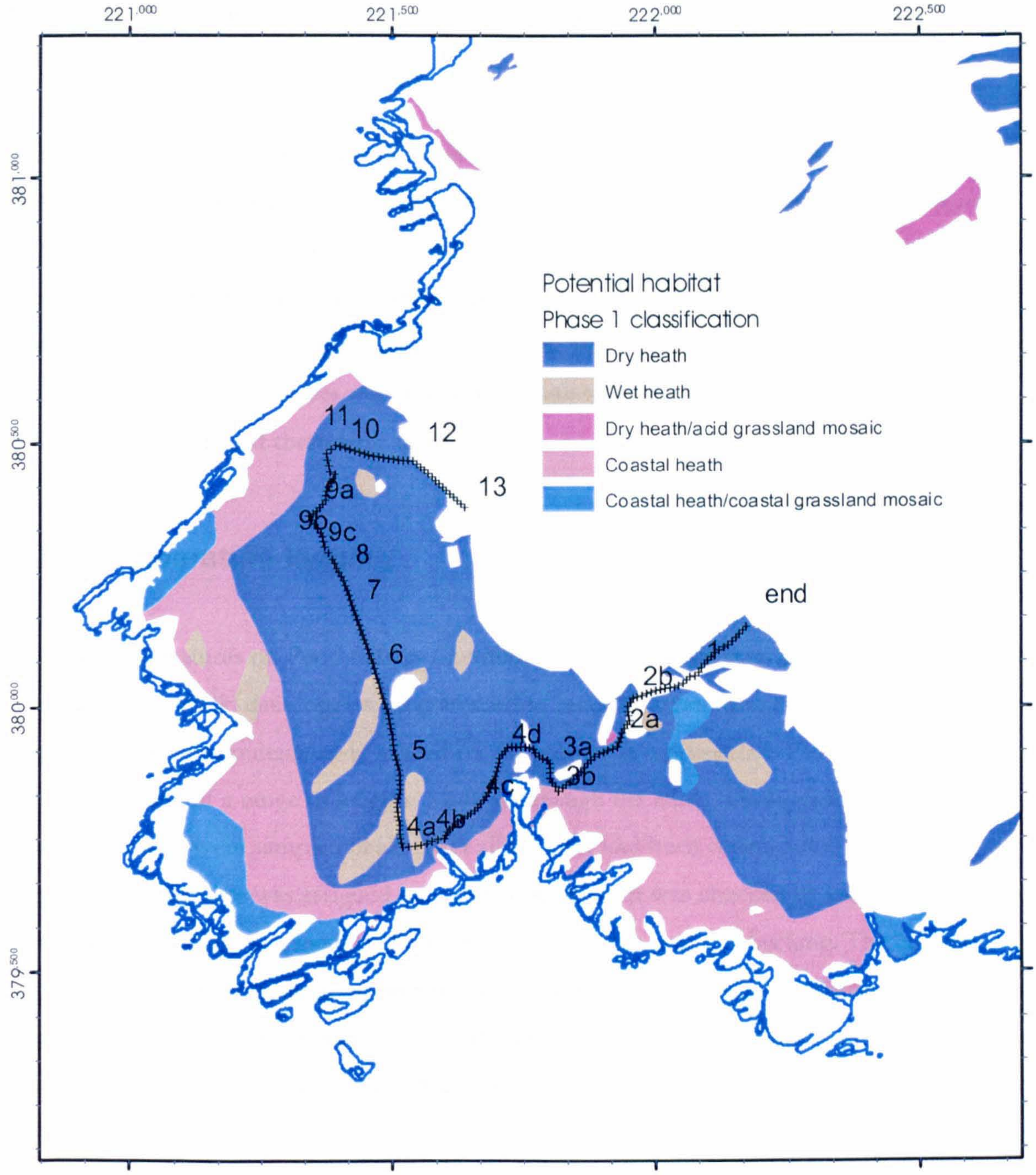


Figure 11: Route of the transect on Penrhosfeilw Common. Each ant bait is marked with a plus, numbers refer to the permanent transect sections used by the RSPB wardens when recording butterfly populations in the summer (numbered in reverse order for historical reasons). Phase 1 habitat classification data was supplied by CCW. There is actually more small-scale habitat variation along the transect than suggested by this classification, including grassy areas and gorse thickets.

The route of the transect mainly follows paths and where it does, baits were placed on the ground amongst the vegetation at the side of the path. Vegetation characteristics (vegetation type, vegetation height (1st and 3rd quartiles), and % bare ground) were recorded for the vegetation within 1m of the bait, not including any path. The surface type of the path, if any, was also recorded. The route of the transect was recorded with a GPS, and this data was used to calculate the shortest distance from each bait to the sea, using ArcMap (ESRI, Redlands, CA).

Ants at the baits were identified to species level where possible, catching specimens to identify with a dissecting microscope where necessary. I did not attempt to distinguish *Lasius niger* and *L. platythorax*. Because the two species are difficult to distinguish, and have only recently been separated (Seifert 1992), no information was available on whether *L. niger*, *L. platythorax* or both are associated with *P. argus* larvae. Henceforth when I refer to *L. niger*, I mean the *L. niger* aggregation. *L. niger* at the baits were counted if there were less than 10, and estimated to the nearest multiple of 10 if there were more.

4.2.2 Temperature logging

Ground temperatures on Penrhosfeilw Common were monitored during the period of the ant study using 'Tinytalk' data loggers programmed to record temperature every 20 minutes. Five loggers were used simultaneously, placed on the ground at representative locations under heather or gorse of a range of heights. Midway through the study, the loggers were moved, so that 10 locations were sampled in all. After all the data had been downloaded from the loggers, a temperature was assigned to each occasion a bait was checked by taking the average of the readings of the five loggers at the time closest to the time of checking. The effect of vegetation height on ground temperature was measured in terms of the deviation of each logger's reading from the geometric mean at each time point. The deviations were averaged over night and daytime periods using published sunrise and sunset times.

4.2.3 Data analysis

Different factors may affect *Lasius niger*'s presence at a bait (e.g. whether the bait lies within the territory of a colony), and the abundance of ants at the bait (e.g. foraging activity levels and the time taken to recruit). To separate the two effects it is helpful to identify false absences, i.e. locations where I would have observed *L. niger* had activity levels been higher at the time of checking. To achieve this I analysed the ant transect data in three stages. R (R Development Core Team 2005) was used for all statistical analyses.

Firstly, I used temperature and time data to predict possible false absences. I applied a linear mixed effect model to log (1+number of *L. niger* observed) including every occasion a bait was checked. The bait station was included as a random factor and the fixed explanatory variables were temperature (degree-2 polynomial) and time (in days since the bait station was first put up). The random factor and both the fixed factors had significant effects. The results allowed me to predict the number of ants expected at each bait if they had been observed at the same temperature and given the same amount of time since baiting. Bait stations where *L. niger* were not recorded on any occasion, but where the predicted number of ants was unusually high, were considered as possible false absences and excluded from the next analysis. (In practice only one station fell into this category.)

Secondly, I used binomial GLMs to model the presence/absence of *L. niger* at each bait station. *L. niger* was considered present if it was observed on any occasion at that bait station. The occurrence of other ant species at the baits was so infrequent that the factors affecting their presence, and whether they interacted with *L. niger*, could not be analysed. The explanatory variables tested with respect to *L. niger* presence were: distance from the sea, path type, vegetation type, percentage of bare ground, and vegetation height (1st and 3rd quartiles). To aid interpretation of the results, I also fitted models where vegetation types were amalgamated into three categories (heath, partially heath and not heath) and path types were amalgamated into three categories (vegetated (or no path), partially vegetated and unvegetated).

Thirdly, I fitted linear models to *L. niger* abundance (transformed as in the first analysis), excluding bait stations where *L. niger* were never seen and stations where there was no heath. All previously mentioned explanatory variables were tested.

Alongside the last two analyses, the influence of spatial autocorrelation was tested by incorporating a functional form for the covariance of errors into a linear mixed effects model (generalised lme model for the case of ant presence)(Venables & Ripley 2002). The methods available to fit these models (lme in the nlme package (Pinheiro *et al.* 2005) and glmmPQL in the MASS package (Venables & Ripley 2002)) are not guaranteed to find the maximum likelihood parameter estimates, which casts doubt on comparisons of goodness-of-fit between these and simpler models. However, it is very useful to see whether any of the explanatory variables lose their significance in a model that incorporates spatial autocorrelation.

4.2.4 Ant-butterfly relationship

It was originally intended to survey *P. argus* larvae at the same spatial scale as the ants. Sweep-netting, beating, and searching of selected host plants by hand were all attempted but were unsuccessful at locating larvae (one larva was seen during the study). However, it was possible to relate ant occurrence and abundance on the 13 sections of the transect (figure 11) to the adult butterfly densities observed in summer. Butterfly numbers by transect section were supplied by the RSPB wardens who manage the site. *P. argus* counts for each transect section were available for 6 separate days throughout the flight season in 2005, and 7 days in 2004. Unfortunately, the surveys in 2005 seem to have missed the fortnight of peak numbers (figure 12).

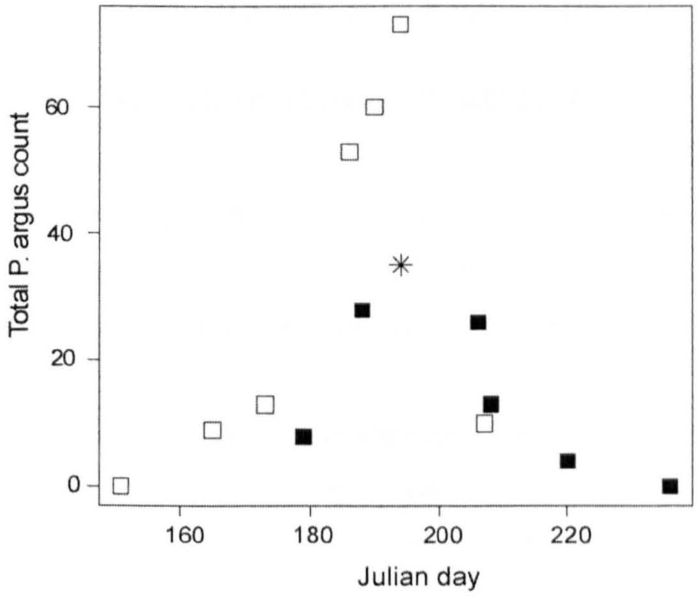


Figure 12: *P. argus* adult transect counts for the whole of the transect route on different dates in 2004 (open symbols) and 2005 (filled symbols). The star shows the total predicted for the 13 July (day 194) 2005, based on a GAM fitted to all the available data. The predictions for each section for this day were used as the estimated 'peak' numbers in 2005.

To arrive at an estimate of peak population density for 2005, I used data from both years to build a GAM where the butterfly count (Poisson distributed) is explained by the factors section and year and a smooth spline curve dependant on the day of the year. I also included a section*year interaction term, because the habitat dynamics change the relative importance of the sections from year to year. I used the GAM to predict section counts for 13 July 2005, which had been the peak date in 2004. It is possible that the peak was later in 2005, but there is not enough data to substantiate this (see figure 12) – if it was later, the densities may be slightly underestimated, but this will not affect the relative densities of the 13 sections. I converted the predicted counts to the population densities per hectare using the section lengths and the formula given in Thomas (1983), which is a fitted relationship between the numbers observed on a transect, and the population size as estimated by mark-release-recapture.

I amalgamated the results of my ant data by transect section, using either observed proportion of baits with ants present, or the averages of the fitted values of the ant models described above (the second and third analyses). I also amalgamated the vegetation height data by transect section. I used both linear models and GAMs to find out which measure of *L. niger* or vegetation was best to predict $\log_{10}$ *P. argus* density.

4.3 Results part 1: Field study

4.3.1 Ant transect and temperature

Lasius niger agg. was the most common ant species observed at the baits; only 35% of bait stations were never visited by *L. niger*. At most of the stations where *L. niger* was not observed, *Myrmica* spp. were observed, the most common of these being *M. rubra*.

Binomial GLMs indicated that vegetation type, path surface and distance from the sea all had significant effects on *L. niger* presence, whichever other variables were included in the model. In models where distance from the sea was not included, vegetation height (either upper or lower quartile) seemed to have a significant (negative) effect on *L. niger* occurrence, but in models where both variables were included, the effect of distance from the sea predominated (table 7 rows 1-4). Distance from the sea was negatively related to the chance of observing *L. niger*, and positively related to vegetation height. The proportion of bare ground amongst the vegetation had no significant effect on *L. niger* presence. As there were 12 vegetation type categories and 14 path surface categories, and many categories where no *L. niger* absences were observed, the fitted values of the GLM including these variables is difficult to interpret. Therefore I amalgamated the categories (see methods), and produced a simpler model that still explained most of the variation explained by the full categorisation (table 7 row 7). In this model there was an interaction between path surface and vegetation type, caused by the fact that when 'bad' vegetation occurs with a 'bad' path surface, the bad effects are less than additive. This effect can be seen in table 8.

Table 7: Significance of variables in a GLM to explain presence of *L. niger* at baits. The selected goodness-of-fit comparisons show the justification for including distance from the sea (shortened to "sea") but not vegetation height (lower or upper quartile), and the justification for amalgamating vegetation heights and path surfaces into fewer categories.

Model to test	Comparison model	Increase in explained deviance	p (χ^2 test)
Veg(lower Q)+sea	Veg(lower Q)	37.8	<0.0001
Veg(lower Q)+sea	sea	1.6	0.2053
Veg(upper Q)+ sea	Veg(upper Q)	35.2	<0.0001
Veg(upper Q)+ sea	sea	0.4	0.5078
12vegtypes+14pathsurfaces+sea	12vegtypes+14pathsurfaces	32.2	<0.0001
12vegtypes+14pathsurfaces +sea	sea	79.1	<0.0001
3vegtypes * 3pathsurfaces +sea	sea	40.7	<0.0001

Table 8: How vegetation type and path surface affect the probability of observing *L. niger* at baits.

			Path surface		
			no veg	part veg	vegatated
Vegetation type	Proportion with *L. niger* present	heath	1.00	0.82	0.57
		part heath	1.00	0.76	0.47
		no heath	0.60	0.31	0.56
	Number of observations	heath	21	34	47
		part heath	14	17	34
		no heath	5	26	18

There was a high degree of spatial autocorrelation in the *L. niger* presence data. The distance-based correlation form fitted by the glmmPQL function had a range of 74m and a 'nugget' of 0.6 (1-nugget gives the maximum correlation between residuals). In this model the effect of distance from the sea was unchanged, but the effects of path surface and vegetation height were no longer significantly different from zero.

L. niger abundance ($\log_{10}$ transformed after adding 1) at stations where it is present (the third analysis described in methods) increased with increasing temperature, but leveled off at the higher temperatures observed in this study. In ordinary linear models the shape of the relationship was best described by a degree 2 polynomial (figure 13). (A slightly better fit could be obtained by using a non-parametric spline smooth within a GAM fitting procedure, the only notable difference being the predictions at the highest observed temperatures, which were higher for the GAM than for the polynomial fit.) *L. niger* abundance also increased with increasing time since the bait was first put out (n.b. food at the bait stations was refreshed regularly). In addition to these factors which changed over time, there were consistent differences in abundance between bait stations, which could be explained by distance from the sea, vegetation type and path surface. As distance from the sea increased, the abundance of *L. niger* decreased. In models where distance from the sea was not included, vegetation height seemed to have a significant (negative) effect on *L. niger* abundance, but in models where both variables were included, the effect of distance from the sea predominated. Percentage of bare ground had no significant effect on *L. niger* abundance. The parameters of the best fitting linear model for *L. niger* abundance are shown in table 9.

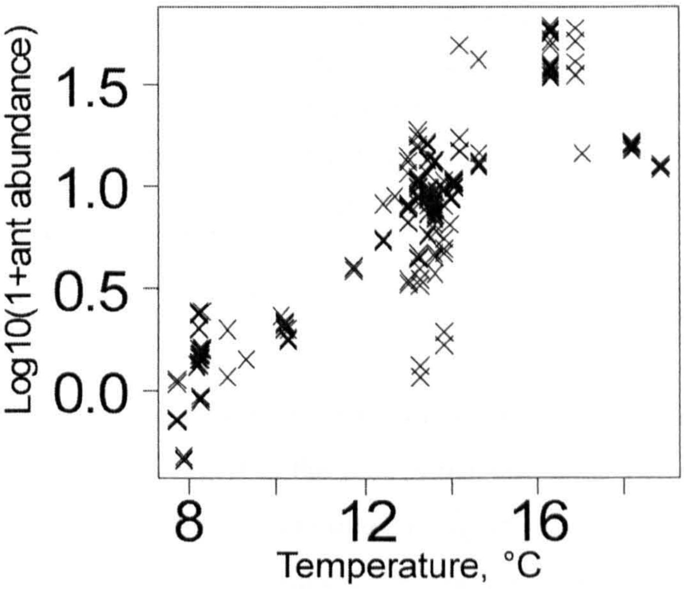


Figure 13: Fitted values of ant abundance against temperature, using degree 2 polynomial fit, other factors affecting abundance are given in table 9.

A linear mixed effects model with distance-based correlation of errors resulted in almost the same parameter estimates as the ordinary linear model. All the variables detailed in table 9 were still significant. The estimated spatial correlation kernel had a 'nugget' of 1, suggesting that there was effectively no spatial correlation effect. However, there was an effect of random differences between days when the baits were checked (which would encompass e.g. weather variables apart from temperature).

Table 9: Parameters of a linear model to explain *L. niger* abundance ($\log_{10}$ transformed after adding 1) at stations where it is present, and not including non-heath vegetation.

Explanatory variable		Parameter Estimate	Std. Error	t value	p
Intercept		9.1E-01	9.0E-02	10.15	<0.001
Polynomial(temperature)1		5.0E+00	5.7E-01	8.78	<0.001
Polynomial(temperature)2		-2.0E+00	5.9E-01	-3.45	0.001
Days since first bait		1.1E-01	2.0E-02	5.37	<0.001
Vegetation types, parameters compared to pure heath	burn (bare ground after heath burning)	-6.2E-02	1.5E-01	-0.43	0.671
	wet grass/heath	-6.5E-02	8.0E-02	-0.81	0.416
	grass/heath	2.3E-01	1.5E-01	1.57	0.119
	coastal grass/heath	-3.2E-01	1.4E-01	-2.29	0.023
	bracken/heath	-3.7E-01	1.8E-01	-2.11	0.036
	bog/heath	-5.1E-01	3.2E-01	-1.60	0.112
Path surfaces, parameters compared to no vegetation	part veg	-1.7E-01	7.5E-02	-2.22	0.027
	vegatated	-2.3E-01	7.7E-02	-2.94	0.004
Sea distance		-9.8E-04	4.3E-04	-2.28	0.023

The temperature values used in the above models were the average of the readings of the temperature loggers at the time of bait checking. The temperatures at different loggers varied according to the vegetation height (figure 14). For this reason, we might expect there to be an interaction between temperature (average) and vegetation height in determining *L. niger* abundance. However this was not apparent in the analysis. I tried modifying temperature according to the vegetation height at each bait station and the daytime temperature differences seen in figure 14: if vegetation was under 10cm, temperature was increased by 1.5 degrees, if vegetation was between 10 and 60cm, temperature was decreased by 0.75 degrees. This adjusted temperature variable gave no improvement in fit to the model of *L. niger* abundance.

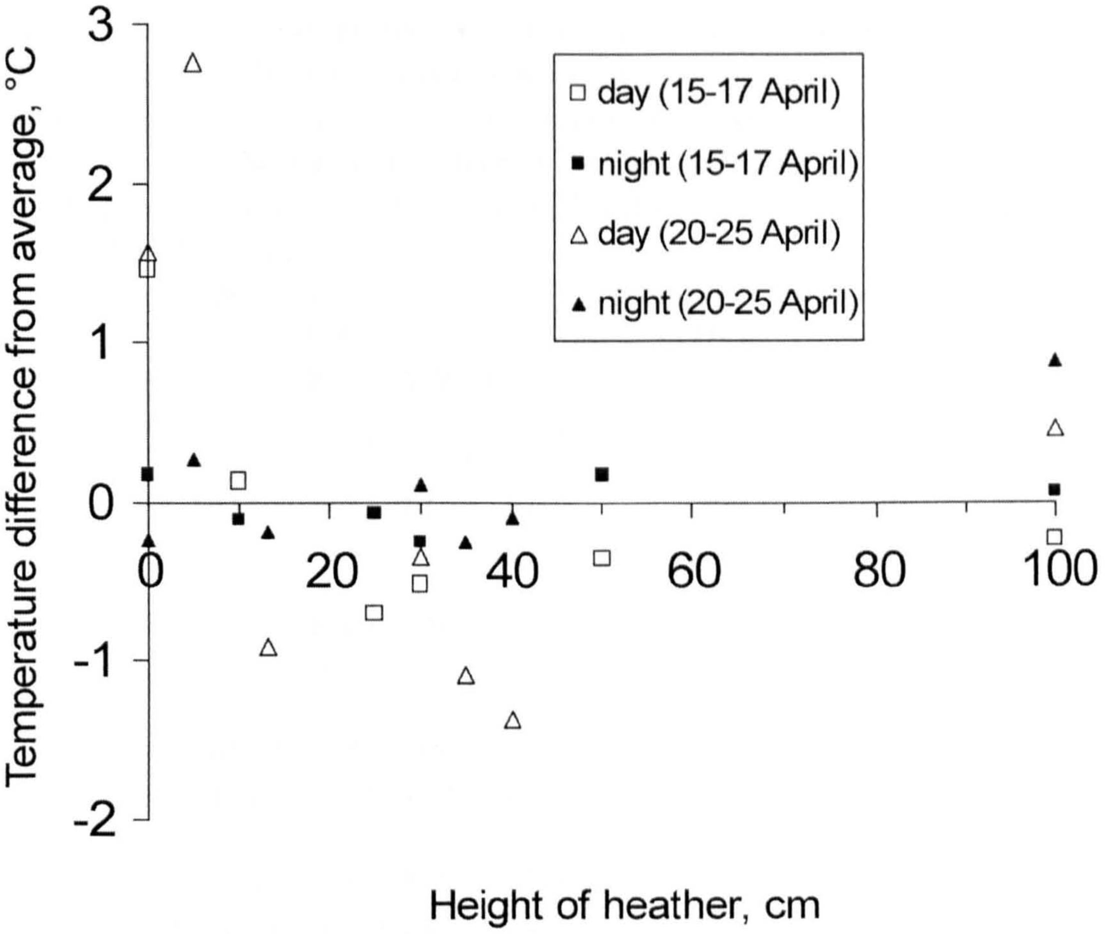


Figure 14: The dependence of ground-level temperature on vegetation height. For each data logger, over all day- or night-time hours, graph shows the average of the difference from the geometric mean temperature at each time point.

4.3.2 Ant-butterfly relationship

The peak density of P. *argus* adults on the 13 sections of the transect was correlated to the presence of L. *niger*. Each measure of L. *niger* occupancy (see methods) gave a significant correlation, but the measure of L. *niger* abundance did not (table 10). The best fit was obtained by using the average of fitted values of the GLM for L. *niger* occupancy (table 10 row 1, figure 15a). Vegetation height by itself was significantly correlated to P. *argus* density (table 10 row 3). When vegetation height and L. *niger* occupancy were both entered into a linear model, both still had highly significant effects (table 10 rows 5-6). In the case of most variables a GAM with a spline based on three nodes gave a significantly better fit than the linear model (table 10). The shapes of the resultant splines show that there is a relationship of 'diminishing returns' - the steepest gradients occur when L. *niger* occupancy is below 0.5, or when vegetation height is above 30cm (figure 15).

Table 10: Significance of variables explaining *P. argus* density on the 13 transect sections in 2005. For linear models the significance is according to an ANOVA comparing the fit with and without the variable in question. For GAMs the significance is according to an ANOVA comparing the GAM to a linear model with the same variable(s).

SIGNIFICANCE OF VARIABLES IN LINEAR MODELS					IMPROVEMENT WITH GAM			
	N	**Sum of Sq**	**F**	**p**	**Increase in Df**	**Sum of Sq**	**F**	**p**
MODELS WITH ONE VARIABLE								
L. niger glm response*	13	44.4	16.2	0.002	0.93	18.1	16.2	0.003
L. niger average occupancy	13	39.8	12.6	0.005	0.80	10.9	5.9	0.04
Veg height	13	36.6	10.6	0.008	0.79	11.6	5.7	0.04
L. niger lm response†	11	1.7	1.0	0.3	0	0	na	na
BOTH VARIABLES TOGETHER								
L. niger glm response	13	23.5	16.2	0.002	1.41	7.8	7.1	0.02
Veg height		15.7	10.9	0.008				

*This is the model in the last line of table 7

†This is the model detailed in table 9

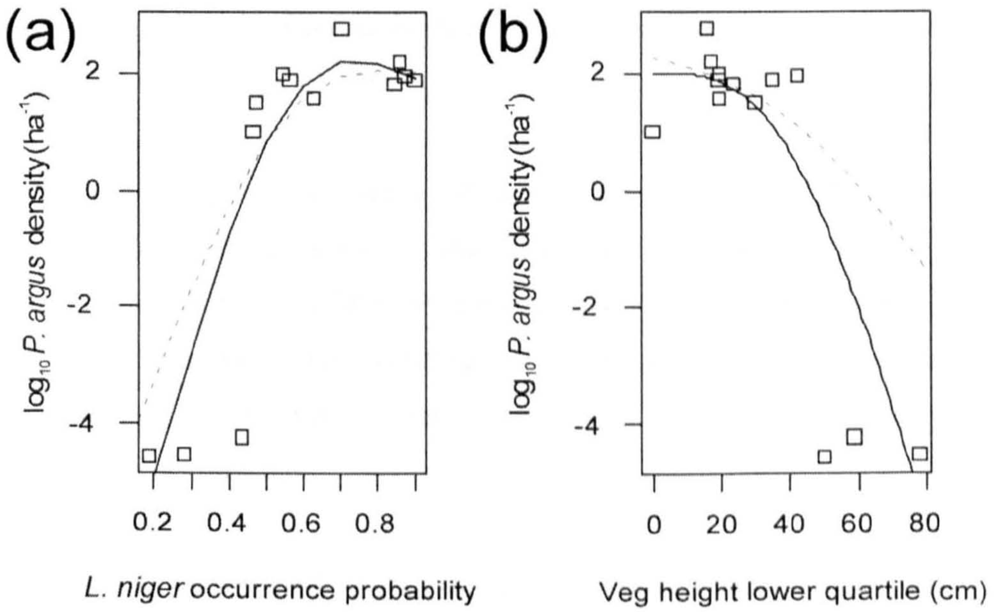


Figure 15: The response of *P. argus* density to (a) the occurrence of *L. niger* and (b) the vegetation height. Solid lines show the predictions of GAMs fitted to each variable individually, dashed lines show the prediction of the GAM fitted to both variables together.

In this study I hypothesised that vegetation height would drive differences in ground-level daytime temperatures, which in turn would drive the abundance of *L. niger* ants, which in turn would drive the abundance of P. *argus* butterflies. This theory is partly substantiated, but there are other complicating factors, including vegetation type and the influence of the sea. The second part of this chapter describes how I took account of the complex relationships described above in setting parameters for simulating this landscape with the MANAGE model.

4.4 Methods part 2: Parameterisation

The results of the ant transect make it clear that proximity to the sea is beneficial for L. *niger* occurrence and abundance, and I therefore concluded that I should include the influence of the sea in my simulations of the P. *argus* metapopulation. One simple way to achieve this within the MANAGE model is to define some permanently suitable patches of habitat around the coastline. Data from the butterfly transect that has been carried out every year between 1984 and 2005 shows that sections 3, 4 and 5 have always had P. *argus* present, whereas the other sections have all shown an absence of P. *argus* in one or more years. Sections 3-5 are also the closest to the sea: each has its closest point between 14 m and 70 m from the sea and the next closest section is (at closest) 125 m from the sea. Based on this data I decided to treat 125 m as a cut-off point between permanently suitable habitat (habitat that is kept permanently open by eg salt spray, wind and cliff erosion), and habitat that only becomes suitable following additional disturbance, e.g. fire.

When attempting to parameterise habitat quality for P. *argus*, we also know that there are some habitats which will not contain P. *argus* food plants, although they may be habitats for L. *niger*. I concluded that bracken, bracken/gorse, bog and wet grassland should be considered permanently unsuitable for modelling. Also, in the context of modelling succession, these habitat types would not be expected to increase in height in the same way that heathland does following a disturbance.

I repeated the GLM predicting L. *niger* presence (analysis 2 in methods part 1) excluding baits that were less than 125m from the sea, and excluding the four habitat types mentioned above. In this model, vegetation height had a significant effect on L. *niger* presence, even when distance from the sea was included as a covariate ($p=0.048$, chi-squared test). Therefore, I decided to parameterise heathland succession based on vegetation height using a 3-step process (figure 16)

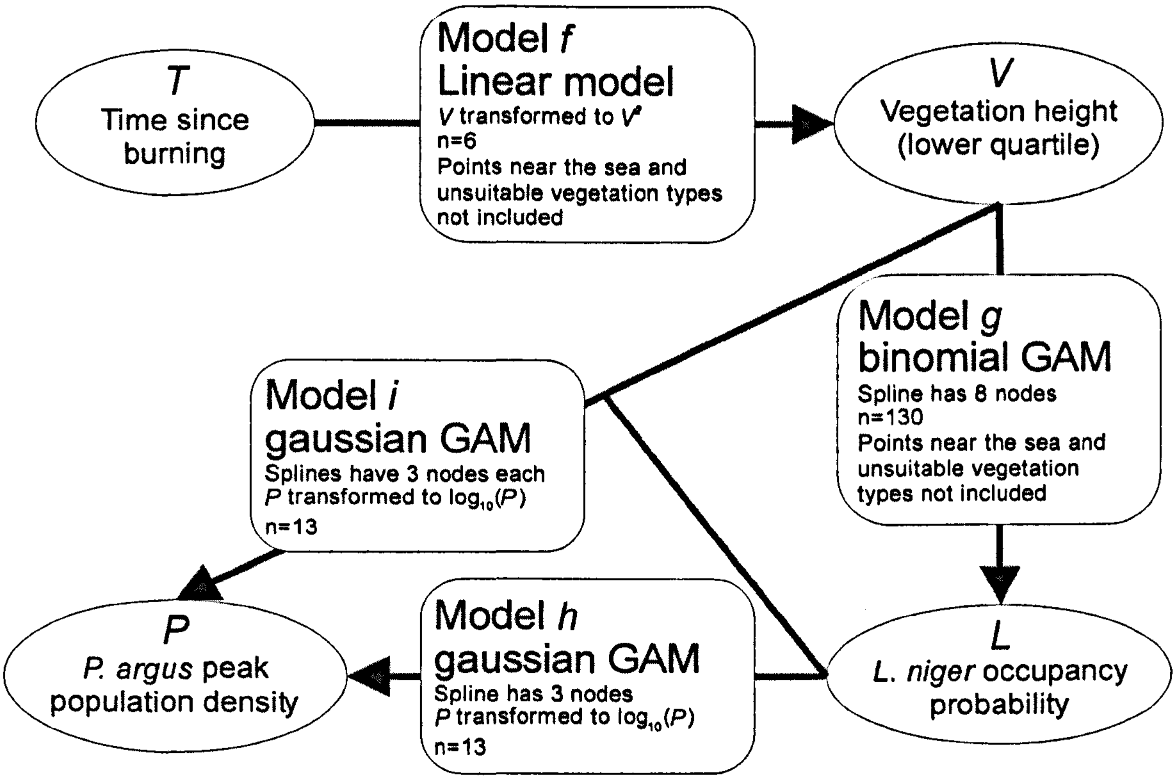


Figure 16: Schematic diagram of the chain of models used to predict *P. argus* density at different time points in the heathland succession. Note that the fits of models *h* and *i* are shown in figure 15.

Data on time since burning were available for the whole of Penrhosfeilw Common, although the longer times are only rough estimates. Each unique time value (each fire or block of similar-aged heath) was considered to be one data point. Data on vegetation height and ant presence were available for every bait station, but the data on *P. argus* was only available as averages over the 13 transect sections (see methods part 1). To relate vegetation height (lower quartile) to time since burning I used a linear model with intercept zero, after transforming vegetation height by squaring it (figure 16, model *f*). (The squared transformation produced a better fit than a simple linear model, and might also be justified because heather plants grow by extending shoots laterally as well as vertically.) To relate the probability of *L. niger* occurrence to vegetation height I used a GAM (figure 16 model *g*). The advantage of a GAM is its flexibility to fit non-linear relationships, which suited this dataset, especially given the variable response to very tall vegetation (see results part 2 and discussion). The disadvantage is that there is not strong theoretical support for extending the predictions of a GAM to new situations, e.g. other geographical areas. To relate *P. argus* density to the occurrence of *L. niger* I used the GAM already described in methods part 1 (figure 16 model *h*, see also table 10 row 1). I used these three statistical models in a chain to generate predictions of *P. argus* density given time since burning. I used a conservative method of propagating the errors around these predictions. If the uncertainty in model *f*s predictions of *V* can be described by the range

$f(T) - \mathrm{SE}(f(T)) < V < f(T) + \mathrm{SE}(f(T))$ where *T* is time, *V* is vegetation height and SE is standard error, and the set of values that satisfy this inequality is denoted as $\mathbf{A}_T$, then the uncertainty in predicting *L. niger* occurrence probability (*L)* based on a particular time, (*T*), denoted as $\mathbf{B}_T$, is taken to be the range between the overall minimum of $g(V) - \mathrm{SE}(g(V))$ where *V* is in $\mathbf{A}_T$, and the overall maximum of $g(V) + \mathrm{SE}(g(V))$ where *V* is in $\mathbf{A}_T$. Similarly, the uncertainty in predicting *P. argus* density, (*P*) based on a particular time, (*T*), is taken to be the range between the overall minimum of $h(L) - \mathrm{SE}(h(L))$ where *L* is in $\mathbf{B}_T$, and the overall maximum of $h(L) + \mathrm{SE}(h(L))$ where *L* is in $\mathbf{B}_T$.

I also tried making predictions of *P* based on the GAM that includes both *L. niger* occurrence and vegetation height (figure 16 model *i*, see also table 10 rows 5-6). In this case the calculation of standard errors is even more complicated, and given that the predictions fell within the standard error ranges calculated in the previous case, I decided that it would not be very informative to calculate them.

Finally, I translated these predictions of *P. argus* density through time to the parameters needed by the MANAGE model. MANAGE models successional changes in habitat quality with a trapezium-shaped quality profile, defined by its height and its 'corners' (*Qmax*, *t1*, *t2* and *t3* as described in section 2.2.3). I found the best-fitting trapezium by fitting linear models to yearly density predictions versus the yearly *Q* values where *Qmax*= 1 and all feasible combinations of *t1*, *t2* and *t3* are used in turn. The combination of *t1*, *t2* and *t3* that gave the lowest residual sum of squares was chosen as the best, and the fitted slope of this model defined *Qmax*.

4.5 Results part 2: Parameterisation

The relationship between the time since burning and the (squared) vegetation height was fitted well by a linear model (fig. 16 model *f*, fig. 17a). By contrast the relationship between vegetation height and the probability of *L. niger* occurrence was strongly non-linear, and the spline fitted by GAM (model *g*) has 4.4 estimated degrees of freedom (figure 17b).

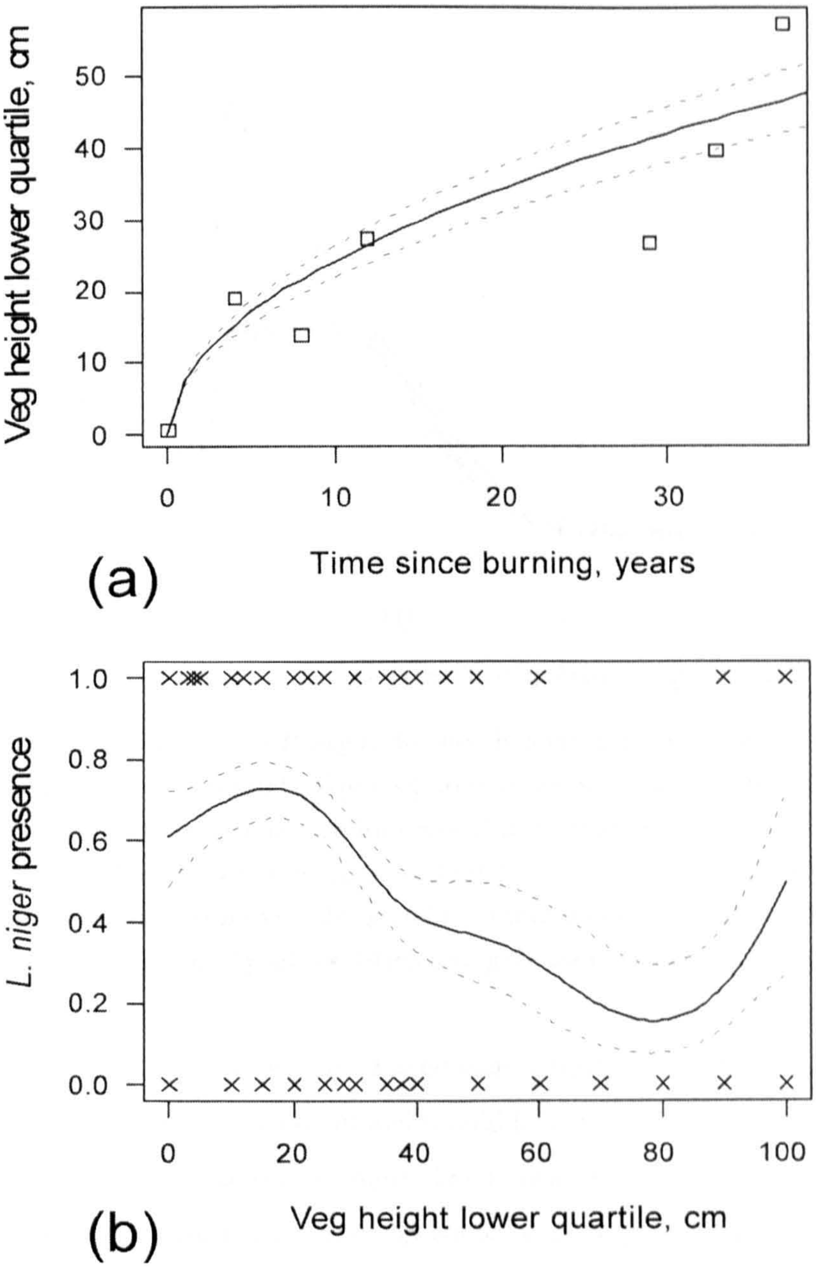


Figure 17: The fit of models explaining (a) the increase in vegetation height with time since burning and (b) the response of *L. niger* occurrence to vegetation height, which I have called models *f* and *g* respectively (see text and figure 16). The points show the data used in fitting, the solid lines show the model predictions and the dotted lines the predictions +/- 1 standard error. For more details about the models see figure 16.

The two alternative models of *P. argus* density (*h* and *i* in figure 16) give rise to quite different predictions of density change with time since burning (figure 18, see also the fits of the models in fig. 15). The differences are primarily in the first three years after burning, with model i producing a higher, sharper peak (figure 18), and although the lines are not statistically significantly different, they could produce quite different results when used to simulate succession.

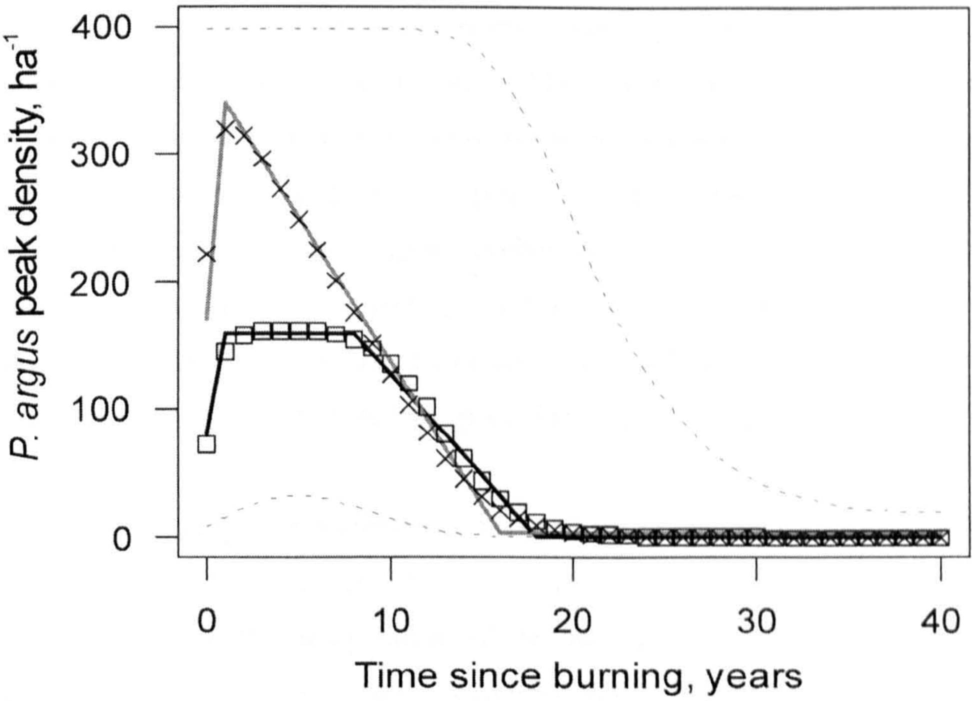


Figure 18: Profiles of *P. argus* density through time in the heathland succession, predicted from a chain of models. Open squares show the yearly predictions when model *f*'s predictions feed into model *g* and then into model *h*. Dotted lines show the propagated standard errors around these predictions (see methods). Crosses show the yearly predictions when model *f*'s predictions feed into model *g* and then into model *i*. Thick solid lines show the best fitting trapezium-shaped profiles, black and grey for the chains using models *h* and *i* respectively.

When fitting the trapezium-shaped quality profiles I assumed that the minimum density (*Qmin*) in the MANAGE model should be zero, which is reasonable as densities late in succession approach zero (figure 18). However, densities in year zero are well above zero. This is because burns usually occur in winter and it is possible for the butterflies to colonise the area in the summer immediately following. Therefore the best fitting trapezium profiles have a corner at zero density in year -1. This merely means that MANAGE will count the year before a fire as year zero of succession, and it should not affect the population dynamics in the model. The other parameters of the succession profile will be *t1*= 2, *t2*= 9, *t3*= 19, and *Qmax*= 158 if model *h* is used, and *t1*= 2, *t2*= 2, *t3*= 17, and *Qmax*= 337 if model *i* is used.

4.6 Discussion

4.6.1 Habitat and microclimate associations of *Lasius niger*

The relationship between heathland vegetation height and *Lasius niger*, via the ground temperature, is more complicated than I predicted. Vegetation height seems to drive differences in ground-level daytime temperatures – particularly high temperatures are found where vegetation is absent or very short. Also, average temperature at the time of bait checking affects the number of ants seen. However, correcting the average temperature based on the vegetation height does not help to explain the number of ants seen. Very short vegetation is associated with higher numbers of ants and a higher probability of ants being present, but it is also correlated to proximity the sea, so it it hard to say where the causal relationships lie. The presence of an unvegetated path seems to have a positive influence on *L. niger*, but a high proportion of bare ground amongst the vegetation does not seem to.

The lack of a simple correspondence between the vegetation's effect on temperature and the vegetation's effect on ants could be due to a number of factors. Firstly, where there is tall vegetation, the ground temperature will be lower than air temperature during the day, but at intermediate levels in the canopy the temperature can be higher than air temperature (Geiger 1965). This leaves open the possibility that ants can behaviourally thermoregulate so as to reach the maximum body temperature possible given the air temperature. Secondly, as mentioned in the introduction, the final "degenerate" stage of heathland succession can be associated with rising ground temperatures as the shrubs' canopy becomes less dense. This could explain the non-linearity in both temperature (figure 14) and *L. niger* occurrence (figure 17b) at the tallest vegetation heights. Also it could be that *L. niger* is favoured by some consequence of physical disturbance (by humans in the case of paths, salt spray and wind close to the sea), other than changes in ground temperature.

As one might expect of such a generalist ant, *L. niger* was found in almost all vegetation types, but it was less likely to be present in non-heath types (including bracken stands, bog, and gorse thickets). *P. argus* is also not associated with these vegetation types, presumably as much related to lack of larval food plants as to the lack of mutualist ants.

4.6.2 The relationship between *P. argus* and *L. niger*

On the scale of transect sections, the proportional presence of *L. niger* helped to explain the abundance of *P. argus* adults. This finding accords with other published studies on the ant association of *P. argus* (Ravenscroft 1990; Jordano *et al.* 1992; Gutierrez *et al.* 2005). It is unfortunate that I could not measure the abundance of *Plebejus argus* caterpillars at the same time, and the same spatial scale, as the ants, because I think the small-scale patterns of spring temperature and ant activity could be responsible for the marked patchiness of the butterfly population on this heath. In the data that were available, butterfly numbers were averaged over quite large areas, so there is the potential for overestimating the species' habitat tolerances and underestimating its maximum density.

The section average vegetation height had a significant effect on *P. argus* density, on top of the effect of *L. niger* (table 10), even though both explanatory variables are correlated. When a model including both variables (model *i*) is used to predict *P. argus* densities through succession, the succession profile has a higher, sharper peak (figure 18). This is easy to explain by considering that in model *g*, short vegetation is beneficial for ant occurrence, and in model *i* both short vegetation and high ant occurrence are beneficial for butterfly density, so using the chain of models, the short vegetation present in the early years 'counts twice' in producing high butterfly densities. This assumption of additivity in the direct effect of vegetation and the indirect effect via the ant occurrence may or may not be realistic, and to disentangle the relationships would require much more data (preferably with examples where high ant occurrence was combined with tall vegetation and vice versa).

Thomas (1983; 1991a) measured temporal autocorrelations in *P. argus* density from the RSPB's permanent transect (an earlier time period than the data used in this chapter), and found that positive correlations lasted about 10 years. This is consistent with the findings in this chapter: the time from peak *P. argus* density to zero density is approximately 10 years (figure 18), (though the time from a density trough to the next peak will depend on the fire return interval, which is not considered here). Understanding how long burned patches provide suitable habitat for *P. argus* is a crucial step towards predicting the population's persistence in this and other heathland landscapes. Not only does habitat longevity combine with disturbance rate to determine the total habitat availability in the landscape, but it also affects the per-patch extinction rate (see section 2.1), and these extinctions must be balanced by colonisations in order for the metapopulation to persist. The results of this chapter are used to inform modelling of *P. argus* metapopulations in chapters 5 and 6.

4.7 Summary

- The relationships between vegetation height and temperature, and temperature and L. niger abundance, were not as straightforward as I had hypothesised. However, there was a negative relationship between vegetation height and L. niger occurrence and abundance.

- Low vegetation height and a high prevalence of L. niger both lead to high P. argus abundance.
- Heathland which is permanently short because of proximity to the coastline may provide permanently suitable habitat for P. argus.
- After burning, heathland may be suitable for P. argus for up to 17 years, but suitability declines rapidly after 8 years.

5 Responses of butterfly metapopulations to patch connectivity and average patch quality are masked by successional habitat dynamics.

5.1 Introduction

Studies of species occurrence at a landscape scale have usually been underpinned by one of two apparently opposing paradigms: the "habitat selection" model or the "metapopulation" model (Armstrong 2005). The former paradigm holds that the pattern of occurrence of populations in a region reflects habitat quality, and that dispersal between habitat patches has a minimal effect on this pattern. The latter holds that dispersal strongly affects the pattern of occupancy and persistence, because there are likely to be stochastic extinctions even in good quality patches. There is increasing recognition that neither paradigm is sufficient by itself (Thomas *et al.* 2001; Franken & Hik 2004; Guisan & Thuiller 2005; Moore & Elmendorf 2006), and that they could be integrated (e.g. Wiens, J.A. 1997; Armstrong 2005). However there has been little discussion of how habitat quality and connectivity could interact with each other, especially in cases where habitat quality changes through time. For species that specialise on one stage of a successional cycle, one expects that habitat quality and connectivity at any location must be variable. Habitat quality and connectivity in previous years could affect whether a location is occupied. So, in typical occupancy studies that examine a snapshot or a long-term average of the landscape, the existence of successional dynamics could obscure the effects of connectivity or the effects of habitat quality.

The early metapopulation models assumed that all suitable habitat could be identified (Lawton & Woodroffe 1991), and its spatial arrangement did not change over time (Hanski 1994; Hanski & Simberloff 1997). There have been modifications of the theory to account for cases where habitat is gradually eroded over time, or a number of patches are suddenly removed (Tilman *et al.* 1994; Gyllenberg & Hanski 1997; Ovaskainen & Hanski 2002). In recent years, more attention has been paid to metapopulations on successional landscapes, where suitable habitat appears and disappears more or less predictably every year (Lindenmayer & Possingham 1995; Stelter *et al.* 1997; Johnson 2000b; Keymer *et al.* 2000; Amarasekare & Possingham 2001; Wahlberg *et al.* 2002; DeWoody *et al.* 2005). In theoretical studies it has been shown that introducing succession makes patch occupancy lower because of the increase in per patch extinction rate (Johnson 2000b). This is the first prediction tested in this chapter:

it is tested by comparing *Plebejus argus* metapopulations inhabiting more and less successional habitat types.

It is a general feature of patch occupancy metapopulation models that colonisation rate (or probability) depends on connectivity to other occupied patches (Hanski 1998; Ovaskainen & Hanski 2004); in some models connectivity also reduces extinction rate (the rescue effect). If either of these are true, and if the model has a positive equilibrium, then the expected occupancy of a patch at equilibrium will be positively related to its connectivity (Ovaskainen & Hanski 2001). Whether or not a positive connectivity-occupancy relationship can be observed in a real metapopulation depends on, among other things, whether the metapopulation is at equilibrium (Hanski 1994; Moilanen 2000), and whether the chosen measure of connectivity is a good enough estimator of the rate of immigrants arriving at a focal patch (Moilanen & Nieminen 2002).

In successional landscapes, the spatial pattern of connections between patches changes over time, and therefore, compared to static landscapes, there is a more complex relationship between patch occupancy and connectivity (Keymer *et al.* 2000). Keymer et al. (2000) applied results from percolation theory to ecology, considering the invasion and persistence of a species on a lattice of equivalent patches, with constant, space-independent rates of disturbance (patches becoming suitable) and successional change (patches becoming unsuitable). They highlighted the fact that, in a landscape with a low proportion of suitable habitat, the habitat dynamics ensured that no patch was permanently isolated from colonisation. But, by the same token, well-connected clumps of patches would not permanently be well-connected. In this chapter I use a model with a finite set of patches that can be of different sizes and located anywhere (not on a grid), but the above conclusions of Keymer et al. (2000) are still applicable.

The model that I use is based on the incidence function model (IFM)(Hanski 1994): a stochastic model where patch colonisation and extinction probabilities are determined by functions of their connectivity and area (see also section 1.2). The dynamical behavior of the IFM when the landscape is static (i.e. patch properties do not change) is already well understood (Hanski 1998; Hanski & Ovaskainen 2000; Ovaskainen & Hanski 2001; Hanski & Ovaskainen 2003). The main theoretical difference between my model and the IFM is the inclusion of a patch quality (expected population density) parameter that changes over time (see equations 1-3 and section 2.2.3). My model is meant to represent a situation where patch quality changes because of succession, and where succession is re-started by disturbance events (which always affect an entire patch). Comparing such a model to its non-successional counterpart, we may expect the realised relationship between the occupancy of a patch and its connectivity at equilibrium to be weaker for two reasons.

Firstly, if disturbance and succession occur independently of species presence this interferes with the positive feedback effect that well-connected patches can have on each other. Positive spatial autocorrelations in occupancy occur in the IFM and similar models at equilibrium because dispersal is limited by distance and nearby patches enhance each other's probability of occupancy. This means that the removal of a patch from a well-connected cluster can leave the other patches significantly above their new expected occupancies (Ovaskainen & Hanski 2001). Likewise, as a new patch appears following a disturbance, its occupancy is necessarily zero but the expected occupancy of this and the surrounding patches will suddenly increase because of the increase in connectivity between them. It will take time for the 'benefit' of new patches to be realized, and so, in a landscape where the relative locations of patches are always changing, the clusters of high occupancy will always lag behind the clusters of patches that are presently close together (the degree of discrepancy depending on the relative rates of habitat dynamics and the species' response to the new habitat distribution). Secondly, at times when patches have a low quality they are less likely to be colonised, whatever their connectivity. The changes in patch quality through time can be considered to add extra 'noise' to the connectivity-occupancy relationship that would be observed at any time point.

For both these reasons one expects a weak *apparent* relationship between connectivity and occupancy in dynamic habitat metapopulations, even though connectivity may ultimately explain colonisations. The true variable of interest to explain occupancy would be some function of a patch's history of connectivity and quality since the last disturbance. Biedermann (2004) found a probable example of this phenomenon in a real metapopulation of leaf beetles on dynamic patches of host plant: data gathered from the field showed that colonisation was more likely in patches with higher connectivity, but that the occupancy state of patches from snapshots was not significantly related to their connectivity. However, Biedermann (2004) did not have any data from static habitat for comparison. The second prediction tested in this chapter is that a static habitat metapopulation will show a steeper relationship between connectivity and occupancy than a dynamic habitat metapopulation.

The relationship between habitat quality and a species distribution can also be complicated by successional dynamics. In a static habitat, quality is simply related to the maximum or average population density at a site, and high quality habitat is more likely to be occupied in the long term (whether metapopulation dynamics are at work or not). In dynamic habitat metapopulation models, habitat occupancy is strongly affected by the temporal pattern of high quality and low (unsuitable) quality phases (Johnson 2000b; Keymer *et al.* 2000; Ellner & Fussmann 2003; Hastings 2003). Therefore, we might expect habitat quality, particularly when averaged over time, to be a poorer predictor of patch occupancy in a dynamic landscape than in a static landscape, and this is the third prediction tested in this chapter.

Although I have used *Plebejus argus* as a case study here to test the above theoretical predictions, there are also conservation implications of this work for a variety of species that inhabit successional landscapes. At least in Britain, about half of all threatened species are associated with early-succession habitats which must either be maintained through the continuous initiation of new successions, or by management intervention that halts succession at a particular seral stage (Thomas *et al.* 1994). The majority of these species are likely to exhibit some kind of metapopulation dynamic, since they must track shifts in the locations of suitable habitats (Thomas 1994), and conversely many species that exhibit metapopulation dynamics apparently inhabit transient habitats (Harrison 1993). With a metapopulation model (an implementation of the Incidence Function Model), modified to include successional habitat dynamics, I show that a frequently used test (the relationship between patch occupancy and connectivity e.g. Watling & Donnelly 2006; Pellet *et al.* 2007) to decide whether a patchily-distributed population is functioning as a metapopulation can give misleading results. The conclusion that a set of populations is or is not a functioning metapopulation can have far-reaching consequences for conservation planning, for example the decision to protect unoccupied but potentially suitable habitat.

Plebejus argus is an ideal case study species to address these questions because it occurs as metapopulations on two different habitat types (biotopes). One biotope, heathland, is dynamic and *P. argus* colonies are restricted to early successional stages (Thomas 1985a, 1985b). In the other, limestone grassland, habitat cycles do not occur because the advance of vegetation succession is prevented by grazing. By comparing long-term census data from the two metapopulations, I provide the first empirical test that a dynamic habitat differs from static habitat according to the expectations from theoretical studies, mentioned above. I also test whether the simulation model including succession is better than the classic IFM at reproducing the empirical patterns observed in the heathland metapopulation.

5.2 Methods

5.2.1 Study species and field surveys

Plebejus argus is a butterfly that is widely distributed across Eurasia, and has evolved to use different habitats and larval food plants in different parts of its range. In Britain it is mainly found on heathland and calcareous grassland, and it feeds on several different ericaceous and leguminous plants, and on *Helianthemum* spp. (Thomas 1985b). Surveys of the distribution of *P. argus* across North Wales were carried out in 1983, 1990, 1997 and 2004 (Thomas 1985a; Thomas & Harrison 1992; Thomas *et al.* 2002, see also section 1.5 and appendix 1). For the analyses presented here, I compare the metapopulation on heathland on Holy Island, Anglesey (appendix figures 32-36), with that on limestone grassland in Conwy, including the area from the Great Orme to the Dulas Valley (appendix figures 37-40). These heathland and limestone metapopulations are far enough apart not to exchange individuals, and they are similar in many respects (table 11). A striking difference between them is that the heathland metapopulation has higher rates of extinction and colonisation (table 11, Thomas & Harrison 1992), which seems to be related to the dynamic, successional nature of this habitat. There is no reason to believe that butterflies were any easier to detect in one biotope than in the other, and MRR studies that have been carried out in both biotopes indicate no significant difference in dispersal distances (Thomas 1985b). In most of the occupied patches it was possible to estimate population density by transect counts, and adjust this to annual peak population density (adults.ha^{-1}) using data from two permanent transects, one for each biotope (Thomas 1985a). Transects were not reliable in 1990 because of poor weather. The recording of empty habitat was slightly different in limestone and heathland because of the dynamic nature of heathland habitat. In limestone the boundaries of unoccupied, suitable patches were mapped. In heathland all potential habitat was searched but there was no attempt to draw patch boundaries where butterfly colonies were not present. In 2005 I systematically mapped the potential habitat within 1km of any observed colonies on Holy Island. I took the Countryside Council for Wales' Phase 1 habitat classification of 1990 as a starting point, selecting all heath-containing vegetation types and disused quarries I visited all accessible patches of this habitat to check whether it was potentially suitable for *P. argus* – sites were discounted if they were mostly gorse (*Ulex spp.*), or mostly grasses.

Table 11: Comparison of essential features of the two metapopulations of *P. argus* in North Wales

Variable	Limestone	Heathland
Total number of patches recorded	67	66
Median patch area	0.28 ha	0.23 ha
Total area of patches that were ever occupied	61.7 ha	75.7 ha
Total area of patches that were never occupied	9.3 ha	Unknown, but total area of potentially suitable heathland on Holy Island is 382 ha
Turnover between surveys 7 years apart (extinctions+ colonisations)/average number of occupied patches	20%	41%

Maps from all *P. argus* surveys were digitized using ArcGIS (ESRI, Redlands, CA, USA). The areas and centroids of each polygon were calculated. For the purposes of the current study, any patches that were observed to merge or split were treated as a single patch at all time points (see appendix table 21). The areas of sub-patches were summed and their centroids were averaged (see appendix table 20 for raw data). Data were further analyzed in R (R Development Core Team 2005).

5.2.2 Analysis of population density

The data on population densities in patches were $\log_{10}$ transformed. Differences in density against $\log_{10}$ patch area and between biotopes, years, and localities within biotopes were tested by ANOVA. The significance of random variation in population density between patches was investigated using linear mixed effect models (Pinheiro *et al.* 2005). If the random patch effect is significant, this gives an indication that different patches have intrinsically different habitat quality. The results of these analyses were used to estimate the regionally correlated stochasticity for use in simulations (as the standard deviation across years, see next section) and to estimate a "quality" for each patch (as its average log population density after controlling for the effect of year).

5.2.3 Fitting IFM parameters using SPOMSIM

I exported the limestone patch survey data to the program SPOMSIM (Moilanen 1999, 2000, 2002, 2004) and used it to estimate IFM parameters for *P. argus*. I used the non-linear regression (NLR) method (the MC method (Moilanen 1999) is potentially better able to account for non-independence of patches, but does not work very well when surveys are very widely spaced in time, as in this case). The occupancy data for the limestone patches was fitted to the model:

$$p[Extinction]_{i,t} = (1 - p[Colonisation]_{i,t}) \cdot \frac{\mu}{A_i^x} \qquad (7)$$

for an occupied patch *i* at time *t*;

$$p[Colonisation]_{i,t} = 1\text{-}e^{-y \cdot S_{i,t}} \quad (8)$$

for an empty patch *i* at time *t* where

$$S_{i,t} = \sum_{j \neq i} z_{j,t} \cdot e^{-\alpha \cdot d_{ij}} \cdot A_j^{\,b} \qquad (9),$$

where *i* and *j* index the number of patches, *z* is patch occupancy state (0 or 1), *d* is distance between a pair of patches (edge-to-edge assuming patches are circles) and *A* is patch area. With regional stochasticity, *A* varies stochastically with time so that

$$A_{effective_{i,t}} = A_i \cdot 10^{r_t}; r \sim N(0,s) \quad (10).$$

I fixed the regional stochasticity parameter *s* at either 0, 0.16 or 0.18, according to estimates from the population density data (see above, and equation 10). Parameter *b* was fixed at 0.85 as estimated from mark-release-recapture data between patches in Lewis (1997).

Parameters α, *y*, *μ* and *x* were allowed to vary in the NLR parameterisation. The parameterisation procedure uses simulations to calculate the likelihood of the observed occupancies and turnover rates given a certain parameter set. It converges on parameter sets with higher likelihood using simulated annealing. The path taken through parameter space and the likelihood at each point are saved, and can be used to calculate confidence intervals by likelihood ratio tests.

Initially I compared parameterisation runs where the patch quality estimated from population density was included (as multiplying A_i in equation 7) or not included. The former gave consistently higher likelihood values, so in subsequent parameterisations I always included patch quality.

I took the parameter set with the highest likelihood from the initial parameterisation runs, and used this as the starting point for 9 more intensive parameterisations (3 replicates with each stochasticity value). I also ran 3 intensive parameterisations where the starting value of α was 3, as this was the value used in previous metapopulation studies of *P. argus* (Thomas *et al.* 2002). I pooled the output from these parameterisation runs by stochasticity value, before applying SPOMSIM's confidence interval calculator.

It was clear from examining the output files that firstly, confidence intervals were very wide and secondly, a large proportion of the points that fell within the confidence intervals failed the likelihood ratio test, and there were even widely differing estimates of the likelihood of a single point in parameter space (figure 19). Therefore I realised that picking the maximum likelihood from each output file would not reliably represent the best parameter set, as each likelihood value was only an estimate of the true likelihood. This problem could be fixed by increasing the number of simulation runs used to estimate each likelihood value, but unfortunately this option cannot be changed within SPOMSIM. Instead, I decided to smooth the likelihood estimates using a GAM (Wood 2004, 2006) in R (making use of the fact that the likelihood should be a smooth function of the parameters), in order to find the region of parameter space that is the best on average.

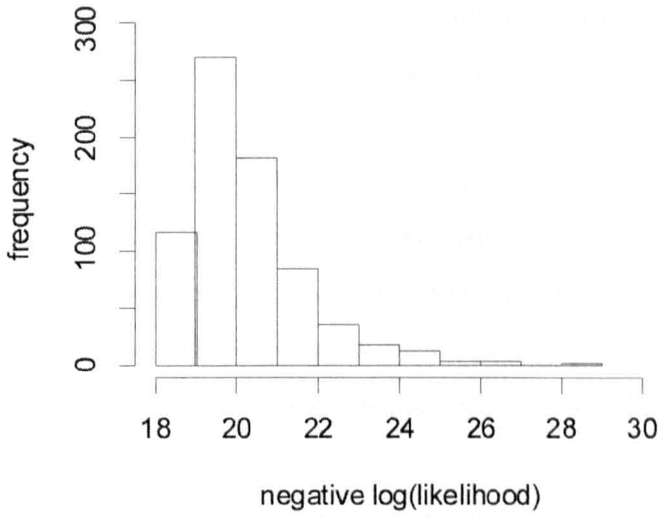


Figure 19: Distribution of point estimates of the likelihood of a single parameter set (α= 1.836, y= 0.197, μ= 0.0515, x= 1.57, s=0.16, chosen simply because it had a particularly large number of repeat estimates during the parameterisation process). The likelihoods vary because each estimate is based on a limited number of simulation runs. Any points with a negative log(likelihood) greater than 20 would fail the likelihood ratio test (i.e. be significantly worse than the maximum likelihood).

Parameters α and y interact to affect colonisation rate, and likewise μ and x interact to affect extinction rate (see equations 7-9 above). Also, extinction rate and colonisation rate interact to affect the overall occupancy. Therefore I fit the GAM using smooth functions of α and of x, and a two-dimensional smooth of $y.e^{-\alpha}$ versus $\mu^{1/x}$ which represents the overall extinction-colonisation balance. Each dimension of the smooth functions was allowed a maximum of 10 degrees of freedom.

5.2.4 Analysis of patch occupancy

The proportion of surveys in which a patch was occupied by *P. argus* is its estimated "occupancy". The effects of biotope, patch area, connectivity and quality on occupancy were tested with binomial GLMs, where patches were weighted by the number of times they were surveyed (usually 4). In this analysis, the area measurements of the same patch in different years were averaged, then $\log_{10}$ transformed, then these patch-wise values were scaled by subtracting the overall mean and dividing by the root mean square. The connectivity (S) of each patch in each year was calculated according to equation 9, but with distances measured edge(j)-to-centre(i) (this ensures that S_i is not positively correlated to A_i, and also means connectivity can be calculated for years when area is not known). Also, in order to make connectivity close to linearly related to logit(occupancy) in GLMs, I applied the transformation $\ln(\exp(yS)-1)$ (the value of y had been estimated using SPOMSIM, see previous section). This transformed connectivity value was averaged across years for each patch, then patch-wise values were scaled by subtracting the overall mean and dividing by the root mean square. The quality of each patch was its mean log population density after controlling for the effect of differences between years (see section 5.2.2). Patches that did not have any population density estimates had their quality predicted from the population density models (see section 5.3.1). Quality was then scaled by dividing by the root mean square of $\log_{10}$ (Area) (so that log population size is proportional to scaled(area)+scaled(quality)).

The significance of biotope, patch area, connectivity and quality were assessed singly and in combination with each other, including the effects of interactions between biotope and the continuous variables. Because area and connectivity data were missing for heathland patches that were never occupied, GLMs were carried out both on the complete data set, and on the set excluding limestone patches that were never occupied.

5.2.5 Modelling

I used MANAGE to model both limestone and heathland metapopulations. When the habitat dynamics options are not used, this simulates exactly the same model as SPOMSIM does (compare equations 1-4 with 7-9), apart from the fact that patch quality can affect colonisation as well as extinction (the A_j in equation 9 becomes A_jQ_j in equation 3). I used the 1983 occupancy of patches as a starting condition. For patches whose occupancy in 1983 was unknown, I used two alternative assumptions and compared the results from each – I either assumed these patches had occupancy 0, or copied the occupancy from the first year when data were available (in practice this option only made a difference to the occupancy for one patch in each biotope). For patches whose quality was unknown, I either used the predicted quality (as in the GLMs, see previous section), or the geometric mean quality for that patch's biotope, and compared the results from each option.

I compared simulation runs to the observed data by sampling occupancy states from the simulations at years 0 (the starting condition), 7, 14 and 21. To each run I fit a binomial GLM including area and connectivity, calculated and transformed in the same way as they were for the real data (see previous section), excluding the data for patches that were never occupied, and compared the model coefficients to the coefficients of the analogous GLM fitted to the real data. For static habitat models I ran 100 replicates. For dynamic habitat models or models with additional patches (see below) I ran 500 replicates, 5 for each of 100 starting conditions.

Recall that in the limestone landscape, the habitat does not undergo much successional change, and the surveyors have mapped all the suitable unoccupied habitat patches. But in the heathland landscape, the habitat is very dynamic, and there is a large amount of potentially suitable heathland that has not been occupied in any survey, and the surveyors could not reliably tell what parts of this habitat were suitable at what times (see table 11). Either the underestimation of patch numbers, or the presence of succession, or both could cause a mismatch between real and simulated heathland occupancy data. I aimed to find out whether either factor or both, when included in the MANAGE simulations, could increase the likelihood of the simulations reproducing the empirical patterns observed in the real heathland metapopulation.

Because the potential habitat had been mapped (see section 5.2.1), but unoccupied suitable patches had not been delimited, I used MANAGE to generate non-overlapping patches randomly within the potential habitat. I did not attempt to estimate exactly how many of these extra patches there were, but I ran sets of simulation scenarios, increasing the number of patches in increments of 20, until the simulations showed that there were too many patches occupied (each 20 patches amounts to c.4.5% of the heathland potentially available). Habitat patch generation simulations were run separately from the 21 year simulations that were compared with the real data. I stopped the former simulations after two years of generating 50 patches per year, and saved the patch co-ordinates and sizes to be entered a starting conditions for the 21 year simulations (picking a random subset of the patches when fewer than 100 were needed). 100 different random landscapes were generated for each of two options:
Each new patch must fit entirely into the available heathland; this option is called "fit" for short (see table 2, section 2.2.3).
Patch centres are selected from within the available heathland, and patch area is truncated to the heathland available within the patch circumference; this option is called "cut" for short (see table 2, section 2.2.3).

The advantage of the "fit" option is that the distribution of patch sizes can be set exactly, and it was set to approximate the distribution of surveyed patch sizes (not including the largest patch). The disadvantage of this option is the restriction on where patches can be placed which means that (a) smaller blocks of heathland are less likely to have patches in them, and

(b) the programme often fails to find places for a hundred patches with the allotted 1000 attempts for each patch. I chose just to use as many random landscapes as were available with the number of patches needed in each simulation scenario: this turned out to be 89 replicates when 60 extra patches were needed, and only 63 replicates when 80 extra patches were needed.

With the "cut" option, there was less restriction on where patches could be placed, and so all 100 random landscapes were available with 100 patches each. But the disadvantage of this option is that the distribution of patch sizes can not be determined exactly: it depends on the interaction of the patch perimeters with the spatial arrangement of habitat. By trial and error, I increased the frequency of larger patches in the "cut" option until the median patch area in the resulting landscapes was the same as in the "fit" option.

When examining the effect of adding extra patches to the landscape, I assumed that all patches (apart from the largest patch at Penrhosfeilw Common) had the same quality: either the mean (0.45) or the geometric mean (0.33) of the surveyed patches. This assumption was necessary, as I had no way of knowing the quality of unsurveyed patches, and justified because patch to patch differences in quality in the heathland were not significant (see results section 5.3.1).

Modelling succession with MANAGE entails many more parameters than modelling a static metapopulation (see chapter 2). These parameters could not be estimated from the heathland occupancy data, and I did not have time to investigate all the feasible options, so I kept the scenarios as simple as possible and estimated the parameters using prior information where possible. The parameters and options used were:

- The largest patch, Penrhosfeilw Common, which was permanently occupied and nearly as big as all the others combined, was treated as permanently suitable and given its original quality, whereas the other 65 patches were successional.
- I used 2 alternative disturbance profiles, which were parameterised in chapter 4 (Estimated from relationships between time since burning, *Lasius* ant occurrence and *P. argus* abundance, see figure 18).
- Disturbance and succession were assumed to be cyclical (patches do not disappear after one successional cycle, but stay 'dormant' until the next disturbance; I varied the dormant phase between 3 and 9 years). Making the patches cyclical enhanced comparability with the static habitat simulations (a fixed number of patches, each one guaranteed to be suitable at some time during the simulation), but also may be justified

because suitable habitat is usually re-created periodically at favorable locations, based on habitat features such as topography, soil & vegetation (Thomas 1985a).

- Each patch follows the same successional cycle, but they have independent phases (i.e. for each of 100 different landscapes, the starting point in the successional cycle for each patch was picked randomly, only ensuring that occupied patches did not start in the dormant phase).
- Mean quality of the successional patches was adjusted to be either 0.33 or 0.45 over the first 21 years of the cycle.

I think that the options used were appropriate as a demonstration of what could be responsible for the differences between the heathland and the limestone metapopulations.

5.3 Results

5.3.1 Determinants of population density

Limestone patches had significantly higher population density ($\log_{10}$ transformed) than heathland patches ($F_{1,163}$=7.1,p<0.001), and population density generally increased with increasing patch area ($F_{1,163}$=4.7, p<0.001), but there were also significant biotope*area ($F_{1,158}$=10.4, p=0.002), biotope*year ($F_{2,158}$=9.9, p<0.001) and biotope*area*year ($F_{2,156}$=3.2, p=0.045) interactions, which implied that there are different determinants of population density in the two biotopes. Therefore I fitted linear models separately to each biotope, retaining only the explanatory variables that were significant for each one.

In limestone, patch area and year were significant determinants of population density, but no interactions were significant, and there was no difference between the two sub-areas (Creuddyn Peninsula and Llandulas)(table 12). A mixed-effects model, where the density values are grouped by patch, fit significantly better than the simple linear model (AIC decreases from 110.8 to 106.4, likelihood ratio= 6.3, p=0.01), this implies that there are consistent differences in quality between limestone patches. However, the same fixed effects were significant (none of the coefficients for the fixed effects differed significantly between the simple linear and mixed-effects model, t tests p>0.5).

In heathland, patch area was a significant determinant of population density, the factor year was almost significant and there were significant differences between the sub-areas of Holy Island (the northern half generally having higher densities), but no interactions were significant (table 12). A mixed effects model offered no improvement on the simple linear model, implying that there is random variation in population density both between years and between patches, but no consistent patch-to-patch differences in quality (however, patch-to-patch differences may be difficult to detect because there are fewer repeat measurements of population density in heathland patches, since occupancy was generally lower than in limestone).

Table 12: Significance of variables in linear models of $\log_{10}$(population density) with respect to patch area, year and locality

	Variable	df	F	p
Limestone	log10(area)	1	7.7	<0.001
	factor(year)	2	1.6	0.035
Heathland	log10(area)	1	5.9	0.018
	factor(year)	2	2.9	0.059
	locality	3	5.1	0.002

An estimate of 'quality' for each patch was obtained by removing the year effect from the population density estimates and then averaging. Patches with no population density estimates had their quality predicted (in one option as the geometric mean of their biotope, and in a second option predicted from the statistical models based on biotope, locality and area).

The standard deviation of year effects in these models provided estimates of the regional stochasticity for using in simulations (because regional stochasticity is modelled as year-to-year random variation in population size that is correlated across all patches in the metapopulation, see equation 10). The estimate for limestone is 0.18 (both for the mixed effect and the simple linear model). The estimate for heathland is 0.16 if the year factor is entered, but the factor is not quite significantly different from 0. With only 3 years of population density measurements, these must be regarded as very rough estimates, and there are not enough degrees of freedom to find out if they are significantly different from each other. However, small differences in stochasticity can have an important effect on the outcome of simulations, and therefore I took the approach of trying all three values (0.18, 0.16 and 0) in the process of parameterising the IFM (see below).

5.3.2 Parameterising the IFM using SPOMSIM

The confidence intervals around the IFM parameters, calculated by likelihood ratio tests, are very large (table 13), but fairly consistent between the different stochasticity values used. As detailed in the methods, I homed in on the most likely parameter values by smoothing the point likelihood estimates using GAMs. As well as being a convenient method to decide which parameters to use, this also revealed some interesting differences between the parameterisations based on different stochasticity values.

As stochasticity increases, the optimal value of x decreases and so does the baseline extinction rate (figure 20). Stochasticity has no consistent effect on the optimal value of α or the baseline colonisation rate. These results are not surprising because the effect of regional stochasticity in a metapopulation model is to increase the extinction rate, especially that of smaller patches. Hence, assuming a higher stochasticity while parameterising, will favour models where the other parameters predict a lower extinction rate, especially for smaller patches (larger x leads to steeper decline of extinction probability with patch area, see equation 7).

Table 13: IFM parameter confidence intervals, and the parameters used for further study. Confidence limits have been rounded (lower ones down, upper ones up) to 2s.f..

Parameter	Stochasticity	Lower	Best for stoch=0.16	Upper
α	0	1.1	2	3.7
	0.16	1.1		3.1
	0.18	1.1		3.5
y	0	0.062	0.2	0.44
	0.16	0.059		0.45
	0.18	0.073		0.45
μ	0	0.051	0.07	0.082
	0.16	0.039		0.110
	0.18	0.047		0.087
x	0	0.65	1.5	2.8
	0.16	0.64		2.8
	0.18	0.61		2.3

Furthermore, the GAMs predict that the likelihood peak for stochasticity= 0.16 is higher than the peaks for the other two stochasticity values, suggesting that a stochasticity of 0.16 is most consistent with the data. The parameter values I used for further simulations (see table 13) are those at the likelihood peak for stochasticity=0.16, rounded to 1s.f. (except in the case of x= 1.5, because rounding down to 1 or up to 2 would have resulted in significantly lower likelihood (difference in smoothed log likelihood >4, see also figure 20)). The GAM-fitted log likelihood of this parameter set is -17.0.

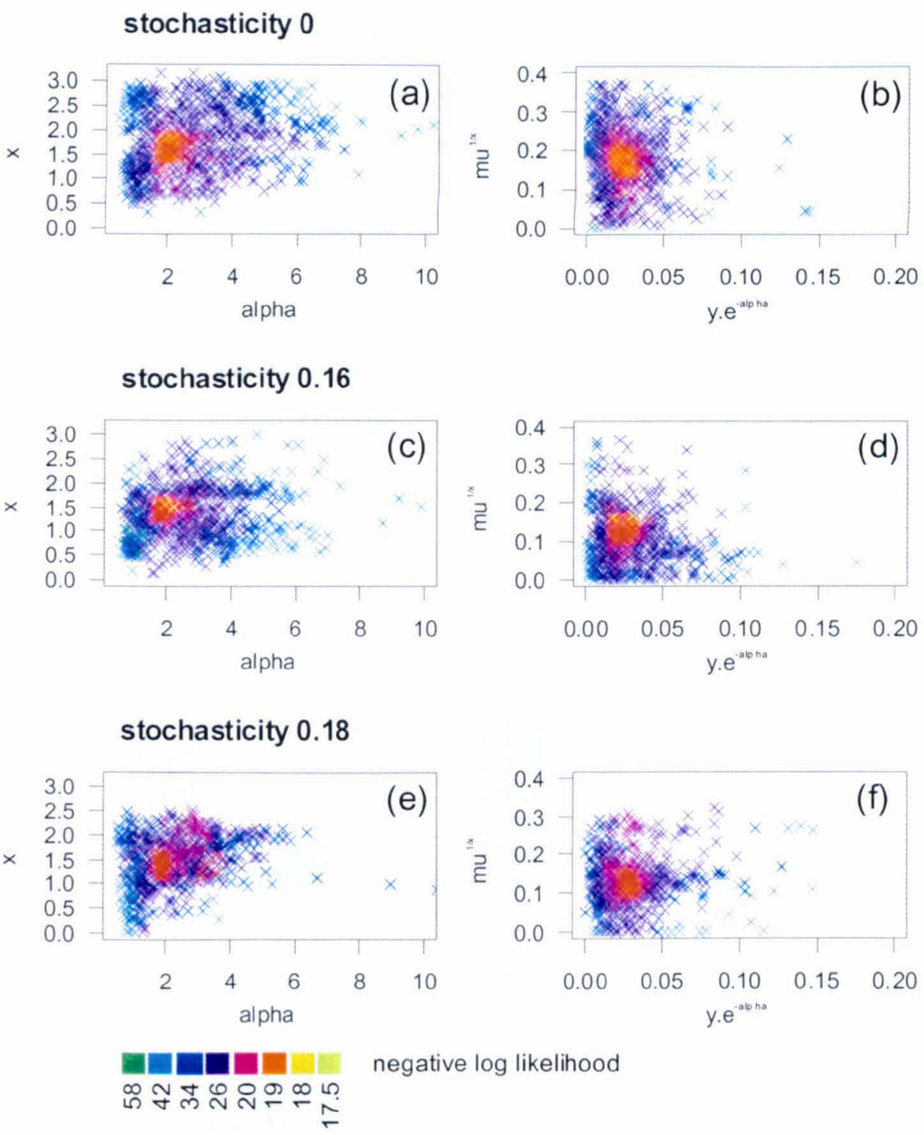


Figure 20: Representation of the smoothed likelihood surface with respect to the metapopulation parameters. Parameter sets and likelihood estimates resulted from NLR parameterisation runs in SPOMSIM, and the likelihood was then smoothed using GAMs in R. Independent parameterisations and GAMs were carried out for 3 stochasticity values:0 (a-b), 0.16 (c-d) and 0.18 (e-f). Likelihood is represented on a colour scale, and is plotted with respect to the parameters α and x (a,c,e) and with respect to composite parameters representing the baseline colonisation rate $y.e^{-\alpha}$ and the baseline extinction rate $\mu^{1/x}$ (d,b,f). Because each data set contains more than 40,000 points, I selected a subset of 1000 to plot in each panel (probability of picking negatively related to number of overlapping points), then overplotted a further 300 points selected from those with negative log likelihood <20.1 (20.1 is the cut-off point for the likelihood ratio test, i.e. these are the best fitting points).

5.3.3 Determinants of occupancy

The prediction that dynamic habitat patches will have lower occupancy on average than static habitat patches was supported by the data from the *P. argus* metapopulations (figure 21). Limestone (static) patches had significantly higher average occupancy according to a GLM where only biotope is included as an explanatory variable (table 14, row 1). Moreover, when patch area, patch connectivity and patch quality had been included in the GLM, limestone patches still had a higher occupancy at median area, connectivity and quality (logit(occupancy) 0.92±0.26 for limestone and 0.19±0.15 for heathland). Note that in the heathland data, patches with occupancy 0 are missing, because their boundaries were not recorded (figure 21), and so for a fair comparison of the average occupancy in GLMs I excluded the limestone patches with occupancy 0.

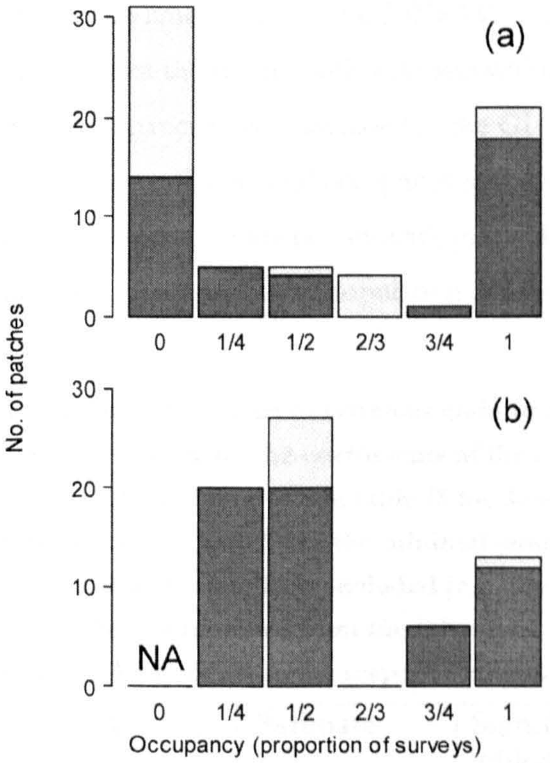


Figure 21: Differences in patch occupancy between the static limestone (a) and more dynamic heathland (b) biotopes. Patch occupancies are the average observed over four surveys spanning 21 years. Dark bars represent patches that were recorded in all 4 surveys; light bars were not recorded in all 4 surveys. The habitat that was never occupied in the heathland could not be counted because individual patches could not be delimited, therefore this data is missing.

Patch area, connectivity and quality all had significant effects on patch occupancy in one or both biotopes according to binomial GLMs (table 14). My second prediction, based on theoretical relationships explained in the introduction, was that the effect of connectivity would be greater in the static limestone metapopulation. This was supported by a significant biotope*connectivity interaction (table 14, row 6). The slope relating connectivity to occupancy was positive for limestone and near zero for heathland (table 15). This relationship also holds if the limestone patches with occupancy 0 are included in the analysis (data not shown), and whether or not patch quality is included in the analysis (table 14, row 6, table 15).

There was a positive relationship between area and occupancy which was similar in both biotopes (table 14, table 15). There was a positive relationship between quality and occupancy in limestone, but not in heathland (table 14, table 15), and this supports my third prediction that the average patch quality will appear to be a less important determinant of patch occupancy in a dynamic habitat. Because quality is actually positively correlated to area (see section 5.3.1), the inclusion of quality in the GLM tended to reduce the estimated effect of area in the limestone biotope (table 15). This makes interpretation a little more difficult, so I have shown the results both with and without quality included (table 15). If limestone patches with occupancy 0 were included in the GLM, there were still positive relationships between occupancy and area, and occupancy and quality for limestone, but the quality effect appeared relatively weaker (data not shown), probably because, by definition, patches with occupancy 0 had no measurements of population density from which to estimate quality.

Table 14: Significance of variables and interactions in GLMs to explain patch occupancy. The estimates given are the coefficients of the minimal model, which are slightly different from those of the full model (see table 15 for these). The minimal model for the main effects is the intercept-only model, but the minimal model for the interaction terms is the model with the two relevant main effects included (e.g. the model A + B + A*B compared to A + B). When a main effect is removed from the full model, all its interactions are also removed. Significance is tested by χ^2 because the response is binomial.

Variable	Estimate		Significance when added to minimal model		Significance when removed from full model	
	Lime	Heath	Change in deviance	p (χ^2 test)	Change in deviance	p (χ^2 test)
Biotope	1.09	0.17	21	<0.001	20	0.001
Area	0.95		55	<0.001	29	<0.001
Connectivity (S)	0.30		2	0.13	17	<0.001
Quality	0.64		24	<0.001	8	0.016
A*B	0.97	0.81	0.2	0.6	-0.5	0.5
S*B	0.86	-0.24	7	0.008	6	0.014
Q*B	1.22	0.06	13	<0.001	7	0.007

Table 15: Significance of individual relationships between occupancy and continuous variables. The z tests on fitted values from GLMs test whether the slope of the relationship is significantly different from zero.

	Relationship	Estimate	z	p
When Q included	Area (Lime)	0.53	1.372	0.17
	Area (Heath)	0.83	4.678	<0.001
	Connectivity (Lime)	1.30	3.315	<0.001
	Connectivity (Heath)	0.10	0.3	0.7
	Quality (Lime)	1.12	2.583	0.001
	Quality (Heath)	-0.10	-0.484	0.6
When Q not included	Area (Lime)	1.24	4.196	<0.001
	Area (Heath)	0.82	4.661	<0.001
	Connectivity (Lime)	1.32	3.301	<0.001
	Connectivity (Heath)	0.11	0.317	0.8

5.3.4 Static and dynamic habitat simulations

Simulation of the limestone patches as a metapopulation with static habitat produced summary statistics not significantly different from the observed ones (figure 22, left boxes). This result was unaffected by the options used for filling NA values in quality or starting occupancy (see methods). By contrast, applying the same parameters and simulation options to the heathland landscape produced simulated results that differed significantly from what was observed. The average number of patches occupied was too low and the connectivity-occupancy relationship was too steep (figure 22, middle boxes). A simple 'fix' of increasing the quality of heathland patches to be the same as the average limestone patch produced improvement in the number of patches occupied, but shifted connectivity and area-occupancy slopes away from their observed values (figure 22, right boxes) (the pink shaded area in figure 22a). My criterion for accepting simulation scenarios on the basis of numbers of occupied patches was that the proportion of simulated surveys with patch numbers in this range had to be greater than 0.05^(1/3). The most straightforward criterion for accepting the simulation scenarios on the basis of connectivity-occupancy slope would be if more than 2.5% (and less than 97.5%) of simulated slopes are less than the observed slope. However, there is uncertainty in the observed slope estimate (see the pink shaded area in figure 22c), and it may not be an unbiased estimate if there are outliers in the data. This prompted me to re-examine the fit of the GLM to the heathland data. The two heathland points with the greatest residuals are patches that have below-average connectivity, but have been occupied in all 4 surveys. Their most obvious feature is that they are patches of heathland regenerating in disused quarries, where the succession is much slower than post-fire succession. This habitat feature may explain their high occupancy, and their low connectivity may be coincidental. If these two points are excluded from the GLM, the estimated slope increases from 0.107 (table 15 last row) to 0.295, although it is still not significantly different from zero, and there is still a significant connectivity*biotope interaction. I have taken the view that the latter value is a more robust estimate of the slope, but in figures 23-24, both values are shown (as red lines) to allow comparison with simulations.

Static habitat simulations with different numbers of patches showed that this factor by itself cannot be responsible for the low observed connectivity-occupancy slope (figure 23). As the number of patches available increased, so did the number occupied, but the connectivity-occupancy slope decreased. This brought the simulated statistics closer to the observed values, but all scenarios remained significantly different with respect to one or both measures (figure 23). At the highest number of patches tried, all scenarios showed too high a number of patches occupied, and connectivity-occupancy slopes that were not low enough (figure 23). This result held true for two alternative patch quality values, and two methods of placing the extra patches (figure 23). Therefore it seems that a static habitat metapopulation model is not adequate to describe this system.

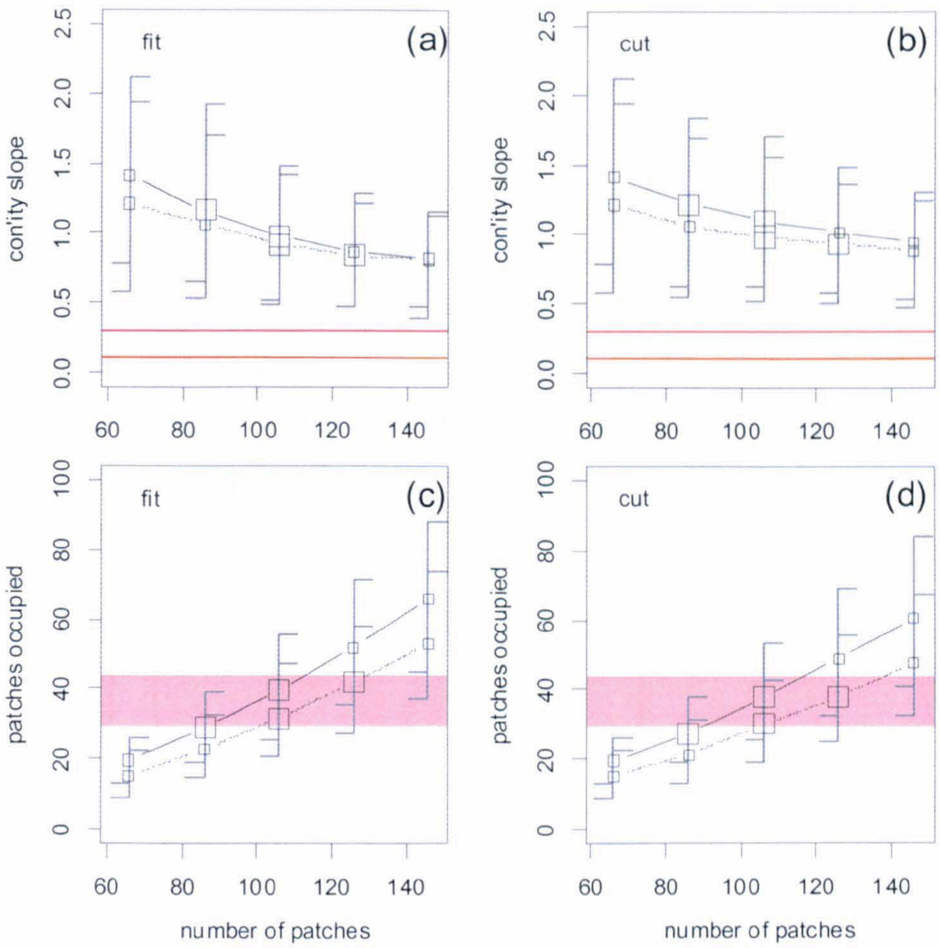


Figure 23: Static habitat heathland simulations showing the effect of adding extra patches in the unoccupied heathland using two placement methods: searching for a location for each patch where it fits completely (a,c), or truncating patches if part of their area falls outside heathland (b,d). Graphs show the medians (squares) and 2.5-97.5 percentiles (grey bars) of 500 simulated summary statistics: the connectivity-occupancy slope ("fit": a,b) and the mean number of occupied patches ("cut": c,d). Larger squares denote simulations that satisfy the criterion that numbers of occupied patches in the 3 simulated surveys should be within the observed range (the pink shaded box) with probability >0.05^(1/3).The red horizontal lines in (a) and (b) show the slope that was fitted to the real heathland data, with (higher) or without 2 outlying points removed. In each panel, points joined by solid lines are simulations where patch quality= 0.45 (the mean of heathland patch qualities) and dashed lines are simulations where patch quality= 0.33 (the geometric mean of heathland patch qualities), but in all cases the very large patch at Penrhosfeilw Common retains its original quality (see methods for more details).

When the habitat patches were made successional in MANAGE simulations, average patch occupancy was reduced, and so was the connectivity-occupancy slope, in agreement with the theoretical predictions (figure 24, appendix 2). Because patch occupancy was reduced, more patches were needed for these simulations to satisfy the criterion of number of patches occupied (figure 24a). Although I have shown that increasing number of patches is associated with lower connectivity-occupancy slopes (figure 23), this is not the only reason that the

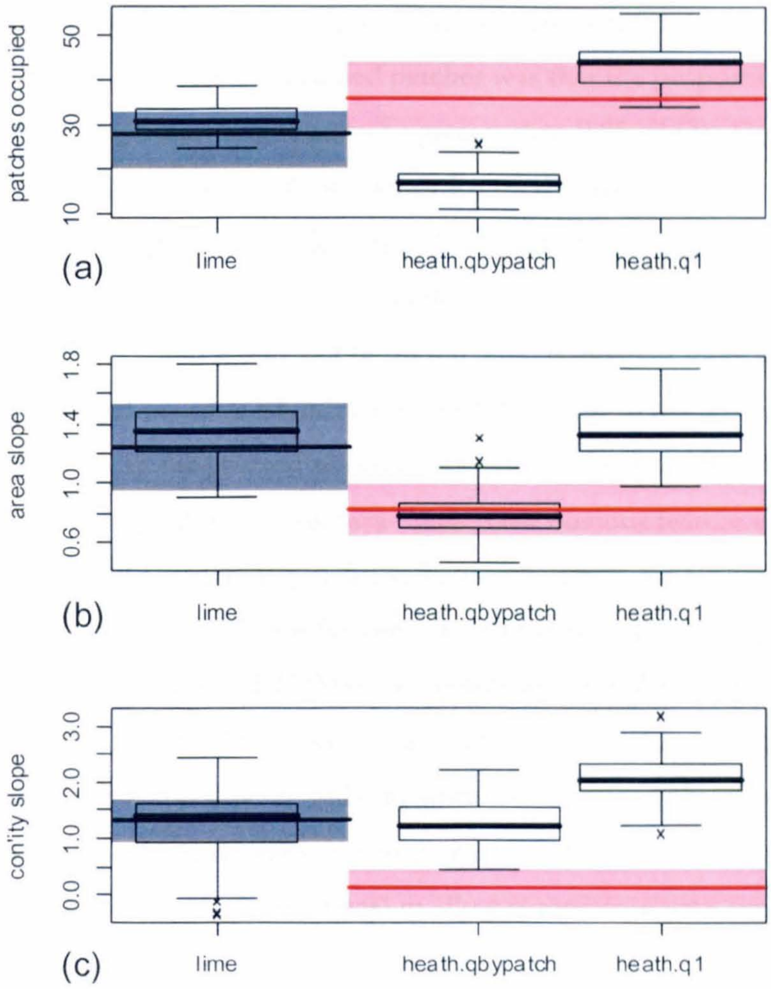


Figure 22: Comparison of observed and simulated summary statistics of the limestone and heathland metapopulations. The summary statistics are number of patches occupied (the mean of years 7, 14 and 21; year 0 is always the same as observed in 1983) (a), area-occupancy slope according to a GLM (b), and connectivity-occupancy slope according to the same GLM (c). Boxplots show the distribution of simulated summary statistics, each comprising 100 simulations. Black and red horizontal lines show the observed values in limestone and heathland respectively. The grey and pink boxes show, for (a), the range of numbers of patches occupied from 1990 to 2004, and for (b) and (c), the range of the slope ±1s.e.. The simulation options used for the left-hand two scenarios are that patches whose occupancy in 1983 is unknown are given occupancy 0 for year 0 of simulation (this only affects one patch in each biotope), and patches whose quality are unknown are given the geometric mean quality for their biotope (1 for limestone and ~0.33 for heathland). The right-hand scenario differs only in that all heathland patches are given quality 1.

The heathland simulations shown in figure 22 ignore the potentially suitable, unoccupied habitat in the landscape, and also ignore the successional dynamics that are such a distinguishing feature of most heathlands. I investigated scenarios that took account of these complicating factors, to see whether they would lead to reduced connectivity-occupancy slopes while retaining the observed numbers of patches occupied. In the 1990, 1997 and 2004 surveys, the number of occupied patches in the heathland system ranged between 29 and 44 succession scenarios come closer to the observed values – scenarios with succession also always had lower connectivity-occupancy slopes than static scenarios with the same number of patches (see appendix 2).

When the time gap between successional cycles was increased, the connectivity-occupancy slope decreased again (figure 24). With increasing gaps, more patches are required to satisfy the criterion of number of patches occupied, but only enough so that the number of patches available at any one time remains the same (figure 24b). With a gap of 9 years, the connectivity-occupancy slopes were not significantly different from the observed slope (the higher estimate).

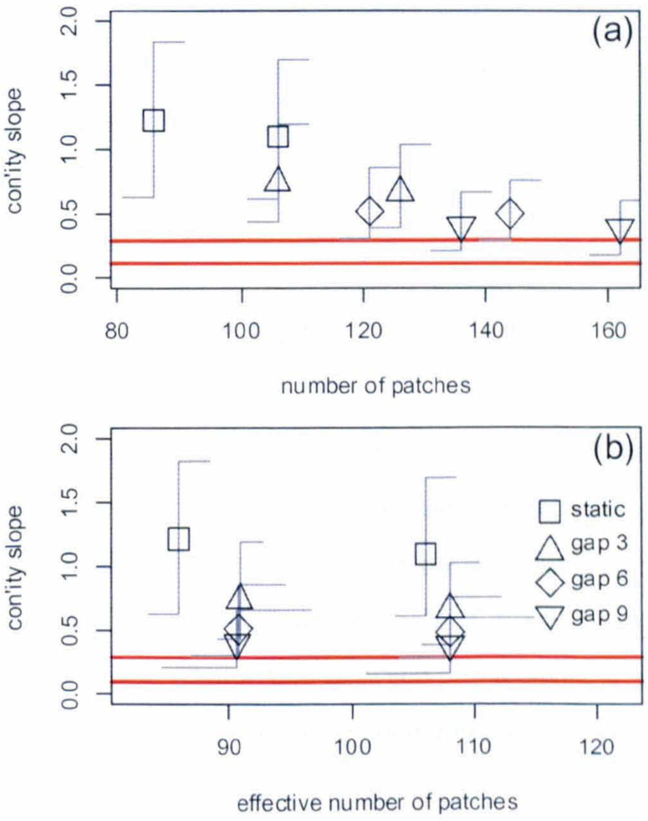


Figure 24: Dynamic habitat heathland simulations compared to static simulations with similar numbers of patches occupied. Graphs show the medians (open shapes) and 2.5-97.5 percentiles (grey bars) of 500 simulated connectivity-occupancy slopes against either the total number of patches in the simulation (a) or the number of patches with non-zero quality at any one time (b). Squares denote static habitat simulations (as in figure 23), other symbols are simulations where patches go through an 18 year successional cycle (black line in figure 18) followed by either a 3, 6, or 9 year gap. The starting point in the cycle is chosen randomly for each patch for each of 100 randomly-generated landscapes (each with 5 replicate simulation runs). The patch addition method is "cut" and average patch quality= 0.45 but the very large patch at Penrhosfeilw Common retains its original quality and is permanently suitable (see methods for more details). Only scenarios that satisfy the criterion of numbers of occupied patches are shown, although many other scenarios were tried (see appendix 2).

Note that in these dynamic simulations I used the options that produced the highest connectivity-occupancy slopes in the static scenarios (quality= 0.45 and patch placement method= "cut"). Further simulations showed that altering these options caused reductions in the connectivity-occupancy slope in succession scenarios just as they did for static scenarios (appendix 2), but the reductions were not as substantial as those caused by increasing the gap period. Using the second quality-time profile parameterised in chapter 4 (grey line in figure 18), which has more extreme variations in quality and a shorter patch lifetime, also produced reductions in the connectivity-occupancy slope (appendix 2). I did not carry out an exhaustive search of which combinations of these parameters might or might not be acceptable, because I never could have claimed to find the "best fitting" model (the number of reasonable landscape dynamics options is so large and the amount of real data relatively small). Rather, this section demonstrates that a combination of summary statistics, which is impossible with reasonable static habitat scenarios, becomes possible when habitat is assumed to be successional.

5.4 Discussion

I have found support for the three predictions that I made based on previous theory: differences in patch occupancy data seen between the two metapopulations of *P. argus* in North Wales are consistent with the differences expected between a static and a dynamic habitat. In the static limestone habitat, firstly, occupancy of patches is higher on average, secondly the relationship between connectivity and occupancy is steeper, and thirdly, the relationship between average patch quality and occupancy is also steeper.

The data on population densities has helped to clarify the differences between the limestone and heathland metapopulations. Density varies from year-to-year and these variations are synchronised to some extent within each metapopulation, but the metapopulations are not synchronised with each other. Population densities are generally lower in heathland. However, the lower population densities do not explain the lower average occupancies on heathland. On heathland there appears to be no relationship between patch quality (population density when occupied) and patch occupancy (proportion of time that a patch is occupied), and, over most of the range of patch qualities seen, limestone patches have higher occupancy for a given patch quality.

The quality estimate used is an average over time, and in heathland, population density varies just as much in repeated measures of the same patch as it does between patches. This may be a sign that the patches do not really have intrinsically different quality, but that they have been measured at different phases of the successional cycle. If this is true, it is unsurprising that I could not detect a relationship between quality and occupancy, (but there is still no reason to doubt that changes in quality within one patch over time are related to extinctions and colonisations in that patch).

There are many more extinction and colonisation events in the heathland metapopulation than the limestone one (table 11, Thomas & Harrison 1992), and so, however colonisation occurs, it is obviously important to the persistence of the heathland system. *P. argus* is sedentary butterfly, which only very rarely colonises habitat beyond 1 kilometre (Lewis *et al.* 1997). It seems reasonable that patch colonisation should depend on proximity to occupied patches, and yet there is no detectable relationship between observed connectivity and occupancy in the survey data on the heathland metapopulation. All my simulations incorporated the same functional relationship between connectivity and the probability of patch colonisation (and patch rescue from extinction). The data sampled from these simulations shows that the connectivity-occupancy relationship can be masked by the habitat dynamics, because of the temporal dimension in the amount of habitat the populations can disperse to and from (see introduction).

I predicted that when I modelled succession in the heathland system and coupled this to the limestone metapopulation parameters, I would get an improved fit of the model to the heathland data. I did not expect the model to be perfect, because of uncertainty about the disturbance history of the patches, the contribution of different disturbance types (e.g. fire, sea spray, and trampling) and the suitability of patches that had never been occupied. In particular, I assumed a strictly cyclical pattern of succession in each patch, where one patch equaled one disturbance and there was a fixed time gap between disturbances. It may have been more realistic to assume that patches disappear after one successional cycle, and that a fresh disturbance in the same place may happen at any time, or not at all, and may be a different size. I chose not to do this because it would have made direct comparisons between dynamic and equivalent static scenarios (in terms of numbers of patches and habitat area available) more difficult, but if I had done, I suspect that such simulations would have showed even less of a connectivity-occupancy relationship. Despite the limitations of the modelling of succession, I succeeded in recreating similar connectivity-occupancy slopes and numbers of patches occupied to those that were seen in heathland data. This was not possible assuming a patch occupancy model in a static landscape.

It is interesting that all the simulation scenarios with just the surveyed 66 heathland patches produced results significantly different from the real data. The fit was improved by including extra patches placed randomly in the habitat that had been searched, but had never been found to be occupied. The surveyors were aware that some of the unoccupied heathland was probably suitable and 'participating' in the metapopulation, but it would not have been reliable to attempt to split this into discrete patches. I would not necessarily expect that placing extra patches randomly in the landscape would work when modelling other species, but it highlights an important point about the conservation of successional stage specialists: the habitat that is occupied at any one time is far from being all of the habitat which will be important for that species' persistence.

Conservation attempts could be wrong-footed if it is assumed that connectivity can be ignored when current patterns of patch occupancy are not closely correlated with connectivity, especially if habitat dynamics are also not considered. The masking of connectivity-occupancy relationships by habitat dynamics could be a widespread phenomenon – in future studies it would be interesting to compare the connectivity-occupancy relationship in many independent metapopulations with different levels of habitat turnover, rather than relying on two very well-studied metapopulations as I have done.

For many species that we might want to conserve or control, in many landscapes, data on the history of disturbance and succession will not be available. In these cases it will be very difficult to make inferences about what really drives the population dynamics. Although I think that a model like MANAGE would be useful for other species when appropriately parameterised, the modelling in this chapter relied heavily on the prior information on relative population density for several years, and knowledge of how long succession takes. When data like this is not available, it may be advisable to assume that connectivity is important (even though there might not be a significant connectivity-occupancy relationship) if it is known that a species specializes on a certain successional stage, and has a limited dispersal range. Efforts should be focused on providing a mosaic of successional stages to conserve the whole assemblage of species on a habitat like heathland. If disturbances can be managed, managers should take into account the dispersal abilities of species to make sure they can always move easily to newly-created patches of habitat.

I see the contrasts between the *Plebejus argus* populations on different habitats as a warning against arguing over a dichotomy between habitat selection and metapopulation models (Armstrong 2005). In the limestone system, the occupancy of patches seems to be mainly due to area and connectivity, in the manner of a classic metapopulation model, but there is also a positive contribution of habitat quality. Extinction and colonisation events are not very frequent; indeed the majority of patches have been occupied in all surveys, or in none. Nevertheless the pattern of occupancy shows that metapopulation processes have shaped these populations in the long term. On the other hand, in the heathland system, extinctions and colonisations are very frequent, and it seems reasonable to assume they are influenced by patch quality and patch connectivity. But in the heathland system, because the quality of each patch changes with disturbance and succession, the relationships between quality or connectivity and occupancy cannot be detected from long-term average values or from a single snapshot. Therefore, counter-intuitively, both connectivity and habitat quality could *appear* less important in landscapes where they actually have more influence on year to year changes in patch occupancy and metapopulation persistence.

5.5 Summary

- Little attention has been paid to developing metapopulation models that include habitat dynamics, and still less to testing the predictions of these models. I tested two predictions from theory about the differences between dynamic habitat metapopulations and their static counterparts, using long-term survey data from two metapopulations of the butterfly *Plebejus argus.*
- As predicted the metapopulation inhabiting dynamic habitat had a lower level of habitat occupancy, which could not be accounted for by other differences between the metapopulations.
- Patch occupancy did not significantly increase with increasing patch connectivity in dynamic habitat, whereas there was a strong positive connectivity-occupancy relationship in static habitat.
- Modelling confirmed that both differences could arise without changing the species' metapopulation parameters - importantly, without changing the dependence of colonisation upon connectivity. Rather, the differences could be due to the contrasting habitat dynamics.

- I conclude that landscape scale studies may often underestimate the importance of connectivity for species occurrence and persistence because habitat turnover can obscure the connectivity-occupancy relationship in commonly available snapshot data.

6 A small percentage of permanent habitat has a disproportionate influence on metapopulation persistence in a dynamic landscape.

6.1 Introduction

The Silver-studded Blue butterfly (*Plebejus argus*) is a species of high conservation priority in the UK (Thomas 1985a). Most of its remaining populations are on heathland habitats (Asher *et al.* 2001), but the only predictive population modelling done for this species has been focused on the limestone grassland populations in North Wales (Hanski & Thomas 1994; Thomas *et al.* 2002). The fact that heathland undergoes cycles of disturbance and succession, and that *P. argus* is restricted to the earlier successional stages, presents a significant challenge to the modeller. Obtaining reasonable parameters for the process of habitat change, and the species' response to it, requires a large amount of data. In the absence of such data, conservation efforts for *P. argus* are probably not being expended as efficiently as they could be. Some populations are managed intensively on a small-scale by using managed fires or mechanical rotavators to create new patches of habitat adjacent to existing populations (e.g. in Sussex, Lewis *et al.* 1997); on the other hand, many populations go unrecorded for years at a time (D. Hoare, personal communication). The availability of a model that captures the essentials of population and habitat dynamics could lead to conservation efforts being expended more wisely. In this chapter I parameterise a model of *P. argus* on heathland on Holy Island, and predict the size of the population assuming the recently observed fire regime should continue.

In chapter 4 I showed that, even though fires created favourable vegetation for *P. argus* on Penrhosfeilw Common, there was also heathland within 125 m of the sea that could provide permanently suitable habitat (because its growth is stunted by wind and salt spray). The data from the *P. argus* population surveys between 1983 and 2004 also show that a few patches have been occupied throughout, including a grazed heath in the far south of the island, and a disused quarry in the far north, as well as parts of Penrhosfeilw Common. It has been shown theoretically and in simulation studies that a metapopulation of static patches has a lower extinction threshold than a dynamic habitat metapopulation (e.g. Johnson 2000b; Keymer *et al.* 2000; Amarasekare & Possingham 2001). It is not known, however, what role a small amount of permanent habitat might play in a largely dynamic metapopulation. One simulation study has shown that a small amount of permanent habitat can increase the overall habitat occupancy (Pulliam *et al.* 1992), but permanent habitat could also act as an important refuge from extinction and a source of colonists for a metapopulation that would otherwise be prone to extinction. I do not know of any studies so far that have quantified this effect theoretically, although it could produce analogous results to theoretical analyses of the case of a parasitoid or pathogen with two hosts of contrasting susceptibility (Anderson 1981).

As shown in chapter 4, much of the variation in *P. argus* abundance in my study area could be explained by the presence of permanent habitat within 125 m of the coast, and as a function of time since burning on the rest of the heathland. In this chapter I aimed to replicate this situation as closely as possible within the MANAGE model, and to extend the results from the study area used in chapter 4 to the whole of Holy Island. Having found that the permanent habitat on Holy Island was crucial to the survival of the metapopulation as a whole, I then extended my analysis to look at the effect of varying the proportion of permanent habitat in the landscape.

The results in this chapter could have quite wide-ranging implications. Just as few real metapopulations fit to Levin's original assumption that all patches have the same size and extinction risk, few real successional systems consist of patches with exactly the same longevity. Most early successional species can access some permanent or quasi-permanent habitat (e.g. weathered rocky outcrops, eroding riverbanks, grazed grassland). The relative conservation value of the permanent and ephemeral habitat will be an important management question for many species, and one that can only be satisfactorily answered with modelling.

6.2 Methods

I was provided with maps of all the fires recorded by the RSPB wardens, for the area that they manage (South Stack Cliffs and Penrhosfeilw Common), between 1991 and 2004. I digitised this data using ArcGIS (ESRI, Redlands, CA, USA), to a polygon layer. I then calculated the area and centroid of each fire. Both the number and total extent of fires were extremely variable from year to year. There was a negative relationship between the number of fires in a year, and the average area of those fires, so I decided to specify the burning rate in MANAGE according to area rather than number of patches. The median area burned per year was 3.63 ha, and the standard deviation of the $\log_{10}$ transformed values was 0.55. Recall that MANAGE samples from a log-normal distribution to set the area to burn each time step, see equation 5, section 2.2.3. In the terms of this equation $A_{m,ds}$= 3.63 and $s_{m,ds}$= 0.55 for the "South Stack" management unit, (which is roughly the region managed by the RSPB). The South Stack management unit contains a little under half of the heathland area of the whole of Holy Island (see figure 25), so when simulating Holy Island, the value of $A_{m,ds}$ was scaled up in direct proportion (3.63*Holy Island area/South Stack area= 6.53 ha), but the standard deviation was not changed (because this is relative to the median anyway, see equation 5, section 2.2.3).

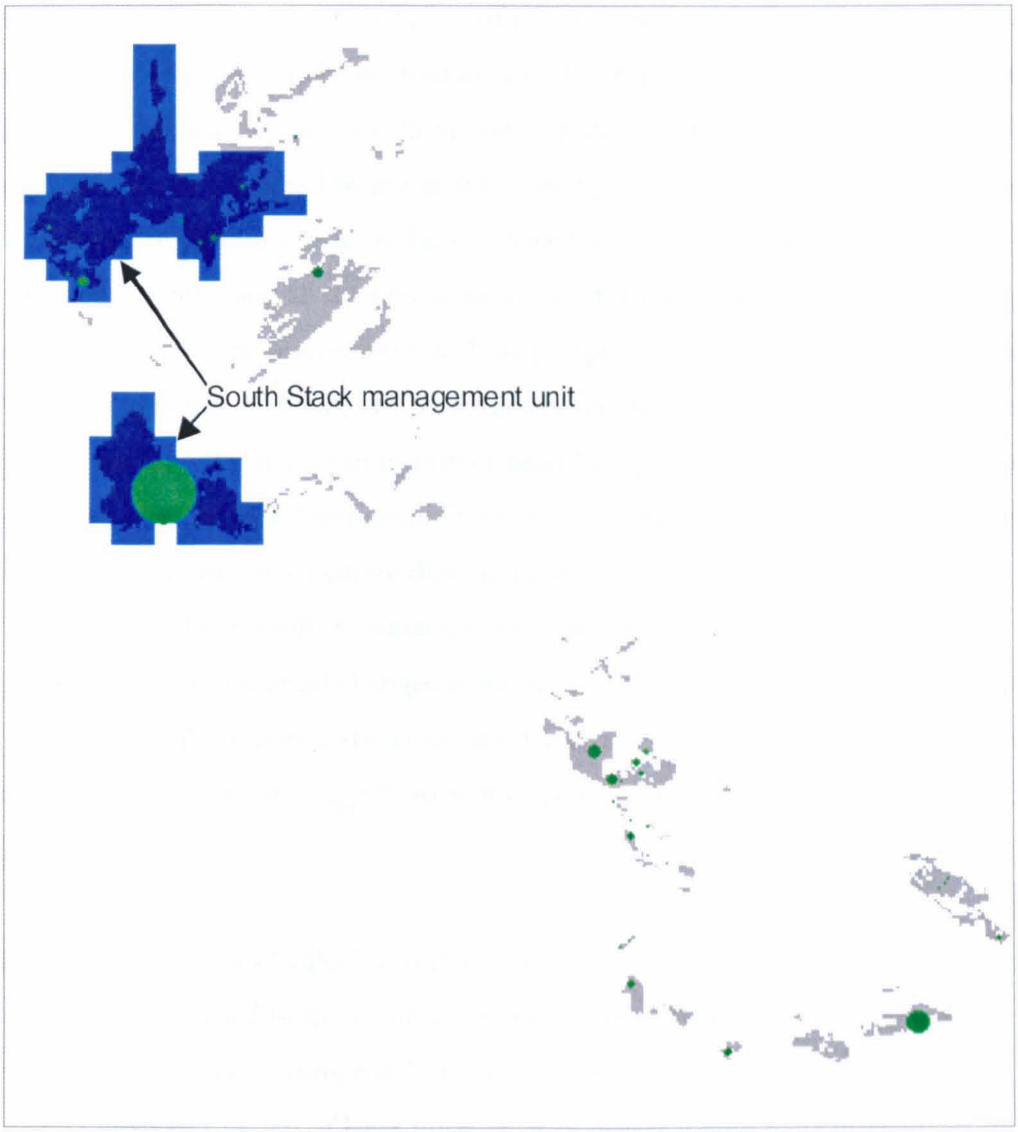


Figure 25: Screen shot of the habitat and management unit maps used for simulating the Holy Island metapopulation with MANAGE. Potential habitat is shown in grey, the South Stack management unit in large blue blocks, and the 2004 occupied patches as green circles.

There were 2 alternative quality-time profiles for burned patches in MANAGE, taken from the parameterisation in chapter 4 (see figure 18), which are henceforth referred to as disturbance types 1 and 2, where 1 is the flat-topped and 2 is the triangular profile. The same disturbance types are used for simulations in chapter 5, but in that chapter I re-scaled both profiles' maximum quality in order to give the same mean quality over 21 years. In this chapter, I use the maximum quality values originally parameterised in terms of population density (adults/ha), and divide these by the average population density in the limestone metapopulation, so that they are scaled appropriately for the population parameters (see section 5.2.3).

To define the habitat that was permanently suitable for *P. argus* I employed two criteria: whether the habitat had been occupied in all four surveys between 1983 and 2004, and whether it was heathland within 125 m of the sea (see section 4.4). To calculate the shapes of these areas I used the "intersect" tool in ArcGIS on the shape files representing each *P. argus* survey (see appendix 1), and the 25 m grid of potential habitat (based on the Phase 1 habitat survey, and ground-truthed by me in 2005; see figure 25 and section 5.2.1), from which I had selected squares within 125 m of the sea (based on the landline OS map data). I decided to run simulations either using all the permanently occupied polygons (which yielded 15 patches, totalling 23 ha), or the intersection of these polygons with the coastal habitat (which yielded 12 patches, totalling 14.5 ha), or no permanent habitat at all. All permanent patches were assigned quality 0.45: the mean quality of heathland patches, see chapter 5. It should be noted that what I have termed "permanent habitat" is heathland where succession proceeds very slowly for some reason, or where there is a constant, low level of disturbance (e.g. grazing), so it will not really be of uniform suitability through space or time, and it still may be at risk from land use and environmental changes in the future. The simulations were started from the population distribution in 2004, assuming that any occupied habitat that was not permanent was successional habitat of age 2 years (the age when maximum quality is first reached, see figure 18).

Fire was modelled as a "killer" disturbance type, because the RSPB data showed that the same point could be burned twice within a very short time period. This means that, as a fire is created, it obliterates existing patches and parts of patches that overlap with it. To calculate the exact areas of overlap of layer-upon-layer of circles would have introduced complication to the model that would be difficult to justify, given that the assumption that patches are circles is an approximation for convenience only. Instead, I used the following approximation for the area that should be obliterated. If patches overlap at all, MANAGE calculates $X = \frac{R_{new}}{R_{old}} \cdot \left(1 - \frac{d_{new,old}}{R_{new} + R_{old}}\right)$, where R is patch radius of either the new (killing) patch or the old (potentially to be killed) patch and *d* is the centre-to-centre distance between them. Then, based on the value of X (which can vary between 0 and R_{new}/R_{old}), MANAGE takes one of three actions: if $X > 0.5$, the old patch will disappear completely; if $X > 0.25$, the area of the old patch will be halved, and otherwise the old patch will be unaffected. I have checked that this approximation works to maintain the maximum area of patches in the landscape close to the total area of potential habitat cells in the landscape, despite the inherent imprecision. It was very important for the results in this chapter that the permanent patches should not be killed by new disturbances, and therefore I added a line to the source code to prevent the killing of permanent patches. As a side effect, this means that fires can overlap and exist at the same time as the permanent patches, but since the permanent patches occupy a maximum of 6% of the potential habitat (23 ha out of 382 ha), I do not think that this caused a serious inaccuracy in the model.

Table 16: The area distribution of fires simulated by MANAGE, based purely on the distribution observed in RSPB fire data, or adjusted for the effect of truncation within the Holy Island landscape.

Area of fire, ha	Relative frequency	Relative frequency after adjusting for "cut" option
0.0484	6	3.181
0.1212	6	5.382
0.1608	6	5.443
0.2511	6	5.284
0.3514	6	5.363
0.5341	6	6.253
0.7592	6	7.460
1.0031	6	8.342
2	1	1.274
6	2	2.409
9	1	1.963
15	1	2.377
90	1	14.196

To define the sizes of individual fires within the MANAGE model, I used the RSPB fire data again. I ranked the 54 fires by area (disregarding the year of the fire) and split them into nine equal-frequency bins. The median of each of bins 1-8 became one of the fire sizes used by MANAGE, but the last bin was broken down further (because it contained fires between 2 and 90 hectares!), so each observation, rounded to the nearest hectare, became one of the fire sizes used by MANAGE (see table 16). When I attempted to simulate these fires assuming that they must be fitted into the potential habitat ("fit" option, see section 2.2.3), there was frequent disturbance failure. However, it proved fairly simple to run a test simulation, assuming that fires are truncated at the edges of potential habitat ("cut" option, see section

2.2.3), then use the output data on the distribution of fire sizes at the end of this simulation to calculate a correction factor for each fire size in the MANAGE input. The adjusted frequencies are given in the last column of table 16, and figure 26 shows how this adjustment brings the patch size distribution in the model closer to the observed fire size distribution.

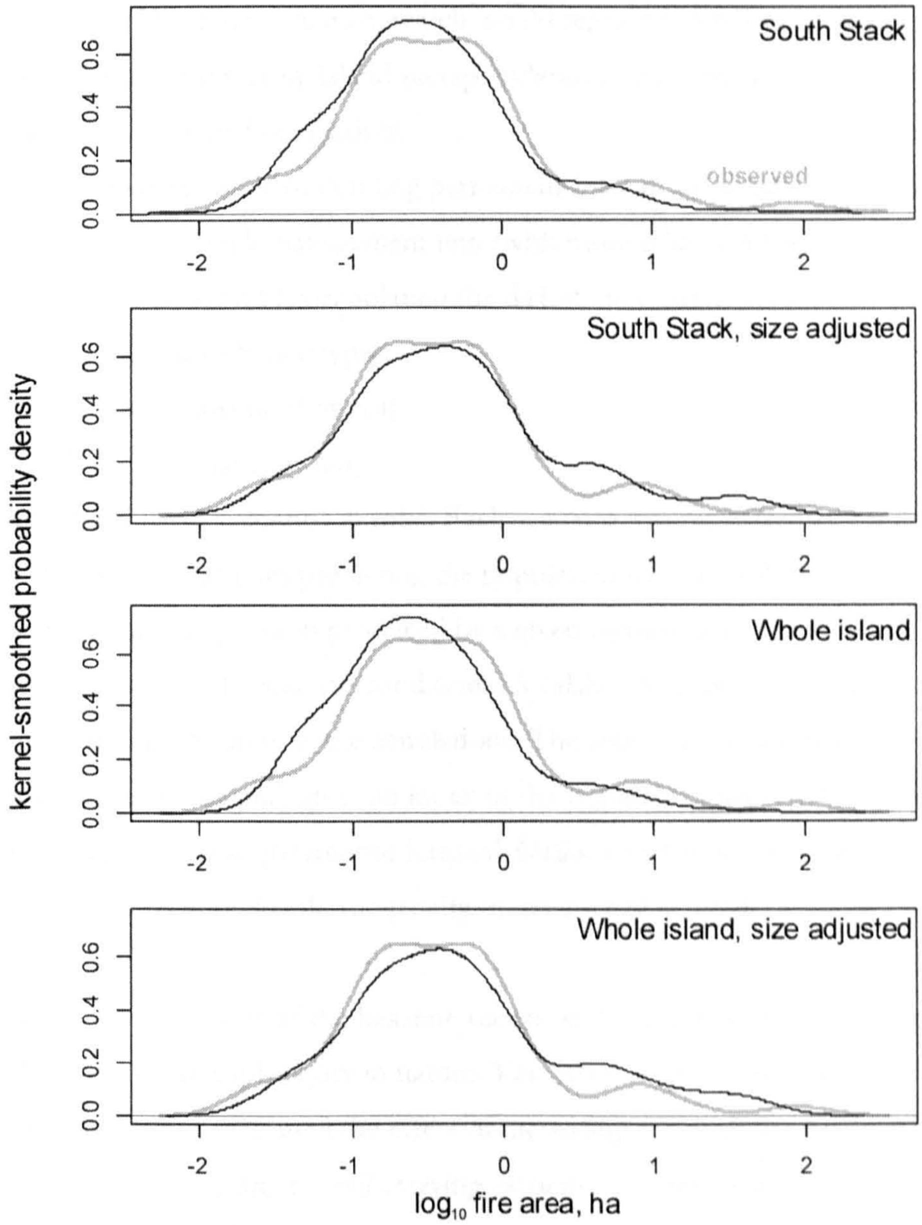


Figure 26: The distribution of fire sizes at the end of simulations (black lines) compared to the distribution observed in the RSPB fire data (thick grey line), for two alternative simulation regions (South Stack management unit alone or whole of Holy Island) and two input size distributions (given in table 16).

Metapopulation parameters for *P. argus* had already been obtained by parameterising the limestone system in North Wales (see chapter 5, table 13). However, for the simulations in this chapter I was concerned about the influence of the rescue effect (R= 1, see equation 1), which had been assumed but not tested in the parameterisation. I suspected that this could be unduly optimistic for a landscape which would contain many small remnants of old fires (see the explanation of patch killing above), which would have low quality, but which would keep getting colonised even if they were certain to go extinct in the next time step. Therefore, for completeness, I ran simulations both with and without the rescue effect.

As a set of baseline scenarios, which would represent the best available prediction of the long-term future of the Holy Island metapopulation, I ran simulations with all combinations of 5 factors that created uncertainty:

1. two methods of defining permanent habitat, or no permanent habitat;
2. South Stack management unit (with more reliable information) simulated alone, or the whole island (extrapolating the disturbance rate);
3. two disturbance types;
4. size adjustment or not;
5. rescue effect or not,

which led to 48 scenarios in total. Each scenario was replicated 100 times for 500 years. This is not to imply that I am predicting the population size in 2504, but that I am sampling the long-term average population produced by a given disturbance regime, which I wanted to be independent of the starting conditions. A GLM was used to analyse which factors affected extinction probability in the simulations. The area of occupied patches multiplied by their quality, then summed, gives an index of the population size. Differences in population index were tested by non-parametric Kruskal-Wallis tests because the data were non-normal and showed considerable inhomogeneity of variance (Zar 1984).

Based on the results of the baseline scenarios, I carried out two sets of follow-up simulations that were more exploratory in nature. The first examined the effect of a reduced burning rate, and the second examined the effect of increasing the portion of permanent habitat while maintaining the same overall carrying capacity. The rationale for these simulations is explained in the results section.

6.3 Results

Based on the current habitat and disturbance regime, MANAGE predicted that the Holy Island metapopulation of *P. argus* has a very low extinction risk, not more than 10% in 500 years for South Stack, and not more than 8% in 500 years for the whole of Holy Island (23 ha and 14.5 ha columns in table 17). However, its survival was crucially dependent on the presence of some permanently suitable habitat: in model scenarios where there was no permanent habitat, MANAGE predicted that the metapopulation is very likely to go extinct within 100 years (right hand two columns in table 17). The binomial GLM (table 18) shows that the extinction risk was increased if the South Stack management unit was modelled in isolation, if disturbance type 1 (flat-topped habitat quality profile) was used, if there was no rescue effect, or if the fire sizes were adjusted (increasing the rate of the largest fires, see table 16), but all these effects were small relative to the effect of removing permanent habitat (table 17 right hand side). There were three significant interactions between factors in the GLM (table 18): region*permanence (lack of permanent patchis is relatively worse for South Stack than for the whole island), disturbance type*size adjustment (size adjustment is especially bad for disturbance type 2) and disturbance type*rescue effect (the rescue effect is especially good for disturbance type 1).

Table 17: Extinction percentages for the Holy Island metapopulation in 500 years of simulation using all combinations of 5 factors: Permanent habitat (15 patches totalling 23 ha; 12 patches totalling 14.5 ha; none), region simulated (ss= South Stack management unit only; whole= whole island; figure in brackets gives the percentage of carrying capacity provided by permanent rather than successional habitat patches), disturbance type (the two disturbance profiles parameterised in chapter 4), size adjustment (if y, frequencies of different fire sizes were adjusted to account for patch truncation at heathland edges, see methods) and rescue effect (if y, *R*= 1). The table body gives number of extinct runs out of 100.

Disturbance type	**Size adjustment**	**Rescue effect**	**Amount of permanent habitat**					
			23 ha		**14.5 ha**		**none (median no. years to extinction in brackets)**	
			ss (27%)	**whole (21%)**	**ss (19%)**	**whole (14%)**	**ss**	**whole**
1	n	y	1	1	1	0	100 (43)	95 (86)
		n	1	1	4	3	100 (29)	99 (72)
	y	y	2	1	5	3	100 (17)	100 (22)
		n	9	5	10	8	100 (17)	100 (19)
2	n	y	0	0	0	0	98 (86)	88 (136)
		n	0	1	2	1	98 (63)	85 (159)
	y	y	1	2	5	5	100 (17)	100 (19)
		n	5	1	10	7	100 (17)	100 (22)

Comparing scenarios with 23 ha versus 14.5 ha of permanent habitat, there was a decrease in extinction risk of the entire metapopulation (table 17, table 18) but there was no significant increase in the population size in the successional habitat (figure 27a-b; Kruskal-Wallis test

$\chi^2=1.5$, $p>0.2$), i.e. the extra permanent habitat did not help to boost the population in the wider landscape. The difference in extinction risk between 0 and 23 ha permanent habitat was more than 10 times larger than the difference in extinction risk between 14.5 ha and 23 ha permanent habitat (in logit transformation, see table 18 right hand side).

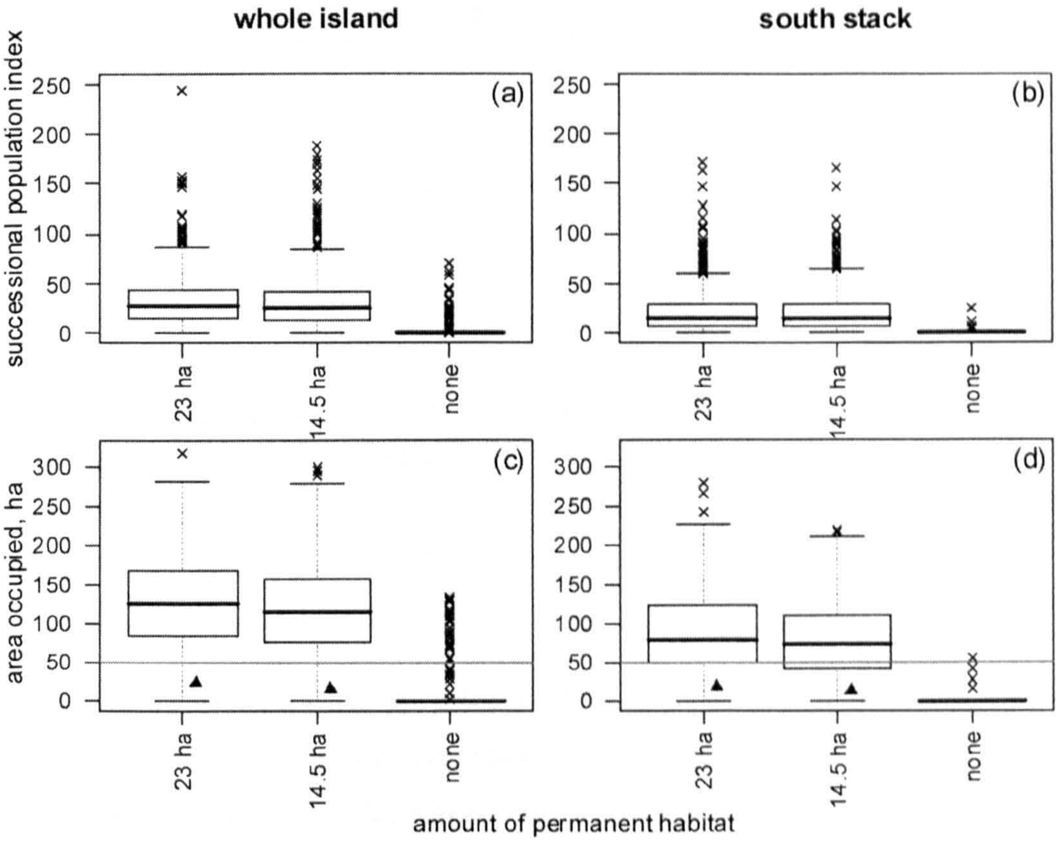


Figure 27: The effect of amount of permanent habitat on the population index of successional habitat (a,b) and the overall area occupied (c,d) after 500 years of simulation. The population index is calculated as occupied area*quality. 800 observations contribute to each box plot (results were pooled with respect to disturbance type, size adjustment and rescue effect). Grey horizontal lines in (c,d) show the area occupied in 2004, the simulation starting condition. Filled triangles in (c,d) show the area of permanent habitat present, in (d) counting just the permanent habitat within the South Stack management unit.

Table 18: Results of a GLM fitted to the data on run extinction after 500 years for all 48 scenarios in table 17, showing which factors influenced extinction rate, and the relative strength of their effects. Factors are as in table 17; whole= whole of Holy Island, ss=South Stack management unit, dt= disturbance type.

Significance of factors			Effect sizes (units are logit (extinction probability))		
factor	**deviance**	**p (χ^2 test)**	**comparison**	**effect**	
region	17.4	<0.001	whole vs. ss (when 23 ha permanent patches)	-0.5	
permanence	5110.8	<0.001		ss	whole
region*permanence	13.4	0.001	14.5 ha vs. 23 ha	+0.7	+0.8
			none vs. 23 ha	+10.6	+8.9
disturbance type (dt)	13.1	<0.001	dt2 vs. dt1 (when no rescue and no size adjustment)	-2.2	
size adjustment	88.8	<0.001		dt1	dt2
rescue effect	14.5	<0.001	size adjust y vs. n	+1.4	+3.2
dt*size	17.8	<0.001	rescue y vs. n	-1.1	-0.3
dt*rescue	4.2	0.04			

The average area occupied in the scenarios that survive for 500 years tended to be higher than that observed in 2004 (the starting condition, see figure 27). This could indicate that these scenarios are overly optimistic, perhaps because the burn rates recorded in the South Stack area are higher than the average across Holy Island, and/or because not all burns produce equally suitable habitat. Therefore, I carried out a series of simulations to evaluate approximately what burning rate would be required to maintain the 2004 area occupied. The results of these scenarios are shown in figure 28 and table 19.

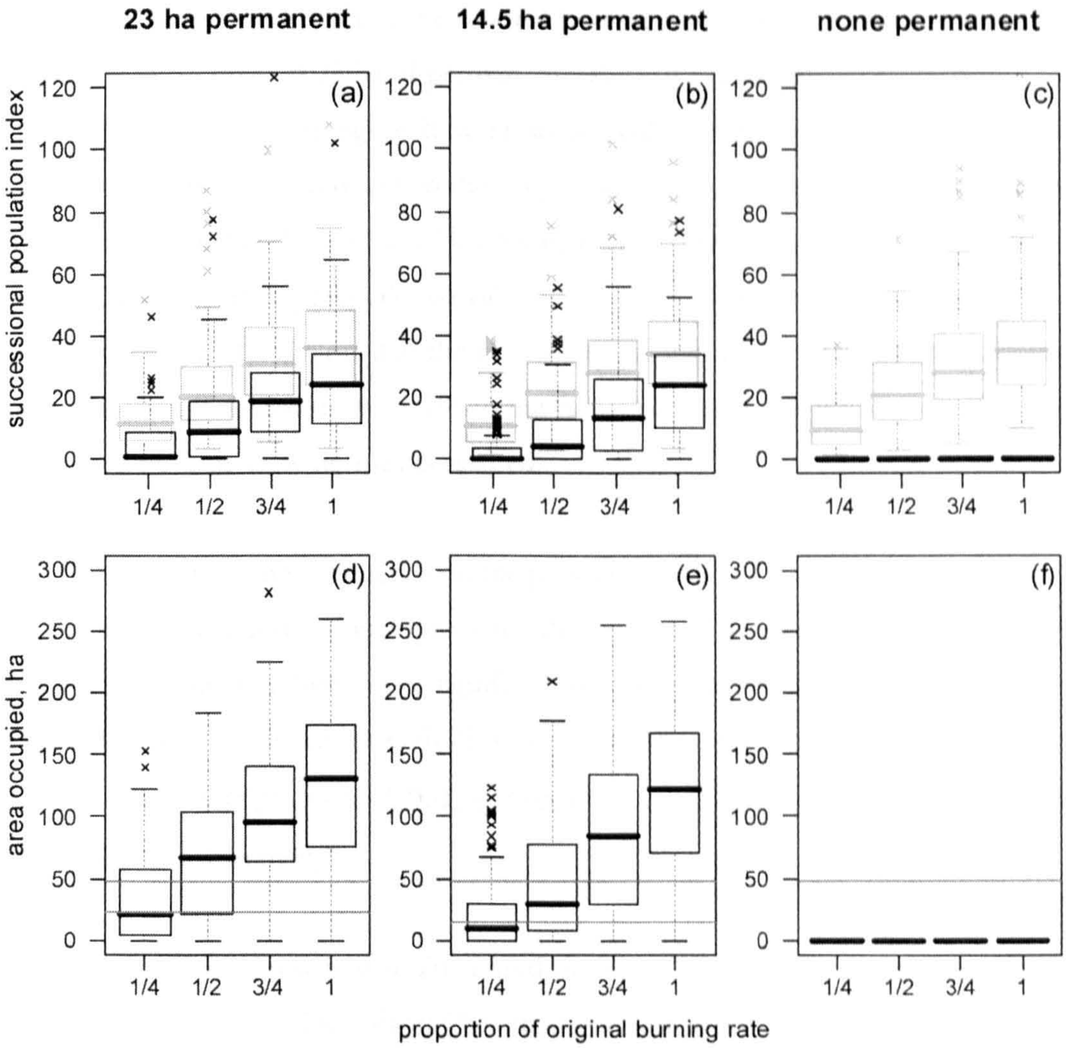


Figure 28: The effect of reducing burning rate on the population index for successional habitat (a-c) and the overall area occupied (d-f) after 500 years of simulation, dependent on the amount of permanent habitat (23 ha a,d; 14.5 ha b,e or none c,f). The grey box plots in (a-c) show the carrying capacity of successional habitat, which reduces as the burning rate reduces (in each of a and b there is one outlying grey point beyond the plotted range). The upper grey horizontal lines in (d-f) show the area occupied in 2004, the simulation starting condition. The lower lines show the area of permanent habitat present. All scenarios used the whole of Holy Island, disturbance type 1, size adjustment and no rescue effect (*R*= 0).

Table 19: The effect of reducing the burning rate on the extinction rate in 500 year simulations. Number of extinct runs out of 100 is shown. All scenarios used the whole of Holy Island, disturbance type 1, size adjustment and no rescue effect (*R*= 0). The scenarios marked with † and ‡ were used as the basis for further simulations, see figure 29.

burning rate	23 ha permanent	14.5 ha permanent	none permanent
original	5	8	100†
¾	6	11‡	100
½	15	22	100
¼	23	40	100
0	50	74	no habitat

Between a quarter and a half of the original burning rate would be expected to maintain the original area occupied if 23 ha of permanent habitat was available (coincidence of box-plots and the upper grey line in figure 28d). However, half to three quarters of the original burning rate would be required to maintain the original area occupied if only 14.5 ha of permanent habitat was available (figure 28e). Those scenarios that reproduced the 2004 occupied area on average, also had an appreciable risk of extinction (more than 10% in 500 years, see table 19 and figure 28), and it is clear that the permanent patches could not sustain a metapopulation by themselves (final row in table 19) so the future of this metapopulation in the absence of continued burning is by no means assured.

The permanent patches' influence on the populations in the successional patches became clearer as the metapopulation approached the extinction threshold. For all the scenarios with a reduced burning rate, there was a significant difference in the population size on successional habitat between the scenarios with 23 and 14.5 ha of permanent habitat (figure 28a-b; Kruskal-Wallis test χ^2=83, $p<0.001$; χ^2=4.5, $p<0.034$; χ^2=4.0, $p<0.046$ when burning rate was ¼, ½ and ¾, respectively).

In all the scenarios presented so far, I used the actual location and estimated amount of permanent habitat on Holy Island (the larger amount, representing all areas that were occupied continually from 1983 to 2004, or the smaller amount, representing the subset of those areas that are within 125 m of the coastline). This is valuable for the planning of conservation on Holy Island, but it is less useful for determining the value of permanent habitat generally. In particular, as the burning rate was decreased in the simulations shown in figure 28, the proportion of permanent habitat increased. To correct for this I ran a set of scenarios with the same overall average carrying capacity, but different proportions of permanent habitat. To set up these scenarios, for each of 100 replicates, the starting set of patches was the set of patches present at the endpoint of one replicate of the scenario marked with † in table 19. I set all these patches to be occupied at t= 0, and I randomly selected patches to be permanent, until the desired area of permanent habitat was reached (and set the quality of the permanent patches to be 0.45, as for the observed permanent patches). I ran 6 scenarios with proportions of permanent habitat (in terms of carrying capacity: area*quality) increasing from 5% to 100%, and the burning rate decreasing so as to produce the same average carrying capacity overall. For comparison between observed and randomly-selected permanent habitat, note that the scenario marked with † had the same carrying capacity on average as the scenario marked with ‡ in table 19, (which has the observed 14.5 ha of permanent patches and ¾ of the original burning rate, leading to 18% of carrying capacity permanent).

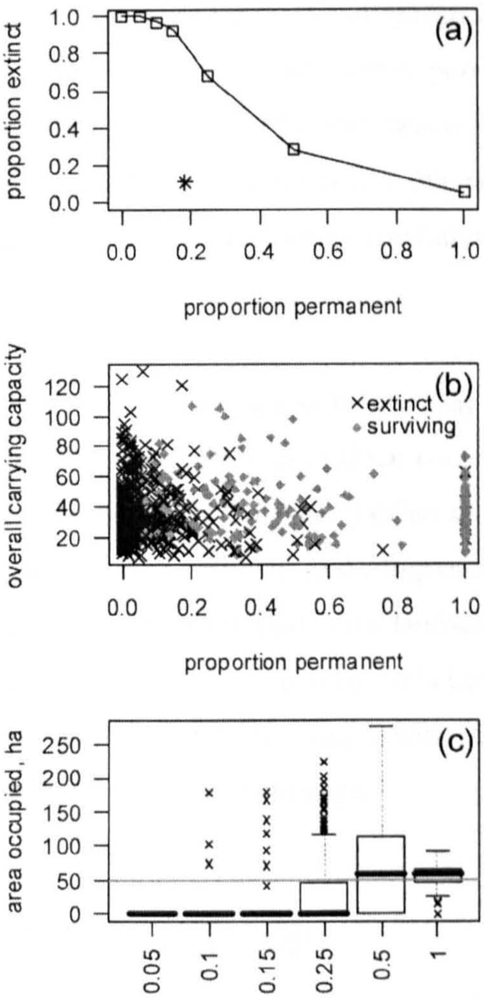


Figure 29: Effects of increasing the proportion of permanent habitat while maintaining the overall carrying capacity. Panel (a) shows the average proportion of runs extinct after 500 years; square symbols are scenarios with randomly-selected permanent habitat (the landscapes used were based on the simulation scenario marked with a † in table 19, see text) and the star shows the result of the scenario with the observed permanent patches (marked with a ‡ in table 19), which had almost exactly the same carrying capacity. Panel (b) shows the extinction status of individual simulation runs against the overall carrying capacity and the proportion of this which was permanent at year 500. Note that overall carrying capacity is affected by stochasticity in the burning rate and by the metapopulation's regional stochasticity, and as a result the proportion permanent varies quite a lot around the discrete categories I used. Black crosses are runs that went extinct, and filled grey diamonds are runs that did not go extinct within 500 years. Panel (c) shows the distribution of area occupied as the proportion of permanent habitat increases. The grey horizontal line shows the area occupied in 2004.

As the proportion of permanent habitat was increased, the extinction probability of the metapopulation gradually decreased (figure 29a-b). A sharp extinction threshold was not evident (figure 29a), which could be due to the considerable variability between runs in the distribution of permanent habitat, and within runs in the amount of successional habitat available (figure 29b). Interestingly, the observed distribution of permanent habitat was much more beneficial for the metapopulation than the same amount of randomly distributed habitat: with the observed distribution of permanent habitat, 18% permanent (by carrying capacity, not by area) led to 11% extinction in 500 years, whereas 25% randomly-distributed permanent habitat led to 67% extinction in 500 years (figure 29a). With randomly selected permanent patches, at least 50% permanent habitat was needed to maintain the 2004 area occupied (figure 29c).

The observed permanent habitat may be better than a random distribution of patches because the observed permanent habitat is concentrated on Penrhosfeilw Common. I calculated the connectivity of permanent patches in the simulated landscapes, assuming only permanent patches were occupied, and compared the sum of these connectivities to the sum of connectivities of the observed landscape with 14.5 ha permanent. Of the random landscapes with 25% permanent habitat, 94% had lower connectivity sums than the observed landscape, and of the random landscapes with 50% permanent habitat, 64% had lower connectivity sums than the observed landscape.

6.4 Discussion

My modelling of *P. argus* on Holy Island was based on integrating a large amount of data from several sources: population parameters based on the limestone grassland metapopulation, habitat quality based on empirical relationships between *P. argus*, *L. niger* and vegetation height, and the fire sizes and frequency based on RSPB records. I have shown that the 2004 population is likely to be maintained and even increased if the recent rate of burning continues, but only if permanent habitat is also present. It is important to note that, although the burning rate could be reduced substantially without risking the metapopulation's survival, the permanent habitat could not sustain a metapopulation on its own.

The metapopulation of *P. argus* could survive almost as well on the South Stack management unit in isolation, as on all of the heathland on Holy Island, which has approximately double the area. The explanation for this is probably that South Stack has the two largest blocks of contiguous heath (figure 25), and the majority of the permanent habitat. The permanent patches are closer to one another than random fire-created patches (as shown by the summed connectivity), and this contributes greatly to the stability of the metapopulation as a whole, by producing extinction-resistant cores (cf. star on figure 29a). The benefit of large contiguous blocks of heath is that a single disturbance is unlikely to affect the whole block, and so the block is unlikely to suffer bottlenecks in habitat availability that might cause local extinction. This is borne out by a study of southern english heaths which found that no heathland block larger than 50 ha had lost its *P. argus* population, although many smaller blocks had (Thomas *et al.* 1998).

If the burning rate was higher than observed (a situation I did not simulate), one might expect that the metapopulation could survive without the permanent habitat. However, while there is more habitat available as the burning rate increases, there is also a higher probability of patches overlapping and "killing" each other (recall that in the model I assumed that fires land randomly and "kill" patches they overlap). The effect of this can be seen in figure 28 (a-c, the grey boxes show that as burning rate increases linearly, the carrying capacity of habitat increases slower than linearly). In the simulations with the observed burning rate, just over half of habitat patches were "killed" before the 18th year of succession, (the mean fire return interval was roughly 26 years). Therefore, I think it possible that, even with a greatly increased burning rate, one could never reduce the extinction rates from over 99% (as resulted from most scenarios without permanent habitat, table 17) to less than 2% in 500 years (as resulted from most scenarios with permanent habitat, table 17). The amount of burning is extremely variable from year to year, and individual burn sizes also vary enormously. If managers are to intervene to help the *P. argus* metapopulation, I think it would be most valuable to even out this burning rate to ensure a reliable supply of suitable habitat. It would obviously also be desirable if managers could prevent a fire killing off an existing population.

In future work it would be valuable to apply this model to heathland landscapes in southern England where there is more concern about *P. argus* declines. Thomas *et al* (1999) attempted to define habitat patches for *P. argus* in Dorset heathland and predicted their likely occupancy by comparing to patches of a similar size and connectivity in the North Wales limestone metapopulation. However, this approach did not take the habitat dynamics into account and, as I have shown in chapter 5, these will tend to result in lower occupancy of heathland patches for a given connectivity and area. Because it is warmer in the south, *P. argus*'s niche it is a little later in the successional cycle. I hoped to find the relationship between ground temperature and habitat suitability for *P. argus*, which could then have been applied to different climates, in chapter 4, but the data I obtained did not allow this. The quality-time profiles that I parameterised in that chapter will probably need some modification to be applicable to southern England. However, even more important than this parameterisation, will be the identification of permanent habitat, or parts of the landscape where succession will be especially slow (for example, the quarries on Holy Island). Even if these represent a small proportion of the total habitat, they could be disproportionately important to the survival of the metapopulation.

I have shown that, even if permanent habitat is randomly selected from the landscape, a few permanent patches can save the metapopulation from extinction. If this is found to be a typical result in many landscapes, it could become the basis of important conservation principles: firstly that maintaining fragments of permanent habitat is almost always worthwhile, but also that the species most at risk will be the ones without access to any permanent habitat.

6.5 Summary

- I used simulations of fires in the MANAGE model to assess the viability of the *P. argus* metapopulation on Holy Island.
- The viability is most strongly affected by the presence of certain areas of permanent habitat - there is much more variability in outcome due to this than due to uncertainty about the size, type and amount of disturbance.
- The observed patches of permanent habitat are highly aggregated in the landscape, which makes them more valuable for metapopulation persistence than the same amount of randomly placed permanent habitat.
- The relative importance of, and the potential for synergy between, successional and permanent habitat will be relevant to many other conservation case studies, and should be a high priority for theoretical research in future.

7 General discussion

This thesis has described the development of a new dynamic landscape metapopulation model, MANAGE, which effectively bridges the gap between those published models that are generalised and those that are very intricately structured. It has proven possible to use this model both to gain an understanding of principles underlying the dynamics of metapopulations occupying temporary habitats, and to identify specific management options to facilitate the conservation of such systems. I have applied the model to two case studies: the Heath Fritillary (*Melitaea athalia*) populations in the Blean Woods, Kent (chapter 3), and the Silver-studded Blue (*Plebejus argus*) in North Wales (chapters 4-6). These are both UK Biodiversity Action Plan priority species, and my work has led to insights into how the populations might be managed: Firstly, I found that the BAP target for the Heath Fritillary could either be met by approximately doubling the coppicing effort, or by concentrating the existing effort into one of the larger woodland blocks (chapter 3). Secondly, I found both heathland burning and the permanently-suitable habitat close to the coast are required to sustain the metapopulation of the Silver-studded Blue in the South Stack area of Anglesey, so both short- and long-lived kinds of habitat are important to conserve, but the permanent habitat is much more important than its area alone would suggest (chapter 6).

I employed different methods for parameterising the MANAGE model for each study species, depending on the types of data available. For the Heath Fritillary I used parallel disturbance (coppicing) and population presence data for a few consecutive years. Consecutive years of data, with exact knowledge of the age of patches, is the ideal type of data to estimate colonisation and extinction parameters in this kind of system; the only drawback to the data set was the lack of isolated patches which would allow one to test the butterfly's long-distance dispersal ability. For the Silver-studded Blue in North Wales, population surveys had been carried out at seven-year intervals, and the disturbance history of most patches was not known, so a different approach to parameterisation was needed. I parameterised habitat quality based on a detailed study of one heath (Penrhosfeilw Common), including the influences of vegetation height, distance from the sea, and the presence of mutualist ants. However, despite the intensive data collection, my resulting model of habitat quality had considerable associated uncertainty (chapter 4). I fitted the parameters of the incidence function model (parameters that govern colonisation and extinction) for the Silver-studded Blue using the population data from the limestone grassland biotope, where the habitat is effectively permanent (chapter 5). For this parameterisation, it was an advantage that the surveys were widely separated in time, because they were able to represent more or less independent samples from the metapopulation's dynamic equilibrium. I used two different approaches to modelling the habitat dynamics of the heathland metapopulation of Silver-studded Blues in chapters 5 and 6, because the aims of the modelling exercises were very different. Firstly (chapter 5), I aimed to test whether the modelling of habitat dynamics was necessary to reproduce the occupancy patterns observed in the heathland metapopulation (it was; a static habitat model was not sufficient). In order to achieve this, I made the habitat dynamics as simple as possible and always included the observed patches. Secondly (chapter 6), I aimed to model a disturbance regime as close as possible to the real disturbance regime, in order to assess the long-term viability of this metapopulation. Therefore I used the fire data provided by the land managers to parameterise the fire regime, and included the permanent habitat for which I had found evidence in chapter 4.

The most important general result in this thesis for ecologists and conservation biologists is the demonstration that temporal changes in habitat can obscure the relationship between patch occupancy and patch connectivity (chapter 5). This has important implications for the debate about whether many real populations actually fit the metapopulation paradigm. If a connectivity-occupancy relationship is not evident from a species distribution, this has frequently been used to argue that metapopulation dynamics do not play a role in shaping that distribution (e.g. Watling & Donnelly 2006; Pellet *et al.* 2007). For this argument to be valid one would need to be sure that the spatial distribution of habitat, and furthermore, the relative quality of habitat patches, had not changed for many generations. In a dynamic landscape of habitat, extinctions are inevitable, and some means of colonising newly appeared habitat is necessary if the population is to survive at all. Therefore, even if dispersal is global, it could be argued that these systems are metapopulations - debate about the label is less important, I believe, than debating whether a spatially explicit model is needed, and if so whether it should be patch based or grid based, etc. Employing a particular model to summarise a particular set of populations is only ever a means to an end: to answer an ecological or management question, and the model that is used can and should be varied according to the question at hand.

7.1 How MANAGE is useful

MANAGE bridges the gap between the simplest simulation models for a dynamic landscape (those with identical patches and simple, universal rates of disturbance and recovery) and the most complex (e.g. those with vegetation growth and within patch population dynamics submodels). For this thesis I have used MANAGE in quite detailed case studies and so my simulations had a large number of parameters (different management units with complex shapes, numerous different patch sizes, different shaped quality profiles, etc). However, MANAGE could also be used to answer very general theoretical questions, with the fewest possible parameters. For example, the landscape could be a uniform expanse of potential habitat, and patches could all be the same size with a uniform quality profile. MANAGE has been designed with the idea of putting it into the public domain (as SPOMSIM is, Moilanen 1999), so other researchers will be able to employ it in a wide variety of case studies in the future.

A unique feature of MANAGE is its range of options for simulating a dynamic landscape. To my knowledge no other dynamic habitat metapopulation model has been designed with such a systematic approach to the habitat variables that really matter from the modelled species' point of view. These variables are: patch sizes, patch locations, the rate of patch creation (and its variability), the overall carrying capacity of the system (which depends on the quality-time profile as well as the other variables), and the question of whether newly created patches can obliterate existing patches. We attempted to design the model so that all of these variables could be controlled, but it soon became clear that in some cases they could not be varied independently. For example, patch size and patch location interact because a large patch cannot be placed in a small fragment of potential habitat– this is of course a feature of the real world as well as of the model. Logically, one or more of the specified landscape parameters (patch size distribution, patch location distribution or overall amount of habitat) has to be relaxed if there is a conflict like this. We decided to allow the user choice over which parameters take precedence, because one can imagine real world scenarios where each parameter might. So, one can either maintain the patch size by searching for a new location (with the side effect that locations are no longer random), or maintain the location by making the patch smaller (with the side effect that the output patch area distribution is no longer the same as the input patch area distribution). In the latter case, one can choose to prioritise the overall amount of habitat by specifying patch creation rate in terms of area rather than in terms of numbers of patches. This is an example of the systematic design approach which allows MANAGE to be used in a wide variety of situations, without becoming overburdened with environmental detail.

7.2 Comment on parameterisation

Previous authors have commented on the difficulty of getting adequate data for parameterising dynamic landscape metapopulation models (e.g. Snall *et al.* 2005b; Wintle *et al.* 2005). The case studies in this thesis are clearly based on more data than would be available for most species and landscapes. Even so, I did not really have enough data to allow it to be split into parameterisation and validation sets. In chapter 5 I used the numbers of occupied patches and the connectivity-occupancy slope to rule out static scenarios that were incompatible with the data, but it was not possible to do such a full enumeration of dynamic landscape scenarios. The best prospects for validating a dynamic landscape metapopulation model arise when the landscape history is known. If the managers of the Blean Woods continue to collect coppicing and population data for a few more years, there would be a great opportunity to test the parameterisation I have used in chapter 3.

As the importance of landscape dynamics becomes more widely recognised, it will hopefully prompt more collection of data on historical and current disturbance regimes. In the meantime, it is still valuable to attempt to derive rules of thumb for use in conservation in dynamic landscapes, based on generalised simulations over a wide range of parameters.

7.3 Possible conservation rules of thumb

Some of the relationships which can be seen in my case studies are probably universal and can be predicted from theory. Most obviously, occupancy is lower in a dynamic landscape than in an equivalent static landscape (chapter 5 and Johnson 2000b; Amarasekare & Possingham 2001). Also, a small amount of permanent habitat alters the extinction threshold of the entire metapopulation, even if it has little effect on the equilibrium population size (chapter 6 and Hastings 2003). Hastings' (2003) analysis suggests that it is always better to have a few long-lived patches than an equivalent lifetime "shared" between many shorter-lived patches. However, this is based on a deterministic model. In a stochastic model, Frank (2005) shows that the benefit of having heterogeneous patch sizes (a few large and many small, versus all the same size) is lessened or reversed compared to the equivalent deterministic model. It seems to me that the same principle might apply with heterogeneous patch lifetimes, and the results of this calculation could lead to a much more robust rule of thumb for conservation.

Temporal variation in the amount of habitat created as a negative impact on the metapopulation size and increases the likelihood of extinction in my simulations and in previously published ones (chapter 3 and e.g. Boughton & Malvadkar 2002). Spatial aggregation in the disturbances has also been predicted to have a negative effect in previous simulation studies (Johst & Drechsler 2003; Vuilleumier *et al.* 2007), but by contrast, an aggregated distribution of disturbance is beneficial in the Blean Woods metapopulation (chapter 3). The reason for this discrepancy is probably the fact that disturbances can't kill existing patches in my simulations (because in coppiced woodland the Heath Fritillary butterflies are eliminated by succession before the trees are ready for cutting again), combined with the fact that concentrations of habitat remain in the same management units throughout the simulation (whereas in the previously mentioned studies the pattern of spatial aggregation was different every time step). Therefore, one cannot express a general rule of thumb about the effect of spatial aggregation - it depends on the details of the habitat dynamics, and probably also on the scale of aggregation relative to the dispersal distance of the organism. There is a clear need for more research in this area.

7.4 Wider implications

If humans are actually to achieve environmental sustainability - stabilising our populations and resource use and the loss of biodiversity - we need to be much smarter about the ways we manipulate landscape dynamics. Disturbance is by definition destructive and causes the extinction of local populations, or at least sets back their growth, but organisms are adapted to certain amounts and modes of disturbance, and some species absolutely require disturbance to create favourable microhabitat conditions or to release them from competition with other species. Hence, it is often held that an "intermediate" level of disturbance maximises biodiversity (e.g. Moloney & Levin 1996, reviewed in Hobbs & Huenneke 1992). Natural disturbance regimes (under which species evolved) cannot play out on a highly fragmented, human dominated landscape, but we may be able to put in place surrogates that play the same role in allowing species to coexist. To do this we must understand how the disturbances and the disturbed communities interact (for example realising that fire suppression causes fires to be bigger and hotter when they do happen).

We know that crop rotation can be an effective way to suppress crop pests because it takes time for the pests to colonise. By the same principles, we must avoid "rotating nature reserves", because this is likely to leave many species unable to keep up, especially species such as parasites that require their host to colonise first. We should be wary of this when habitat restoration is suggested as a means to mitigate development. On the other hand, we might be able to use landscape dynamics as a tool to limit the spread of invasive species. For example if a certain invasive plant is favoured by domestic grazing animals, one might be able to graze a small area for a short time, then move the animals a good distance away and leave the natural vegetation to regenerate.

Climate warming is likely to lead in some regions to a higher frequency and severity of some disturbance types, especially storms and fires. Planning for biodiversity needs to take this into account: we will need greater areas of natural habitat to combat the increased extinction risk. Furthermore, the climate change itself will change the distribution of suitable habitat for each species. The "creation" of new habitat patches at range margins where the climate is improving (new favourable microclimates and habitats), and loss of suitable locations where climate is deteriorating (loss of suitable microclimate) are similar in some respects to the processes modelled here. Possibly, manipulating succession to create a small-scale patchwork of contrasting micro-climates could aid species in adjusting their geographic range to the new climate.

7.5 Conclusion

In any situation where habitat suitability fluctuates through time, this is predicted to have a negative impact on the equilibrium amount of habitat occupied (all else being equal). This means that classical metapopulation models, if applied to such situations, are likely to give overly optimistic results, with potentially serious consequences for conservation. A dynamic habitat metapopulation model, like MANAGE, can help us to understand the large-scale and long-term impacts of landscape dynamics on individual species. It can help in conservation planning in the face of uncertainty: for example, future disturbance regimes can be explored by using different scenarios, and one can also quantify the effect of different manmade disturbance strategies. Many, if not most, habitat types that occur as discrete patches are also temporary. Therefore, although a dynamic habitat model requires more parameters than a classical patch occupancy metapopulation model, it is potentially applicable to many more species and landscapes. Ultimately, a better understanding of the spatio-temporal constraints on species distributions can help us to understand how species co-exist with each other, and to understand how we might avoid the loss of biodiversity in a rapidly changing world.

Appendix 1: Raw data from the *P. argus* surveys of North Wales 1983-2004

Appendix table 20: Data from the four North Wales *P. argus* surveys, including patches of unoccupied, suitable limestone grassland habitat. The co-ordinates are measured on the British National Grid, and are averaged across all years a patch was surveyed. Density is the estimated density of adults at the peak flight period, based on a transect count. The localities used for the analyses in chapter 5 are Silver Bay, South Stack Cliffs, Penrhosfeilw and Trearddur (all on Holy Island, Anglesey) and Creuddyn Peninsula, Great Orme, and Llandulas (all on mainland). The Id numbers can be used to identify each of the patches in these localities on the maps in figures 32-40.

Id	Biotope	Locality	X co-ord average, m	Y co-ord average, m	Area 1983, ha	Area 1990, ha	Area 1997, ha	Area 2004, ha	Occupancy 1983	Occupancy 1990	Occupancy 1997	Occupancy 2004	Density 1983, ha^{-1}	Density 1997, ha^{-1}	Density 2004, ha^{-1}
55	Heath	Cae-brych Lligwy	248,650	385,950	~	~	~	~	1	0	0	~	~	~	~
56	Heath	Cors Erddreiniog	247,211	381,362	0.900	0.900	~	~	1	0	0	~	34	~	~
57	Heath	Marford Quarry	335,767	355,896	1.506	1.506	~	~	1	1	0	0	105	~	~
54	Heath	Mynydd Bodafon	247,250	385,550	~	~	~	~	1	0	0	~	~	~	~
61	Heath	Prees Heath	355,736	336,925	0.106	0.130	0.050	~	1	1	1	0	109	1,908	~
62	Heath	Prees Heath	355,706	336,385	0.139	0.141	0.084	~	1	0	1	0	682	159	~
63	Heath	Prees Heath	355,802	336,311	0.125	0.117	0.155	~	1	0	1	0	259	2,695	~
64	Heath	Prees Heath	355,923	336,795	4.057	4.471	3.963	4.315	1	1	1	1	557	3,250	436
66	Heath	Prees Heath	355,868	337,333	0.222	0.121	0.247	~	1	1	1	0	394	1,709	~
67	Heath	Prees Heath	355,780	337,472	0.408	0.408	0.185	~	1	0	1	0	180	166	~
68	Heath	Prees Heath	355,821	337,602	0.368	0.384	0.114	~	1	0	1	0	932	395	~
123	Heath	Prees Heath	355,790	336,904	~	0.043	~	~	0	1	0	0	~	~	~
124	Heath	Prees Heath	355,725	336,669	~	0.478	0.677	0.642	0	1	1	1	~	1,617	1,466
125	Heath	Prees Heath	355,756	337,114	~	0.138	0.093	~	0	1	1	0	~	3,170	~
126	Heath	Prees Heath	355,764	337,289	~	0.175	0.451	0.317	~	1	1	1	~	3,808	373
129	Heath	Prees Heath	355,761	337,533	~	0.023	~	~	~	0	0	~	~	~	~
225	Heath	Prees Heath	355,782	337,060	~	~	0.163	~	~	0	1	0	~	2,613	~
226	Heath	Prees Heath	355,802	337,235	~	~	0.184	0.249	~	0	1	1	~	345	651
36	Heath	Silver Bay	228,602	375,035	3.978	5.372	4.542	5.114	1	1	1	1	335	306	517

Appendix table 20, continued

Id	Biotope	Locality	X co-ord average, m	Y co-ord average, m	Area 1983, ha	Area 1990, ha	Area 1997, ha	Area 2004, ha	Occupancy 1983	Occupancy 1990	Occupancy 1997	Occupancy 2004	Density 1983, ha^{-1}	Density 1997, ha^{-1}	Density 2004, ha^{-1}
37	Heath	Silver Bay	229,345	375,871	6.025	4.488	2.985	0.541	1	1	1	1	475	84	30
38	Heath	Silver Bay	229,100	376,133	1.295	2.217	~	~	1	1	0	0	437	~	~
305	Heath	Silver Bay	225,976	375,779	~	~	~	0.060	0	~	~	1	~	~	30
306	Heath	Silver Bay	225,897	375,724	~	~	~	0.077	0	~	~	1	~	~	19
307	Heath	Silver Bay	226,000	375,382	~	~	~	0.806	0	~	~	1	~	~	349
308	Heath	Silver Bay	226,877	374,755	~	~	~	0.601	0	~	~	1	~	~	12
309	Heath	Silver Bay	228,809	376,255	~	~	~	0.069	0	~	~	1	~	~	119
310	Heath	Silver Bay	228,890	376,340	~	~	~	0.106	0	~	~	1	~	~	367
311	Heath	Silver Bay	228,868	376,295	~	~	~	0.044	0	~	~	1	~	~	36
1	Heath	South Stack Cliffs	220,725	382,163	0.250	0.413	0.356	~	1	1	1	0	893	420	~
2	Heath	South Stack Cliffs	220,949	382,257	0.147	~	~	~	1	0	0	0	171	~	~
3	Heath	South Stack Cliffs	220,886	382,343	0.599	0.233	~	~	1	1	0	0	234	~	~
4	Heath	South Stack Cliffs	220,766	382,459	0.225	~	~	~	1	0	0	0	364	~	~
5	Heath	South Stack Cliffs	221,154	382,071	0.270	~	0.066	~	1	0	1	0	497	413	~
6	Heath	South Stack Cliffs	221,476	382,489	0.237	0.233	~	~	1	1	0	0	757	~	~
7	Heath	South Stack Cliffs	221,853	382,366	0.279	0.415	0.226	0.026	1	1	1	1	1,586	553	75
8	Heath	South Stack Cliffs	222,339	383,558	1.005	1.223	~	~	1	1	0	0	732	~	~
9	Heath	South Stack Cliffs	222,668	383,489	0.265	0.215	~	~	1	1	0	0	546	~	~
10	Heath	South Stack Cliffs	222,631	383,377	0.498	0.617	0.331	~	1	1	1	0	1,070	76	~
11	Heath	South Stack Cliffs	222,922	383,096	0.284	0.225	0.155	0.118	1	1	1	1	446	330	~
12	Heath	South Stack Cliffs	221,027	381,522	0.260	~	~	~	1	0	0	0	926	~	~
13	Heath	South Stack Cliffs	221,049	381,883	0.243	~	~	~	1	0	0	0	957	~	~
14	Heath	South Stack Cliffs	220,814	381,869	1.810	0.370	0.303	1.135	1	1	1	1	196	479	~
107	Heath	South Stack Cliffs	221,021	382,011	~	0.051	~	~	0	1	0	0	~	~	~
108	Heath	South Stack Cliffs	220,955	382,015	~	0.058	0.048	~	0	1	1	0	~	11	~
109	Heath	South Stack Cliffs	221,000	382,210	~	0.251	~	~	0	1	0	0	~	~	~
110	Heath	South Stack Cliffs	220,620	382,308	~	0.521	0.246	0.201	0	1	1	1	~	389	157
111	Heath	South Stack Cliffs	221,780	382,386	~	0.135	~	~	0	1	0	0	~	~	~
113	Heath	South Stack Cliffs	222,012	382,153	~	0.083	0.166	0.203	0	1	1	1	~	1,001	673
114	Heath	South Stack Cliffs	222,110	382,113	~	0.082	~	~	0	1	0	0	~	~	~
115	Heath	South Stack Cliffs	222,167	382,209	~	0.093	0.271	0.321	0	1	1	1	~	91	640
116	Heath	South Stack Cliffs	222,213	382,261	~	0.105	~	~	0	1	0	0	~	~	~

Appendix table 20, continued

Id	Biotope	Locality	X co-ord average, m	Y co-ord average, m	Area 1983, ha	Area 1990, ha	Area 1997, ha	Area 2004, ha	Occupancy 1983	Occupancy 1990	Occupancy 1997	Occupancy 2004	Density 1983, ha^{-1}	Density 1997, ha^{-1}	Density 2004, ha^{-1}
117	Heath	South Stack Cliffs	222,385	382,492	~	0.042	~	~	0	1	0	0	~	~	~
118	Heath	South Stack Cliffs	222,427	382,561	~	0.474	~	~	0	1	0	0	~	~	~
119	Heath	South Stack Cliffs	222,208	382,589	~	0.110	0.085	~	0	1	1	0	~	92	~
120	Heath	South Stack Cliffs	222,503	383,347	~	0.188	~	~	0	1	0	0	~	~	~
203	Heath	South Stack Cliffs	220,694	382,241	~	~	0.034	~	0	0	1	0	~	92	~
204	Heath	South Stack Cliffs	222,310	382,667	~	~	0.076	~	0	0	1	0	~	115	~
205	Heath	South Stack Cliffs	222,394	382,663	~	~	0.102	0.137	0	0	1	1	~	1,391	83
206	Heath	South Stack Cliffs	222,432	383,212	~	~	0.494	~	0	0	1	0	~	37	~
300	Heath	South Stack Cliffs	223,122	381,892	~	~	~	1.172	~	~	~	1	~	~	144
15	Heath	Penrhosfeilw	221,843	379,900	47.579	41.701	47.375	30.146	1	1	1	1	667	2,058	420
21	Heath	Penrhosfeilw	222,454	379,562	0.347	0.230	~	~	1	1	0	0	531	~	~
22	Heath	Penrhosfeilw	222,726	379,617	0.159	0.107	~	~	1	1	0	0	420	~	~
23	Heath	Penrhosfeilw	222,634	379,751	0.471	0.263	~	~	1	1	0	0	445	~	~
24	Heath	Penrhosfeilw	222,730	379,736	0.641	0.202	0.351	0.231	1	1	1	1	452	844	105
25	Heath	Penrhosfeilw	222,792	379,862	0.196	0.105	~	~	1	1	0	0	99	~	~
26	Heath	Penrhosfeilw	222,921	379,902	0.222	0.041	~	~	1	1	0	0	141	~	~
27	Heath	Penrhosfeilw	222,971	379,969	0.127	~	~	~	1	0	0	0	137	~	~
28	Heath	Penrhosfeilw	223,136	379,972	0.134	~	0.191	~	1	0	1	0	148	156	~
106	Heath	Penrhosfeilw	222,857	379,899	~	0.090	0.094	~	0	1	1	0	~	429	~
29	Heath	Trearddur	225,696	377,522	5.340	5.985	3.881	2.276	1	1	1	1	165	143	322
30	Heath	Trearddur	226,133	377,377	2.778	3.164	0.449	0.907	1	1	1	1	75	79	13
31	Heath	Trearddur	225,933	377,139	1.100	0.192	0.483	~	1	1	1	0	380	74	~
32	Heath	Trearddur	225,848	377,240	0.125	0.216	0.324	1.293	1	1	1	1	245	143	52
33	Heath	Trearddur	225,830	377,046	0.617	0.671	0.328	0.148	1	1	1	1	247	78	155
35	Heath	Trearddur	225,998	376,721	1.500	1.109	0.676	0.927	1	1	1	1	16	75	15
101	Heath	Trearddur	225,493	377,515	~	0.093	~	~	0	1	0	0	~	~	~
102	Heath	Trearddur	225,459	377,788	~	0.061	0.028	~	0	1	1	0	~	196	~
103	Heath	Trearddur	226,135	377,547	~	1.045	~	0.288	0	1	0	1	~	~	~
104	Heath	Trearddur	226,139	376,834	~	0.101	~	0.202	0	1	0	1	~	~	273
105	Heath	Trearddur	226,098	376,528	~	0.664	~	~	0	1	0	0	~	~	~
201	Heath	Trearddur	225,939	377,241	~	~	0.119	0.058	0	0	1	1	~	267	28
301	Heath	Trearddur	226,099	377,312	~	~	~	0.487	0	0	0	1	~	~	203

Appendix table 20, continued

Id	Biotope	Locality	X co-ord average, m	Y co-ord average, m	Area 1983, ha	Area 1990, ha	Area 1997, ha	Area 2004, ha	Occupancy 1983	Occupancy 1990	Occupancy 1997	Occupancy 2004	Density 1983, ha^{-1}	Density 1997, ha^{-1}	Density 2004, ha^{-1}
304	Heath	Trearddur	226,002	376,886	~	~	~	0.158	0	0	0	1	~	~	196
143	Lime	Creuddyn Peninsula	281,309	382,165	~	1.021	0.755	1.575	0	0	0	0	~	0	0
144	Lime	Creuddyn Peninsula	281,819	382,539	~	0.215	0.239	0.081	0	0	0	0	~	0	0
145	Lime	Creuddyn Peninsula	281,823	382,350	~	0.432	~	~	0	0	0	~	~	~	~
146	Lime	Creuddyn Peninsula	281,769	381,717	~	0.394	0.264	0.068	0	0	0	0	~	0	0
147	Lime	Creuddyn Peninsula	281,702	381,646	~	0.152	0.110	0.024	0	0	0	0	~	0	0
148	Lime	Creuddyn Peninsula	281,582	381,748	~	0.350	0.183	0.050	0	0	0	0	~	0	0
150	Lime	Creuddyn Peninsula	281,324	381,905	~	0.101	0.058	~	0	0	0	0	~	0	~
151	Lime	Creuddyn Peninsula	281,277	381,636	~	0.106	~	~	0	0	0	~	~	~	~
152	Lime	Creuddyn Peninsula	281,018	382,043	~	0.430	0.229	~	0	0	0	0	~	0	~
153	Lime	Creuddyn Peninsula	279,867	380,961	~	0.990	1.180	1.910	0	0	1	0	~	~	0
155	Lime	Creuddyn Peninsula	280,028	378,668	~	1.076	0.371	0.586	0	0	0	0	~	0	0
156	Lime	Creuddyn Peninsula	280,268	378,719	~	0.338	0.225	~	0	0	0	0	~	0	~
157	Lime	Creuddyn Peninsula	280,524	378,881	~	0.262	0.468	0.334	0	0	0	0	~	0	0
158	Lime	Creuddyn Peninsula	281,128	378,937	~	0.188	0.308	~	0	0	0	0	~	0	~
159	Lime	Creuddyn Peninsula	282,215	379,750	~	0.394	0.763	0.242	0	0	1	0	~	~	0
160	Lime	Creuddyn Peninsula	283,100	379,761	~	0.686	0.961	0.629	0	0	0	0	~	0	0
216	Lime	Creuddyn Peninsula	283,161	379,817	~	~	0.275	~	~	0	0	0	~	0	~
217	Lime	Creuddyn Peninsula	283,242	379,827	~	~	0.199	~	~	0	0	0	~	0	~
320	Lime	Creuddyn Peninsula	282,053	379,599	~	~	~	0.121	0	0	0	0	~	~	0
321	Lime	Creuddyn Peninsula	280,278	381,464	~	~	~	0.585	~	~	0	0	~	~	0
322	Lime	Creuddyn Peninsula	280,139	381,499	~	~	~	0.061	~	~	0	0	~	~	0
323	Lime	Creuddyn Peninsula	281,075	381,553	~	~	~	0.267	~	~	0	0	~	~	0
324	Lime	Creuddyn Peninsula	280,493	381,197	~	~	~	1.149	~	~	0	0	~	~	0
325	Lime	Creuddyn Peninsula	281,391	382,282	~	~	~	0.452	~	~	0	0	~	~	0
326	Lime	Creuddyn Peninsula	281,478	382,482	~	~	~	0.336	~	~	0	0	~	~	0
327	Lime	Creuddyn Peninsula	278,185	379,439	~	~	~	0.027	~	~	0	0	~	~	0
71	Lime	Great Orme	276,168	383,016	17.000	22.958	55.594	48.614	1	1	1	1	5,439	2,065	4,848
76	Lime	Great Orme	277,169	382,659	1.369	0.902	0.406	0.337	1	1	1	1	1,375	597	1,172
77	Lime	Great Orme	277,936	382,866	0.291	0.417	0.661	0.531	1	1	1	1	496	1,529	2,659
78	Lime	Great Orme	277,831	383,150	1.531	3.232	4.449	7.624	1	1	1	1	690	1,955	2,991
80	Lime	Great Orme	277,595	382,696	0.306	0.365	0.297	0.255	1	1	1	1	401	3,901	4,804

Appendix table 20, continued

Id	Biotope	Locality	X co-ord average, m	Y co-ord average, m	Area 1983, ha	Area 1990, ha	Area 1997, ha	Area 2004, ha	Occupancy 1983	Occupancy 1990	Occupancy 1997	Occupancy 2004	Density 1983, ha^{-1}	Density 1997, ha^{-1}	Density 2004, ha^{-1}
141	Lime	Great Orme	278,008	382,982	~	0.234	~	~	0	0	0	~	~	~	~
208	Lime	Great Orme	277,377	382,937	~	~	0.036	0.120	~	0	1	1	~	55	257
209	Lime	Great Orme	277,777	383,401	~	~	0.366	0.197	~	0	1	1	~	230	202
210	Lime	Great Orme	278,263	382,886	~	~	0.155	0.083	~	~	1	1	~	3,469	504
211	Lime	Great Orme	278,127	382,868	~	~	0.276	0.154	~	~	1	1	~	4,490	3,775
212	Lime	Great Orme	278,062	382,881	~	~	0.061	0.100	~	~	1	0	~	119	0
213	Lime	Great Orme	277,692	382,678	~	~	0.064	0.007	~	0	1	1	~	176	327
81	Lime	Llandulas	289,010	377,259	2.062	1.542	1.396	0.822	1	1	1	1	3,967	1,711	479
82	Lime	Llandulas	289,738	376,524	2.083	1.666	0.578	0.437	1	1	1	1	1,398	768	225
84	Lime	Llandulas	290,217	376,429	0.236	0.682	0.203	0.593	1	1	1	1	144	648	750
85	Lime	Llandulas	290,376	376,335	0.283	0.504	0.409	0.176	1	1	1	1	472	333	786
86	Lime	Llandulas	290,596	376,539	1.348	1.537	1.342	0.686	1	1	1	1	5,716	2,098	5,449
87	Lime	Llandulas	290,686	376,756	0.842	1.378	1.099	0.474	1	1	1	1	327	591	6,237
88	Lime	Llandulas	290,516	376,831	1.010	1.192	1.236	0.757	1	1	1	1	794	2,822	1,680
89	Lime	Llandulas	290,663	376,999	1.168	1.365	1.370	0.511	1	1	1	1	1,002	1,002	2,788
90	Lime	Llandulas	290,598	377,359	0.068	0.104	0.061	0.010	1	1	0	0	74	0	0
91	Lime	Llandulas	291,287	376,469	2.036	1.497	2.444	0.875	1	1	1	1	1,712	1,330	5,070
92	Lime	Llandulas	291,630	375,896	0.696	0.377	0.837	0.697	1	1	1	1	178	928	140
94	Lime	Llandulas	291,707	376,203	0.800	0.697	0.591	1.053	1	1	1	1	191	1,279	458
95	Lime	Llandulas	291,521	377,203	0.317	0.451	0.345	4.031	1	1	1	1	96	373	1,602
96	Lime	Llandulas	291,331	377,726	4.093	2.409	2.439	0.470	1	1	1	1	1,328	1,244	5,195
161	Lime	Llandulas	288,167	377,554	~	0.139	0.106	0.211	0	0	1	0	~	41	0
162	Lime	Llandulas	288,645	377,301	~	0.138	0.038	0.015	0	0	1	1	~	450	107
163	Lime	Llandulas	291,303	376,164	~	0.540	1.580	0.655	0	1	1	1	~	2,255	~
218	Lime	Llandulas	290,392	376,998	~	~	0.235	0.199	0	0	1	0	~	68	0
219	Lime	Llandulas	290,667	377,249	~	~	0.204	~	0	0	0	0	~	0	~
220	Lime	Llandulas	291,710	377,088	~	~	0.177	0.590	0	0	0	1	~	0	317
221	Lime	Llandulas	291,602	376,880	~	~	0.352	0.584	~	0	1	1	~	168	148
222	Lime	Llandulas	291,915	376,999	~	~	0.167	0.348	0	0	1	1	~	591	3,737
223	Lime	Llandulas	291,708	376,043	~	~	0.167	0.285	0	0	1	1	~	123	840
328	Lime	Llandulas	288,422	377,400	~	~	~	0.226	~	~	0	0	~	~	0
332	Lime	Llandulas	291,445	377,232	~	~	~	0.054	~	~	~	1	~	~	553

Appendix table 20, continued

Id	Biotope	Locality	X co-ord average, m	Y co-ord average, m	Area 1983, ha	Area 1990, ha	Area 1997, ha	Area 2004, ha	Occupancy 1983	Occupancy 1990	Occupancy 1997	Occupancy 2004	Density 1983, ha^{-1}	Density 1997, ha^{-1}	Density 2004, ha^{-1}
333	Lime	Llandulas	294,780	376,045	~	~	~	0.021	~	~	~	0	~	~	0
334	Lime	Llandulas	293,488	377,187	~	~	~	0.028	~	~	~	0	~	~	0
335	Lime	Llandulas	293,808	376,605	~	~	~	0.015	~	~	~	0	~	~	0
336	Lime	Llandulas	293,771	376,639	~	~	~	0.032	~	~	~	0	~	~	0
98	Lime	Penmon	262,817	380,319	~	2.345	2.382	0.710	1	0	0	0	~	0	0
131	Lime	Penmon	262,856	380,589	~	1.504	1.125	0.102	0	0	0	0	~	0	0
132	Lime	Penmon	263,028	380,776	~	0.084	~	~	0	0	~	~	~	~	~
133	Lime	Penmon	263,531	380,714	~	1.427	2.174	~	~	0	0	~	~	0	~
139	Lime	Penmon	263,067	381,194	~	0.129	0.182	~	0	0	0	0	~	0	~
140	Lime	Penmon	262,745	381,623	~	0.078	~	~	0	0	0	~	~	~	~
207	Lime	Penmon	263,443	380,915	~	~	0.195	~	~	0	0	~	~	0	~
312	Lime	Penmon	263,201	380,869	~	~	~	0.008	~	~	0	0	~	~	0
313	Lime	Penmon	262,708	381,495	~	~	~	0.060	~	~	0	0	~	~	0
97	Lime	Prestatyn	305,944	380,329	~	1.852	0.713	2.546	1	1	1	1	~	1,241	1,596
167	Lime	Prestatyn	306,256	378,334	~	6.985	7.042	1.933	0	0	0	0	~	0	0
169	Lime	Prestatyn	305,704	379,307	~	0.448	0.139	0.048	0	0	0	0	~	0	0
170	Lime	Prestatyn	305,778	379,489	~	0.502	0.235	0.083	0	0	0	0	~	0	0
171	Lime	Prestatyn	305,993	379,895	~	0.775	0.230	0.339	0	0	0	0	~	0	0
172	Lime	Prestatyn	306,679	380,785	~	0.490	0.160	0.017	0	0	0	0	~	0	0
173	Lime	Prestatyn	306,732	381,007	~	0.757	0.508	0.141	0	0	0	0	~	0	0
175	Lime	Prestatyn	306,818	381,032	~	0.283	0.018	0.016	~	0	0	0	~	0	0
176	Lime	Prestatyn	306,809	381,114	~	0.218	~	0.024	~	0	~	0	~	~	0
177	Lime	Prestatyn	306,500	380,322	~	0.387	0.138	0.101	0	0	0	0	~	0	0
179	Lime	Prestatyn	306,269	379,004	~	0.527	0.102	0.049	0	0	0	0	~	0	0
180	Lime	Prestatyn	306,124	378,894	~	0.255	0.119	0.025	0	0	0	0	~	0	0
181	Lime	Prestatyn	308,705	380,066	~	0.574	2.162	0.261	0	0	0	0	~	0	0
182	Lime	Prestatyn	307,144	381,920	~	0.324	~	~	0	0	0	~	~	~	~
183	Lime	Prestatyn	307,085	381,826	~	0.321	~	~	0	0	0	~	~	~	~
184	Lime	Prestatyn	307,188	382,045	~	0.525	~	~	0	0	0	~	~	~	~
185	Lime	Prestatyn	307,250	382,150	~	0.142	~	~	0	0	0	~	~	~	~
214	Lime	Prestatyn	306,791	380,919	~	~	0.037	0.004	~	~	0	0	~	0	0
215	Lime	Prestatyn	306,740	380,640	~	~	0.087	0.025	~	0	0	0	~	0	0

Appendix table 20, continued

Id	Biotope	Locality	X co-ord average, m	Y co-ord average, m	Area 1983, ha	Area 1990, ha	Area 1997, ha	Area 2004, ha	Occupancy 1983	Occupancy 1990	Occupancy 1997	Occupancy 2004	Density 1983, ha^{-1}	Density 1997, ha^{-1}	Density 2004, ha^{-1}
314	Lime	Prestatyn	306,874	381,093	~	~	~	0.017	~	~	0	0	~	~	0
316	Lime	Prestatyn	306,829	380,888	~	~	~	0.034	~	~	0	0	~	~	0
224	Lime	Tremeirchion	308,521	371,895	~	~	0.131	0.380	~	0	1	0	~	~	0
58	Moss	Hafod Garregog	260,104	344,646	4.491	3.269	3.175	~	1	1	1	~	1,654	2,133	~
121	Moss	Hafod Garregog	260,445	344,840	~	1.769	1.982	1.970	0	1	1	1	~	243	119
122	Moss	Hafod Garregog	260,483	344,636	~	0.778	1.503	~	~	1	1	~	~	1,353	~

Appendix table 21: Details of patches that split or merged from one survey to the next. Sometimes this represents a true change in the habitat, but it could also be a difference in the surveyors' interpretation of where patch boundaries are (see maps in figures 32-40 for more details). The Id number is the same as that in table 20, and on the maps; the code is the identification code used by the surveyors in a particular year.

Id	Locality	Biotope	Year 0	Year 7	Code Yr0	Code Yr7	No. sub patches	Split or merge	X co-ord Yr0	Y co-ord Yr0	X co-ord Yr7	Y co-ord Yr7	Area Yr0	Area Yr7	Occupancy Yr0	Occupancy Yr7
61	Prees Heath	Heath	1983	1990	S1	S1b	2	s	355,743	336,922	355,752	336,904	0.106	0.102	1	1
61	Prees Heath	Heath	1983	1990	S1	S1a	2	s	355,743	336,922	355,680	336,979	0.106	0.028	1	0
64	Prees Heath	Heath	1983	1990	S4	S4-5	2	m	355,916	336,791	355,932	336,839	3.439	4.471	1	1
64	Prees Heath	Heath	1983	1990	S5	S4-5	2	m	355,945	336,796	355,932	336,839	0.618	4.471	1	1
68	Prees Heath	Heath	1990	1997	S8	C	2	m	355,813	337,609	355,835	337,601	0.368	0.114	0	1
68	Prees Heath	Heath	1990	1997	S15	C	2	m	355,818	337,583	355,835	337,601	0.016	0.114	0	1
126	Prees Heath	Heath	1990	1997	S11	I	3	m	355,770	337,251	355,757	337,289	0.097	0.451	1	1
126	Prees Heath	Heath	1990	1997	S12	I	3	m	355,776	337,300	355,757	337,289	0.064	0.451	1	1
126	Prees Heath	Heath	1990	1997	S13	I	3	m	355,728	337,284	355,757	337,289	0.014	0.451	1	1
7	South Stack Cliffs	Heath	1990	1997	H14(1)	H	2	m	221,844	382,341	221,866	382,399	0.156	0.226	1	1
7	South Stack Cliffs	Heath	1990	1997	H14(3)	H	2	m	221,835	382,444	221,866	382,399	0.259	0.226	1	1
14	South Stack Cliffs	Heath	1983	1990	H9(2)	H9(2)	2	s	220,809	381,867	220,729	381,923	1.81	0.239	1	1
14	South Stack Cliffs	Heath	1983	1990	H9(2)	H9(2)	2	s	220,809	381,867	220,865	381,823	1.81	0.131	1	1
14	South Stack Cliffs	Heath	1997	2004	A	129	2	s	220,848	381,844	220,803	381,872	0.173	0.066	1	1

Appendix table 21, continued

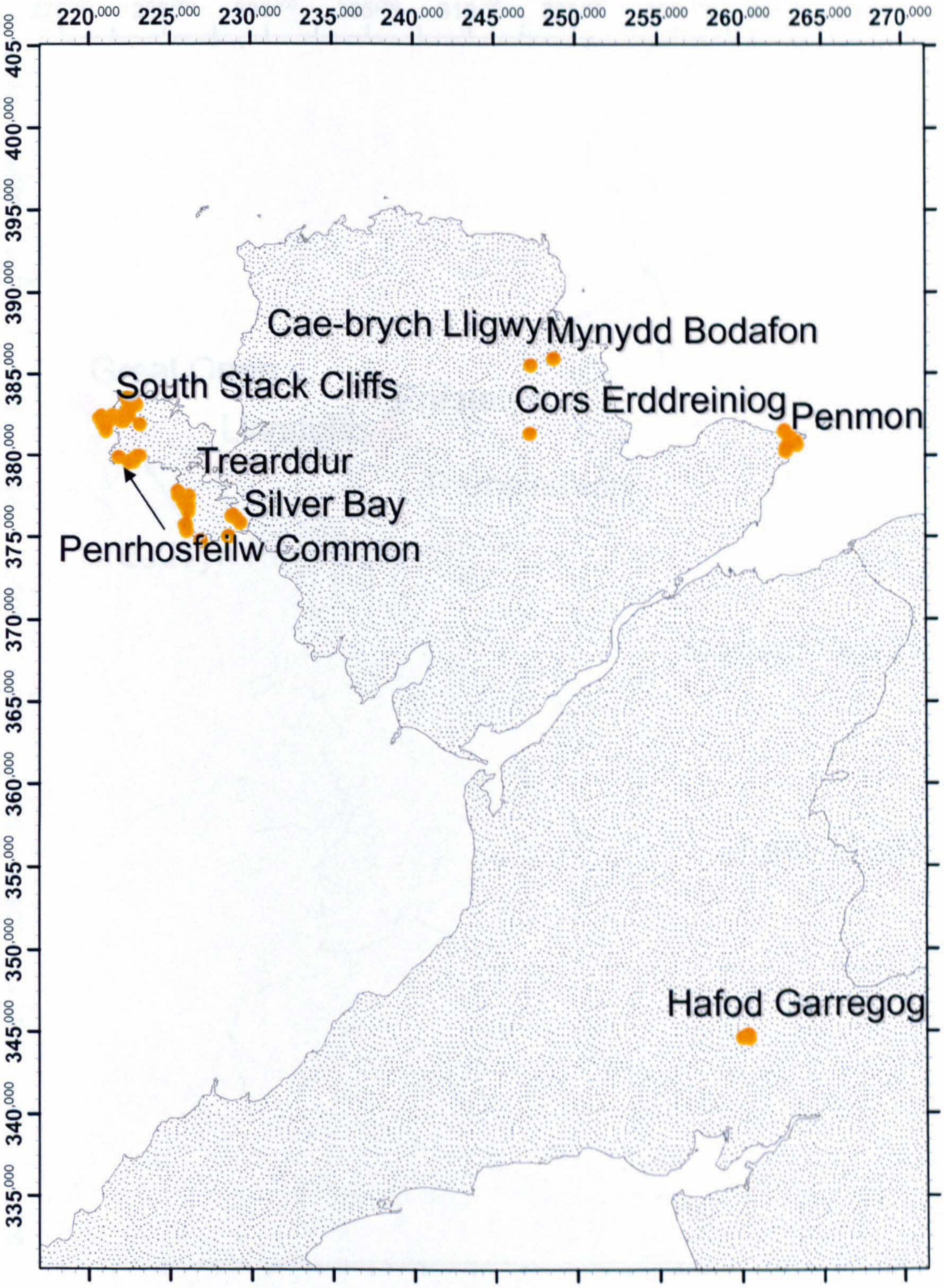
Id	Locality	Biotope	Year 0	Year 7	Code Yr0	Code Yr7	No. sub patches	Split or merge	X co-ord Yr0	Y co-ord Yr0	X co-ord Yr7	Y co-ord Yr7	Area Yr0	Area Yr7	Occupancy Yr0	Occupancy Yr7
14	South Stack Cliffs	Heath	1997	2004	A	107	2	s	220,848	381,844	220,957	381,803	0.173	1.069	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	5	s	221,430	380,075	221,383	380,003	38.017	26.281	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	5	s	221,430	380,075	221,757	380,007	38.017	0.411	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	5	s	221,430	380,075	221,754	379,896	38.017	0.286	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	5	s	221,430	380,075	221,696	379,752	38.017	0.093	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	5	s	221,430	380,075	221,775	379,823	38.017	0.058	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	4	m	221,986	379,830	222,144	379,758	6.068	14.572	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	4	m	222,190	379,857	222,144	379,758	0.716	14.572	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	4	m	222,287	379,767	222,144	379,758	0.343	14.572	1	1
15	Penrhosfeilw	Heath	1983	1990	H1	H1	4	m	222,319	379,598	222,144	379,758	2.24	14.572	1	1
15	Penrhosfeilw	Heath	1990	1997	H1	A	6	m	222,144	379,758	221,602	379,950	14.572	47.195	1	1
15	Penrhosfeilw	Heath	1990	1997	H1	A	6	m	221,383	380,003	221,602	379,950	26.281	47.195	1	1
15	Penrhosfeilw	Heath	1990	1997	H1	A	6	m	221,757	380,007	221,602	379,950	0.411	47.195	1	1
15	Penrhosfeilw	Heath	1990	1997	H1	A	6	m	221,754	379,896	221,602	379,950	0.286	47.195	1	1
15	Penrhosfeilw	Heath	1990	1997	H1	A	6	m	221,696	379,752	221,602	379,950	0.093	47.195	1	1
15	Penrhosfeilw	Heath	1990	1997	H1	A	6	m	221,775	379,823	221,602	379,950	0.058	47.195	1	1
15	Penrhosfeilw	Heath	1997	2004	A	113.1	2	m	221,602	379,950	221,703	379,884	47.195	30.146	1	1
15	Penrhosfeilw	Heath	1997	2004	B	113.1	2	m	222,107	379,983	221,703	379,884	0.18	30.146	1	1
31	Trearddur	Heath	1983	1990	H5(1)	H5(1)	3	s	225,951	377,146	225,963	377,153	1.1	0.1	1	1
31	Trearddur	Heath	1983	1990	H5(1)	H5(1)	3	s	225,951	377,146	225,867	377,109	1.1	0.046	1	1
31	Trearddur	Heath	1983	1990	H5(1)	H5(1)	3	s	225,951	377,146	225,845	377,151	1.1	0.046	1	1
33	Trearddur	Heath	1983	1990	H5(3)	H5(3+4)	2	m	225,782	377,065	225,823	377,034	0.385	0.671	1	1
33	Trearddur	Heath	1983	1990	H5(4)	H5(3+4)	2	m	225,860	377,037	225,823	377,034	0.232	0.671	1	1
153	Creuddyn Peninsula	Lime	1997	2004	A	24	2	m	279,812	381,063	279,878	381,038	0.844	1.91	1	0
153	Creuddyn Peninsula	Lime	1997	2004	J	24	2	m	279,915	380,813	279,878	381,038	0.336	1.91	0	0
71	Great Orme	Lime	1990	1997	GO1	M	5	m	275,175	383,867	276,059	383,106	2.661	55.594	1	1
71	Great Orme	Lime	1990	1997	GO2	M	5	m	275,804	383,280	276,059	383,106	10.751	55.594	1	1
71	Great Orme	Lime	1990	1997	GO3	M	5	m	276,444	382,713	276,059	383,106	2.336	55.594	1	1
71	Great Orme	Lime	1990	1997	GO4	M	5	m	276,691	382,443	276,059	383,106	3.637	55.594	1	1
71	Great Orme	Lime	1990	1997	GO5	M	5	m	277,208	382,337	276,059	383,106	3.573	55.594	1	1
76	Great Orme	Lime	1990	1997	GO6	A	2	s	277,137	382,647	277,155	382,637	0.902	0.085	1	1
76	Great Orme	Lime	1990	1997	GO6	B	2	s	277,137	382,647	277,256	382,719	0.902	0.321	1	1

Appendix table 21, continued

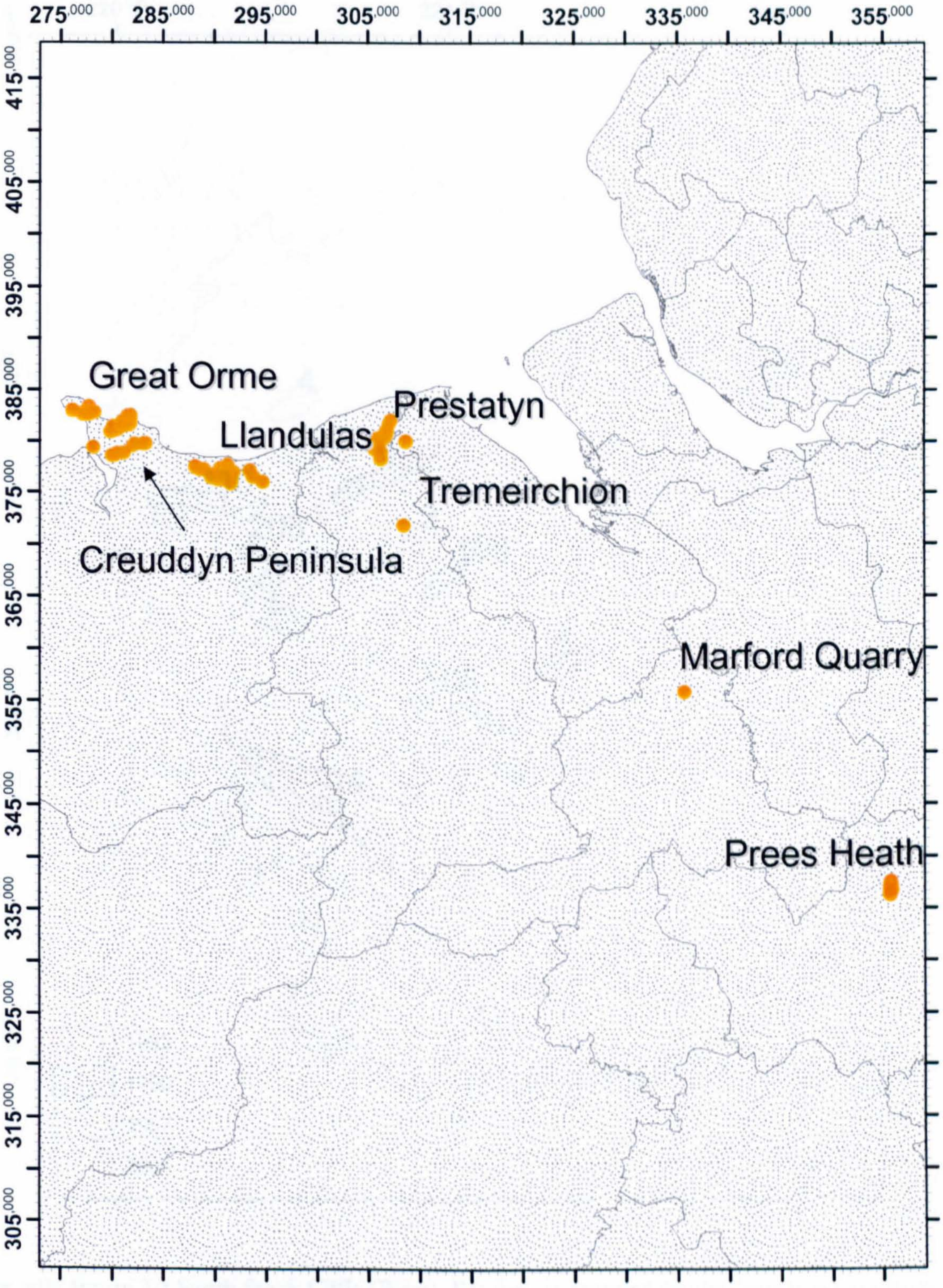
Id	Locality	Biotope	Year 0	Year 7	Code Yr0	Code Yr7	No. sub patches	Split or merge	X co-ord Yr0	Y co-ord Yr0	X co-ord Yr7	Y co-ord Yr7	Area Yr0	Area Yr7	Occupancy Yr0	Occupancy Yr7
77	Great Orme	Lime	1997	2004	J	10	3	s	277,957	382,866	277,964	382,850	0.661	0.319	1	1
77	Great Orme	Lime	1997	2004	J	9.1	3	s	277,957	382,866	277,855	382,866	0.661	0.125	1	1
77	Great Orme	Lime	1997	2004	J	9.2	3	s	277,957	382,866	277,837	382,895	0.661	0.087	1	0
78	Great Orme	Lime	1990	1997	GO9	D	3	m	277,823	383,300	277,842	383,118	0.694	4.449	1	1
78	Great Orme	Lime	1990	1997	GO8	D	3	m	277,673	383,010	277,842	383,118	1.476	4.449	1	1
78	Great Orme	Lime	1990	1997	GO11	D	3	m	278,069	383,164	277,842	383,118	1.062	4.449	1	1
211	Great Orme	Lime	1997	2004	G	12.1	2	s	278,117	382,867	278,142	382,860	0.276	0.089	1	1
211	Great Orme	Lime	1997	2004	G	12.2	2	s	278,117	382,867	278,131	382,877	0.276	0.065	1	1
82	Llandulas	Lime	1983	1990	DV2	DV2-3	2	m	289,516	376,575	289,767	376,504	0.689	1.666	1	1
82	Llandulas	Lime	1983	1990	DV3	DV2-3	2	m	289,910	376,493	289,767	376,504	1.394	1.666	1	1
82	Llandulas	Lime	1990	1997	DV2-3	D	2	s	289,767	376,504	289,518	376,570	1.666	0.33	1	1
82	Llandulas	Lime	1990	1997	DV2-3	E	2	s	289,767	376,504	289,948	376,476	1.666	0.248	1	1
91	Llandulas	Lime	1990	1997	DV11	Q	2	s	291,270	376,513	291,282	376,584	1.497	0.574	1	1
91	Llandulas	Lime	1990	1997	DV11	R	2	s	291,270	376,513	291,309	376,353	1.497	1.87	1	1
91	Llandulas	Lime	1997	2004	R	38.1	2	s	291,309	376,353	291,309	376,416	1.87	0.18	1	1
91	Llandulas	Lime	1997	2004	R	38.2	2	s	291,309	376,353	291,390	376,295	1.87	0.64	1	1
92	Llandulas	Lime	1997	2004	T	40	2	m	291,479	375,915	291,642	375,901	0.395	0.697	1	1
92	Llandulas	Lime	1997	2004	U	40	2	m	291,716	375,893	291,642	375,901	0.442	0.697	1	1
95	Llandulas	Lime	1997	2004	N	35.1	2	s	291,552	377,258	291,526	377,373	0.345	3.188	1	1
95	Llandulas	Lime	1997	2004	N	35.2	2	s	291,552	377,258	291,611	377,177	0.345	0.843	1	1
163	Llandulas	Lime	1990	1997	DV18	S	2	m	291,257	376,247	291,297	376,157	0.382	1.58	1	1
163	Llandulas	Lime	1990	1997	DV19	S	2	m	291,385	375,983	291,297	376,157	0.158	1.58	1	1
163	Llandulas	Lime	1997	2004	S	37	2	s	291,297	376,157	291,248	376,283	1.58	0.158	1	1
163	Llandulas	Lime	1997	2004	S	39	2	s	291,297	376,157	291,335	376,157	1.58	0.497	1	1
133	Penmon	Lime	1990	1997	Q2	C	2	s	263,584	380,617	263,494	380,628	0.759	0.224	0	0
133	Penmon	Lime	1990	1997	Q2	D	2	s	263,584	380,617	263,690	380,617	0.759	0.629	0	0
133	Penmon	Lime	1990	1997	Q5	F	2	m	263,495	380,820	263,591	380,875	0.13	1.049	0	0
133	Penmon	Lime	1990	1997	Q6	F	2	m	263,390	380,855	263,591	380,875	0.208	1.049	0	0
97	Prestatyn	Lime	1990	1997	GF1	A	2	m	305,987	380,226	305,887	380,324	1.214	0.713	1	1
97	Prestatyn	Lime	1990	1997	GF2	A	2	m	305,881	380,326	305,887	380,324	0.638	0.713	1	1
167	Prestatyn	Lime	1990	1997	2	M	3	m	306,133	378,624	306,217	378,368	2.316	7.042	0	0
167	Prestatyn	Lime	1990	1997	1	M	3	m	306,265	378,167	306,217	378,368	3.861	7.042	0	0

Appendix table 21, continued

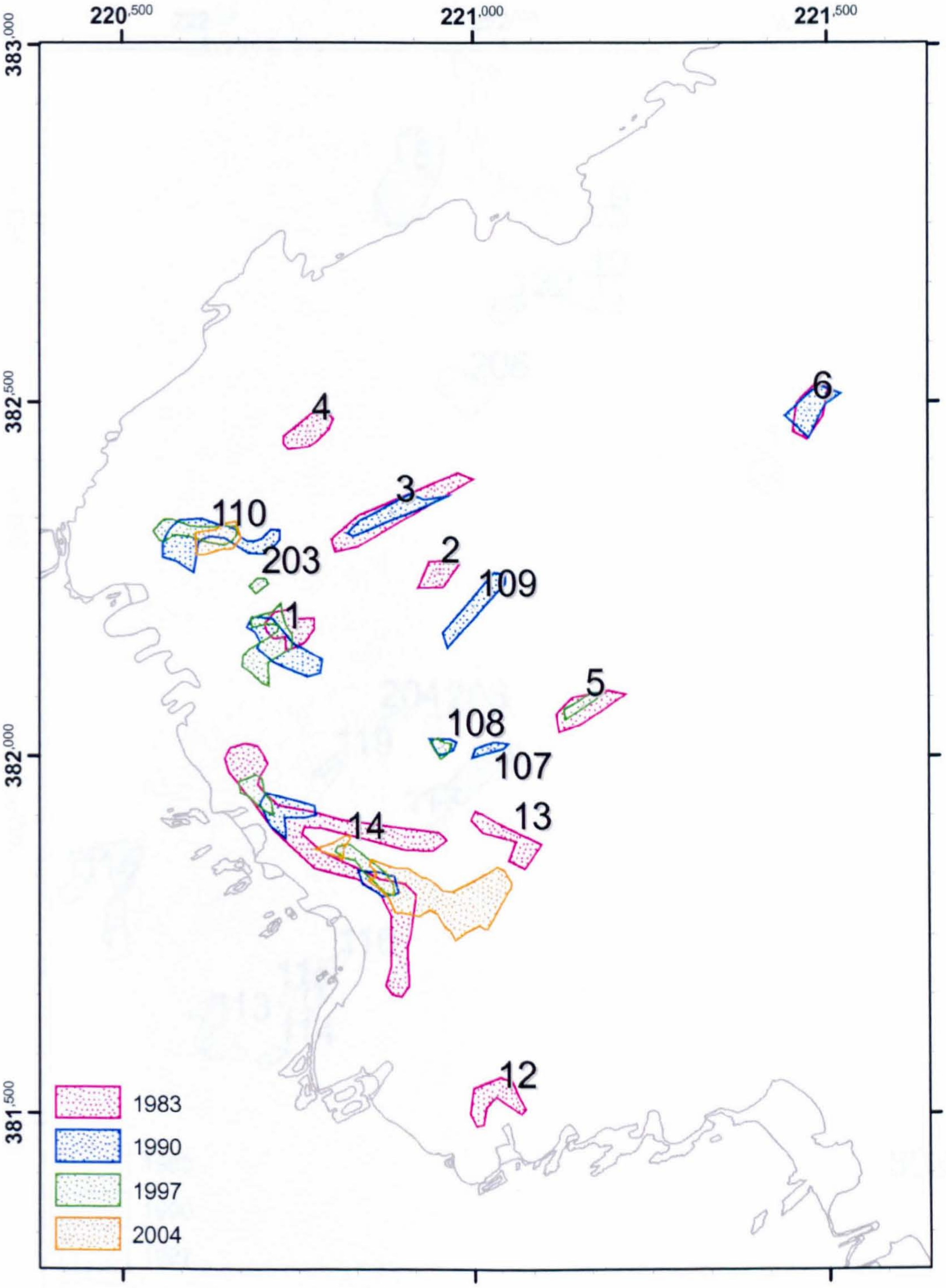
Id	Locality	Biotope	Year 0	Year 7	Code Yr0	Code Yr7	No. sub patches	Split or merge	X co-ord Yr0	Y co-ord Yr0	X co-ord Yr7	Y co-ord Yr7	Area Yr0	Area Yr7	Occupancy Yr0	Occupancy Yr7
167	Prestatyn	Lime	1990	1997	11	M	3	m	306,576	378,147	306,217	378,368	0.808	7.042	0	0
173	Prestatyn	Lime	1990	1997	7	F	2	m	306,726	380,966	306,721	381,016	0.427	0.508	0	0
173	Prestatyn	Lime	1990	1997	8	F	2	m	306,733	381,038	306,721	381,016	0.33	0.508	0	0
58	Hafod Garregog	Moss	1983	1990	C1-1	C1	3	m	260,079	344,687	260,099	344,643	1.191	3.269	1	1
58	Hafod Garregog	Moss	1983	1990	C1-2	C1	3	m	260,187	344,668	260,099	344,643	2.329	3.269	1	1
58	Hafod Garregog	Moss	1983	1990	C1-3	C1	3	m	260,050	344,568	260,099	344,643	0.971	3.269	1	1



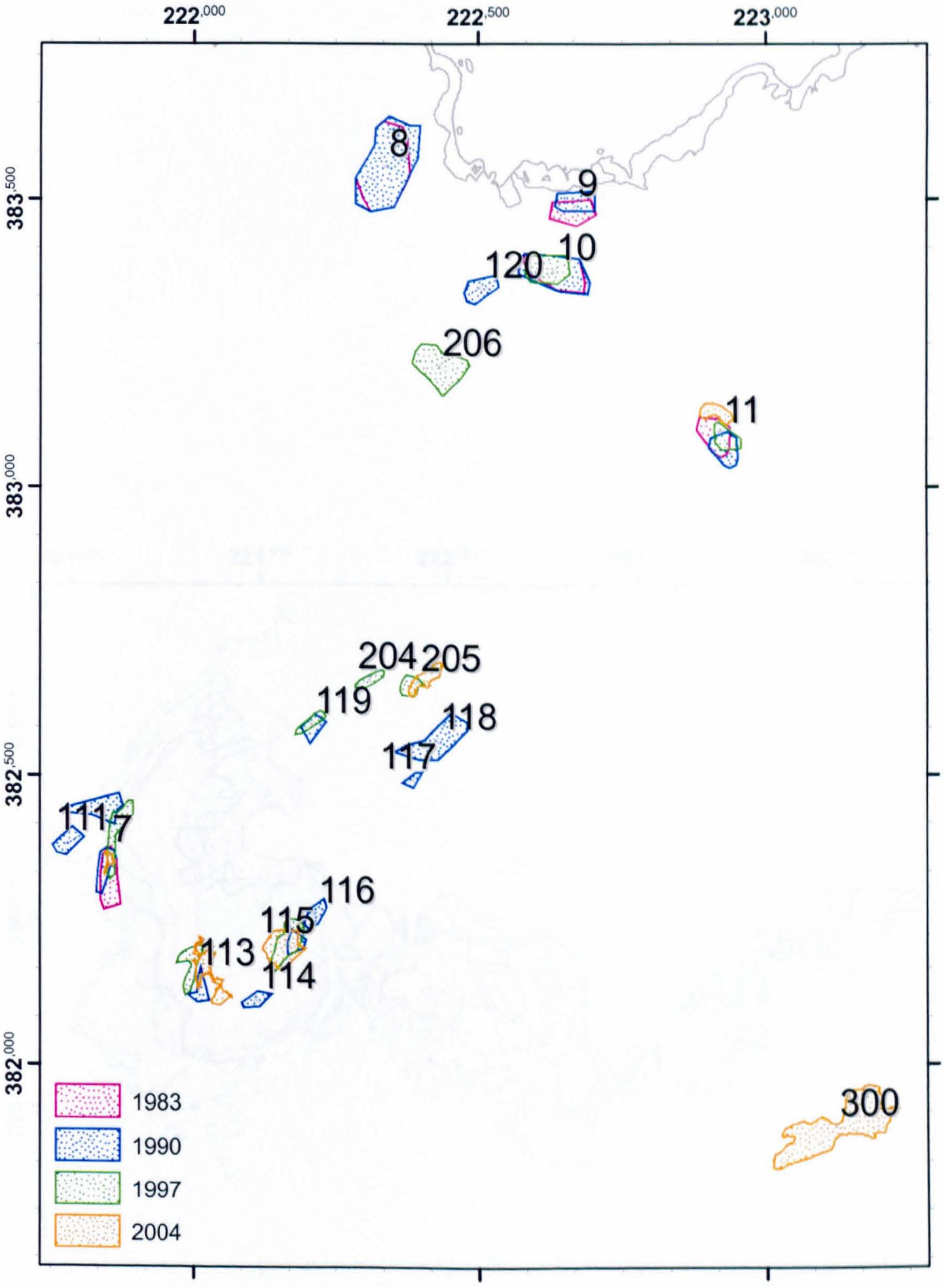
Appendix figure 30: Overview map of North Wales *P. argus* populations – western half. The labels refer to the localities given in tables 20-21. More detailed maps of the patches used in the analyses in chapter 5 are given in figures 32-36.



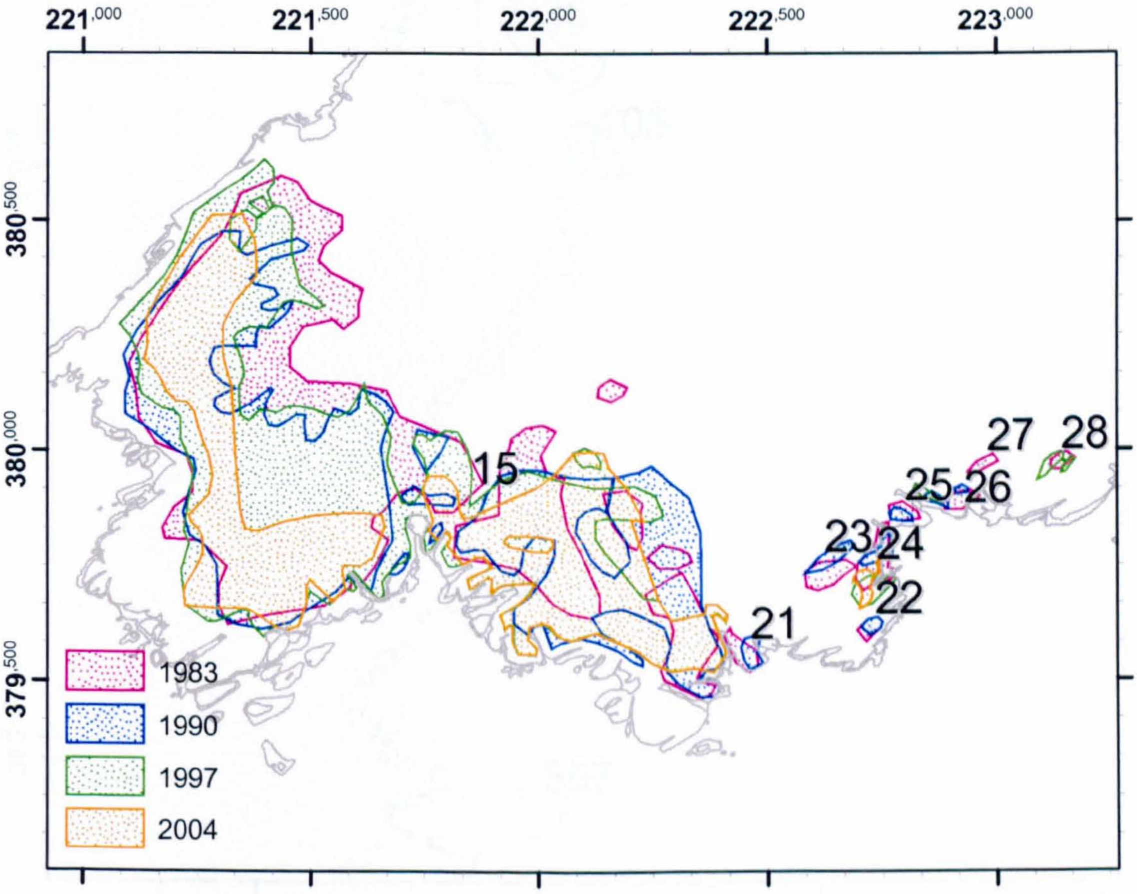
Appendix figure 31: Overview map of North Wales *P. argus* populations – eastern half. The labels refer to the localities given in tables 20-21. More detailed maps of the patches used in the analyses in chapter 5 are given in figures 37-40.



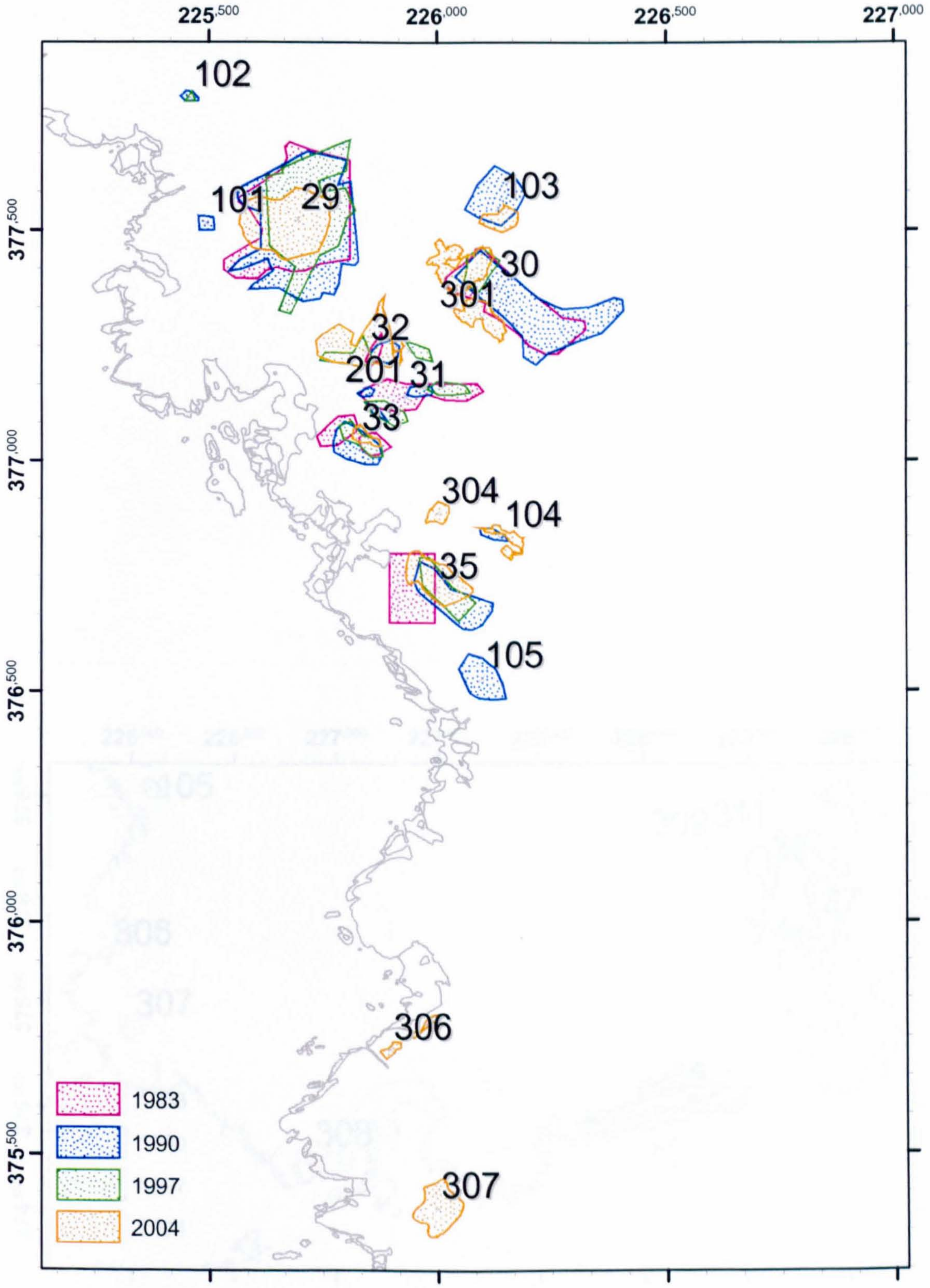
Appendix figure 32: South Stack Cliffs (West). Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



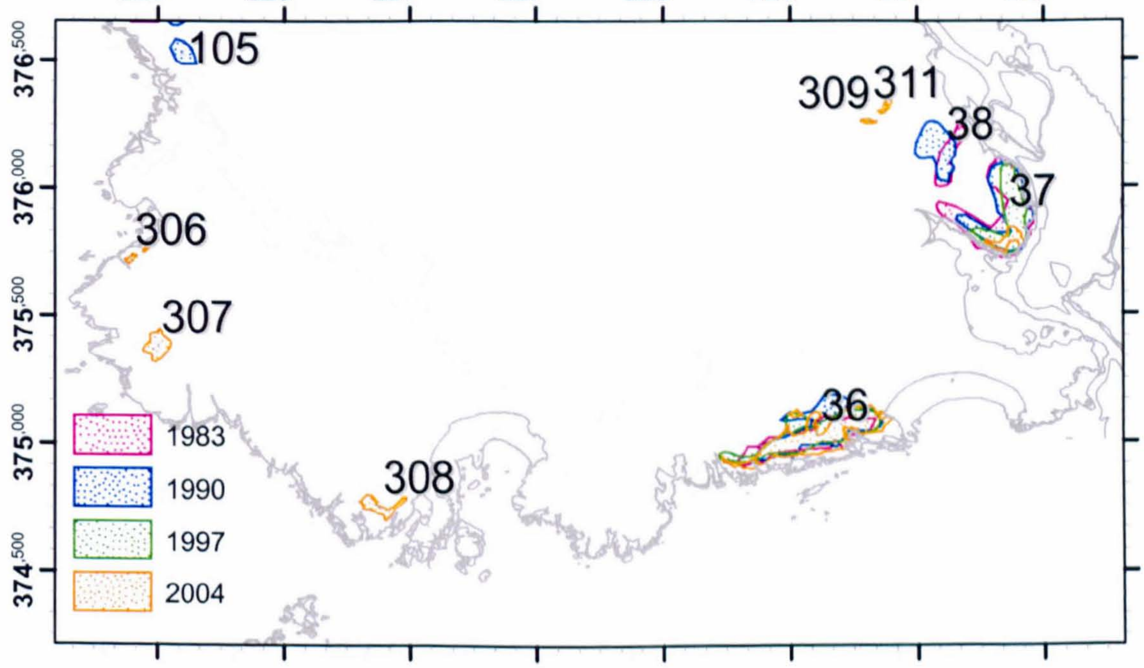
Appendix figure 33: South Stack Cliffs (East). Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



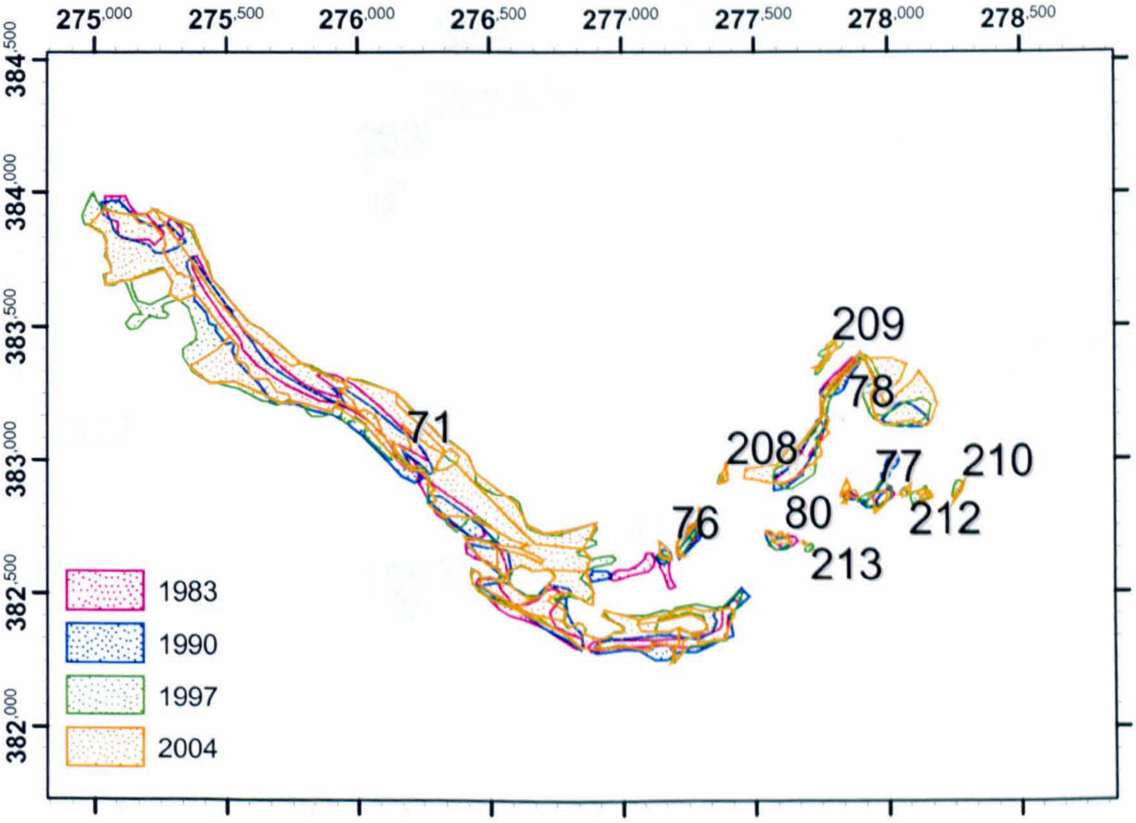
Appendix figure 34: Penrhosfeilw Common. Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



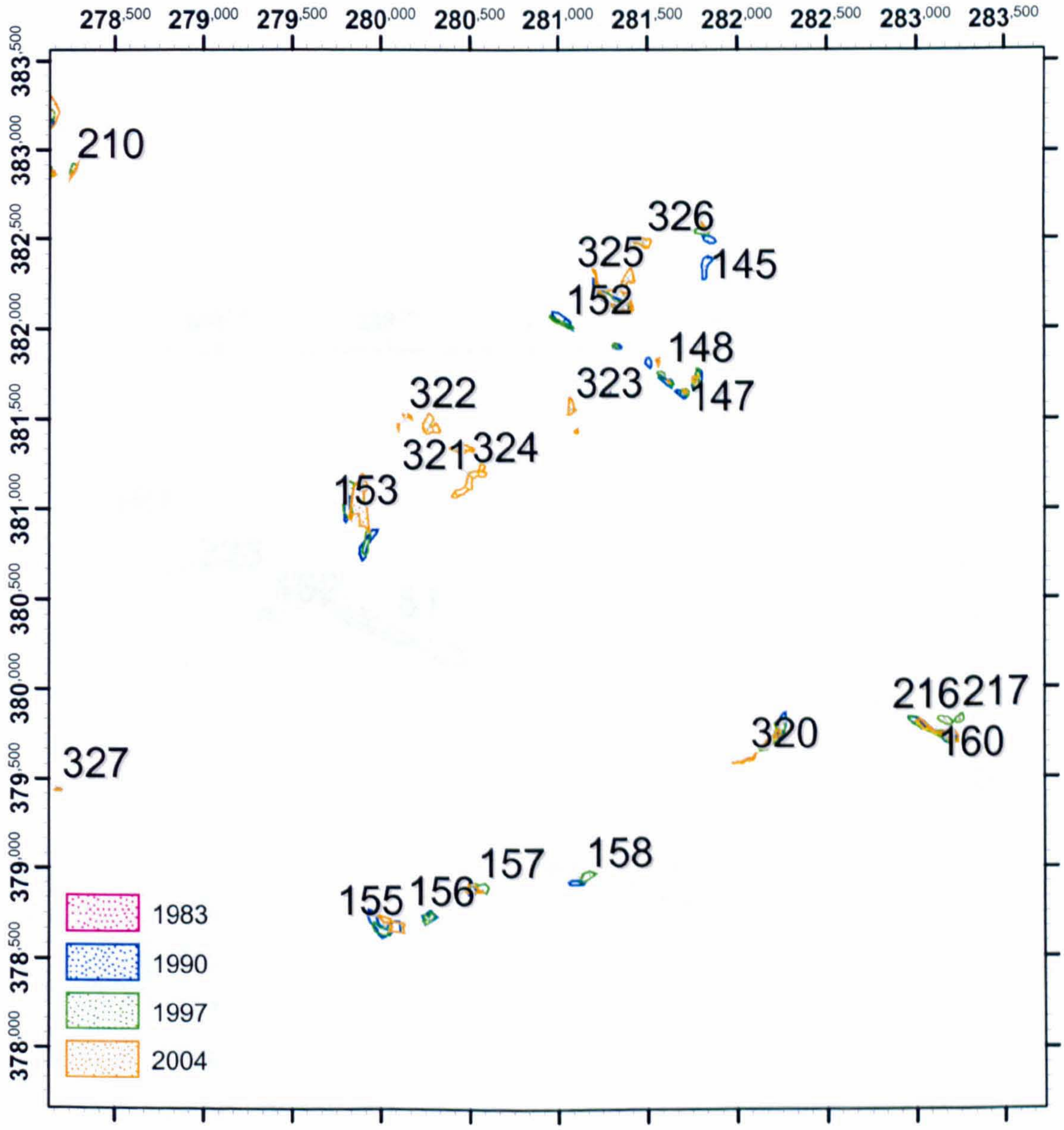
Appendix figure 35: Trearddur. Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



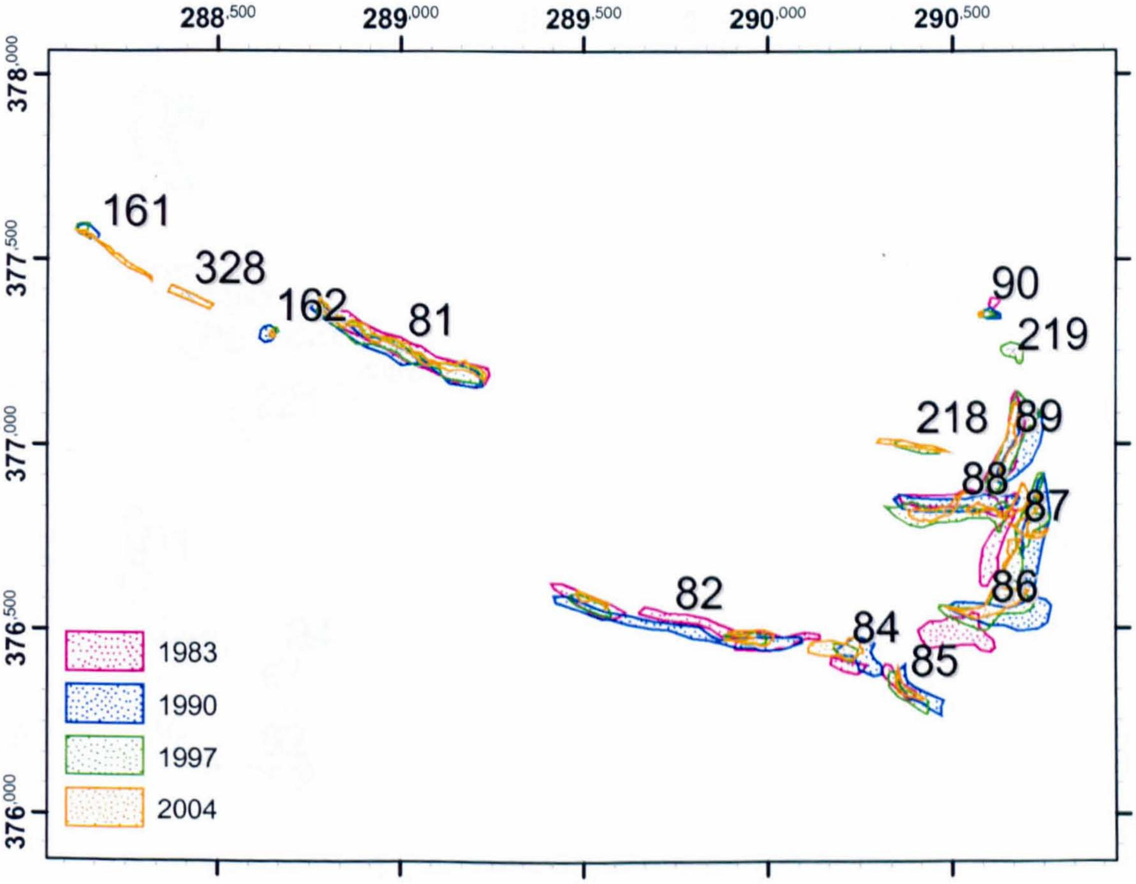
Appendix figure 36: Silver Bay. Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



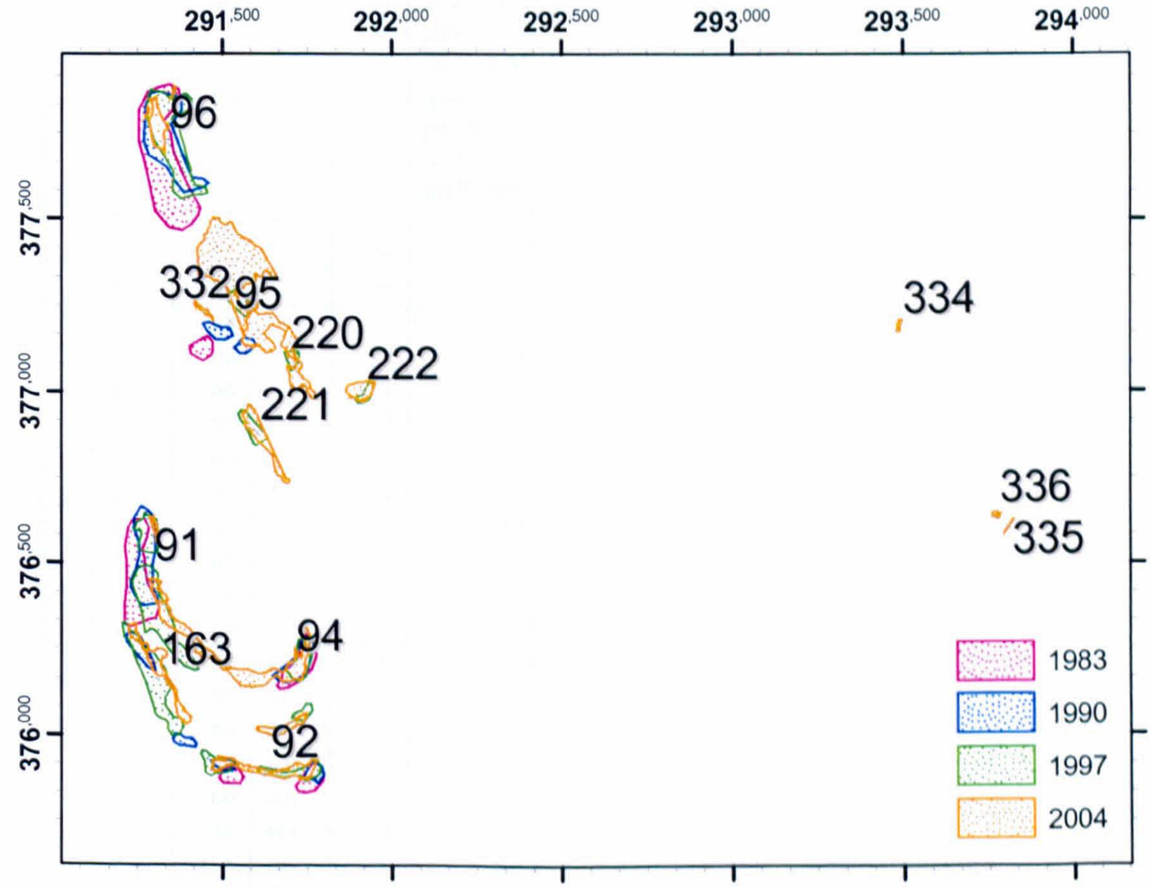
Appendix figure 37: Great Orme. Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



Appendix figure 38: Creuddyn Peninsula. Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



Appendix figure 39: Llandulas (West). Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.



Appendix figure 40: Llandulas (East). Patches as mapped by the surveyors; numbers refer to the Id numbers given in tables 20-21.

Appendix 2: Supplementary data on simulations carried out for chapter 5

Appendix table 22: Summary of simulation scenarios that were tried, but where connectivity-occupancy slopes were too high to match the observed slope.

	Succession	Number of patches	cut/fit	Disturbance type	Quality	*S* slope 2.5 percentile	*S* slope median	*S* slope 97.5 percentile	Median number of patches occupied	Does number of occupied patches fit the data?
basic scenarios with increasing quality	7	66	~	~	quality by patch (NAs 0.33)	0.60	1.22	1.97	16.7	7
	7	66	~	~	quality by patch (NAs predicted)	0.65	1.25	2.01	17.7	7
	7	66	~	~	0.33	0.58	1.21	1.93	15.3	7
	7	66	~	~	0.45	0.79	1.42	2.10	19.7	7
	7	66	~	~	1	1.31	2.03	2.81	44.3	3
	7	66	~	~	1.4	1.25	2.01	2.84	44.0	3
adding succession to 66 patch scenarios	7	66	~	~	0.33	0.58	1.21	1.93	15.3	7
	3	66	~	1	0.33	0.54	0.96	1.51	11.0	7
	3	66	~	2	0.33	0.52	0.86	1.25	9.7	7
	7	66	~	~	0.45	0.79	1.42	2.10	19.7	7
	3	66	~	1	0.45	0.59	1.07	1.65	13.7	7
	3	66	~	2	0.45	0.59	0.95	1.40	12.0	7
	7	66	~	~	1	1.31	2.03	2.81	44.3	3
	3	66	~	1	1	0.82	1.41	1.94	26.7	3
	3	66	~	2	1	0.71	1.18	1.59	22.3	7
adding extra patches, with or without succession	7	86	fit	0	0.33	0.54	1.06	1.69	23.0	7
	3	86	fit	1	0.33	0.41	0.70	1.12	17.7	7
	3	86	fit	2	0.33	0.39	0.62	0.93	15.0	7
	7	86	cut	0	0.33	0.55	1.06	1.68	21.3	7
	3	86	cut	1	0.33	0.46	0.78	1.36	16.3	7
	3	86	cut	2	0.33	0.38	0.62	1.02	14.3	7
	7	106	fit	0	0.33	0.49	0.92	1.42	31.7	3
	3	106	fit	1	0.33	0.37	0.63	1.02	24.7	7
	3	106	fit	2	0.33	0.32	0.51	0.79	22.0	7
	7	106	cut	0	0.33	0.53	0.98	1.55	30.0	3
	3	106	cut	1	0.33	0.42	0.66	1.08	22.7	7
	3	106	cut	2	0.33	0.33	0.55	0.86	20.0	7
	7	126	fit	0	0.33	0.48	0.84	1.22	42.0	3
	3	126	fit	1	0.33	0.36	0.57	0.82	32.3	3
	3	126	fit	2	0.33	0.32	0.47	0.67	28.3	3
	7	126	cut	0	0.33	0.51	0.94	1.36	38.0	3
	3	126	cut	1	0.33	0.37	0.63	0.95	30.0	3
	3	126	cut	2	0.33	0.32	0.51	0.73	26.0	7

Succession	Number of patches	cut/fit	Disturbance type	Quality	*S* slope 2.5 percentile	*S* slope median	*S* slope 97.5 percentile	Median number of patches occupied	Does number of occupied patches fit the data?
7	146	fit	0	0.33	0.39	0.82	1.15	53.0	7
3	146	fit	1	0.33	0.33	0.53	0.75	41.0	3
3	146	fit	2	0.33	0.28	0.45	0.65	37.0	3
7	146	cut	0	0.33	0.47	0.89	1.24	47.7	7
3	146	cut	1	0.33	0.36	0.58	0.88	38.3	3
3	146	cut	2	0.33	0.29	0.47	0.71	34.0	3
7	86	fit	0	0.45	0.65	1.16	1.91	29.0	3
3	86	fit	1	0.45	0.45	0.77	1.26	21.3	7
3	86	fit	2	0.45	0.38	0.64	1.00	17.7	7
7	86	cut	0	0.45	0.63	1.22	1.82	27.3	3
3	86	cut	1	0.45	0.51	0.88	1.46	20.3	7
3	86	cut	2	0.45	0.43	0.68	1.10	17.3	7
7	106	fit	0	0.45	0.52	0.98	1.48	39.7	3
3	106	fit	1	0.45	0.37	0.67	1.07	30.7	3
3	106	fit	2	0.45	0.32	0.53	0.83	26.3	7
7	106	cut	0	0.45	0.62	1.10	1.69	37.7	3
3	106	cut	1	0.45	0.44	0.74	1.20	28.3	3
3	106	cut	2	0.45	0.36	0.59	0.92	24.7	7
7	126	fit	0	0.45	0.47	0.87	1.29	52.0	7
3	126	fit	1	0.45	0.38	0.60	0.95	40.7	3
3	126	fit	2	0.45	0.30	0.49	0.74	35.3	3
7	126	cut	0	0.45	0.58	1.02	1.49	49.0	7
3	126	cut	1	0.45	0.39	0.66	1.02	37.3	3
3	126	cut	2	0.45	0.34	0.54	0.80	32.3	3
7	146	fit	0	0.45	0.47	0.81	1.13	65.7	7
3	146	fit	1	0.45	0.35	0.56	0.82	51.7	7
3	146	fit	2	0.45	0.29	0.45	0.66	45.0	3
7	146	cut	0	0.45	0.54	0.94	1.30	60.7	7
3	146	cut	1	0.45	0.40	0.64	0.96	48.5	7
3	146	cut	2	0.45	0.31	0.50	0.77	41.7	3

Appendix table 23: Summary of scenarios with succession and with increasing gap period between disturbance events.

number of patches	effective number of patches	gap period, years	cut/fit	disturbance type	quality	*S* slope 2.5 percentile	*S* slope median	*S* slope 97.5 percentile	median number of patches occupied	does number of occupied patches fit the data?	does the connectivity-occupancy slope fit the data?
86	74	3	cut	1	0.45	0.51	0.88	1.46	20.3	7	7
111	74	9	cut	1	0.45	0.26	0.46	0.71	21.0	7	3
106	91	3	cut	1	0.45	0.44	0.74	1.20	28.3	3	7
121	91	6	cut	1	0.45	0.31	0.51	0.85	29.0	3	7
136	91	9	cut	1	0.45	0.21	0.41	0.66	29.7	3	3
126	108	3	cut	1	0.45	0.39	0.66	1.02	37.3	3	7
144	108	6	cut	1	0.45	0.30	0.49	0.76	39.3	3	7
162	108	9	cut	1	0.45	0.17	0.38	0.60	39.3	3	3
146	125	3	cut	1	0.45	0.40	0.64	0.96	48.5	7	7

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