

IMPACTS OF ENVIRONMENTAL CHANGE ON ECOLOGICAL COMMUNITIES

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Impacts of environmental change on ecological communities

Sally A. Keith

ABSTRACT

The impacts of environmental change on ecological communities are poorly understood relative to impacts on species. Impacts on inter-community (beta-) diversity are particularly neglected. As a result, our ability to forecast the impacts of environmental change on communities, and on individual species constrained by those communities, is seriously limited. However, as conservation efforts increasingly emphasise broad-scale approaches in terms of multi-species coverage and spatial scale, it is imperative that understanding of biodiversity change at these scales is enhanced so that conservation can be based on appropriate scientific evidence. Within this thesis I aimed to conduct multi-species analyses over multi-decadal temporal scales at the spatial meso-scale to improve our understanding of such issues in both terrestrial and marine ecosystems. I discussed my findings in the theoretical context of Gleasonian and Clementsian views of species distributions (i.e. limitations to individualistic species responses) and their impact at the community scale. The temporal extent provided the opportunity to empirically test emerging concepts, including non-analogous communities, biotic homogenization, metacommunities and climate tracking responses at an appropriate meso-scale. Although no evidence for non-analogous communities was found, biotic homogenization was supported and appeared to be caused by increased nitrogen and decreased light availability. An intertidal assemblage also converged but appeared to be driven by a reduced sea surface temperature gradient. Woodland plant metacommunity structure was demonstrated to be Clementsian for woodland plants despite experiencing biodiversity loss. Hydrodynamic features were demonstrated to act as meso-scale dispersal barriers that limited intertidal invertebrates in tracking of climate (sea surface temperature) over the last 20 years. These barriers appear to alter when modelled under a scenario of sea level rise. Overall, results suggest that species are responding individually but that these responses are bounded by extrinsic constraints.

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AUTHOR'S DECLARATION

I confirm that this thesis is my own work with the following exceptions of the manuscripts below. As senior author on all the papers below, I led all aspects, including idea development, data collection, analysis and interpretation. I also led the preparation of these manuscripts. The only exception was data collection for Chapter 4, which was undertaken by the MarClim project. The use of other material has been properly and fully acknowledged throughout this thesis.

N.B. Bullock replaced Bealey as a supervisor for this thesis in 2009 owing to employment changes amongst my supervisory team.

Chapter 2 is published in collaboration with my supervisors as: Keith, S.A., Newton, A.C., Herbert, R.J.H., Morecroft, M.D., & Bealey, C.E. (2009) Non-Analogous Community Formation in Response to Climate Change. *Journal for Nature Conservation* 17:228-235

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Chapter 6, Part I is submitted in collaboration with two of my supervisors, Norton of ABPmer and Hawkins of Bangor University as: Keith S.A., Herbert, R.J.H., Norton, P., Hawkins, S.J. & Newton A.C. (submitted) Meso-scale dispersal barriers generate individualistic limitations of climate-induced range expansions. *Diversity and Distributions*

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Chapter 1

Introduction

1.1. ENVIRONMENTAL CHANGE AND BIODIVERSITY

The complex and rapid environmental change that characterises the modern era represents a major challenge to ecological understanding and biodiversity conservation. Sala et al. (2000) determined the five biggest threats to terrestrial biodiversity according to scenarios of biodiversity change for 2100. These threats were listed as changes in land use, climate, nitrogen deposition, biotic exchange and atmospheric CO₂ (Sala et al. 2000), and are largely echoed in the marine environment, with the notable addition of over-exploitation (Myers & Worm 2003; Worm et al. 2006). The impact of recent climate change on biodiversity is well documented (McCarty 2001; Parmesan & Yohe 2003; Root et al. 2003; Rosenzweig et al. 2007; Sala & Knowlton 2006; Walther et al. 2002) and non-climatic change, such as habitat loss and modification, are also significant drivers affecting biodiversity (Pimm 2008). These drivers act additively and synergistically to exacerbate biodiversity loss (Travis 2003). For a broad overview of the evidence for environmental change and its impacts on biodiversity see Appendix I.

The Gleasonian view of species distribution suggests species are organised individualistically along environmental gradients owing to species specific variation in physiological tolerance and life history traits (Gleason 1926). This view implies that species are expected to respond to changes in those environmental gradients individualistically – an idea that is supported by palaeoecological evidence from past 'climate flickers' (Roy et al 1996). These responses are commonly manifested through changes in a species' geographical range extent as suitable environmental conditions are tracked (Walther et al 2005). In turn, this will contribute to altered biodiversity at higher organisational scales as community compositions and regional species pools are re-organised (Gilman et al. 2010; Walther 2010).

However, there are two substantial problems with this assumption: 1) the current climate change episode differs from past 'climate flickers' because the additional impacts of habitat loss and degradation may prevent climate tracking, and, 2) inter-specific interactions are assumed to have no effect on species distribution. Consideration must be afforded to such limitations on species responses if we are to better understand and forecast impacts of environmental change on multiple scales of biodiversity. Although the second issue is well debated in community ecology and alternative hypotheses exist (e.g. Clements 1916), it is only recently that this has begun to be considered in the context of forecasted responses to environmental change (Gilman et al. 2010; Walther 2010). One way to achieve such consideration is to conduct analyses that encompass multiple species in an attempt to implicitly encapsulate these limitations.

However, the vast majority of analyses regarding impacts of environmental change on biodiversity have focused on single species and evidence for impacts on higher levels of organization is scarce by comparison (Gilman et al. 2010; Walther 2010). Extrapolation of impacts from lower levels of organisation is not advisable because of the potential for emergent properties (Gaston & Blackburn 1999; Woodward et al. 2010). As conservation efforts increasingly emphasise broad-scale approaches in terms of multi-species coverage and spatial scale (Guichard et al. 2004; Hannah et al. 2002; Opdam et al. 1995; Opdam & Wascher 2004; Whittaker et al. 2005), it is imperative that understanding of biodiversity change at these levels is enhanced so that conservation can be based on appropriate scientific evidence (Sutherland et al. 2004).

In this introductory chapter I will briefly clarify essential definitions and the spatial scale on which this thesis will focus. I subsequently review observed and expected impacts of environmental change on ecological communities, considering first the effect of individualistic species responses and, second the constraints imposed by inter-specific interactions. This is followed by an overview of impacts on multiple communities, with concentration on beta-diversity and the metacommunity concept. I

subsequently present an explanation for the use of terrestrial and marine data within this thesis. Finally, I outline my aims and objectives, and detail the structure of this thesis.

1.1.1. Definition of biodiversity, community and scale

Biodiversity has many different definitions (Botkin et al. 2007; Peters 1991). The definition of biodiversity I adhere to throughout this thesis is provided by the United Nations Environment Programme (UNEP) Global Biodiversity Assessment: “‘Biological Diversity’ means the variability among living organisms from all sources, including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.” (Heywood et al. 1995).

Throughout this thesis, a biological community shall be defined as: “The individuals of all species that *potentially* interact within a single patch or local area of habitat” (Holyoak et al. 2005). Communities are therefore a collection of interdependencies determined by complex intra- and inter-specific interactions. To assume the implicit capture of these interactions it is necessary for data to encompass an entire community. When the community is only represented sparsely, one cannot assume interactions are implicitly captured and instead can only assume that this is a collection of species that share geographic space. This latter case is distinguished by the term ‘assemblage’. Within this thesis I refer to both communities and assemblages to reflect this difference. Explicit consideration of species interactions is outside the scope of this thesis.

The scale at which biodiversity is analysed is an essential consideration (Schneider 2001). To assess impacts on multiple ecological communities it is appropriate to employ the spatial scale of landscapes (Urban et al. 1987) and seascapes (Ray 1991). These scales encompass spatially and temporally variable habitat mosaics. The inherent variability of these scales necessitates consideration of pattern and process across time and space. Therefore, pattern and process in landscapes and seascapes are

appropriately explored through hierarchical analyses of multiple abiotic or biotic (e.g. community, metacommunity, ecosystem) organizational levels and temporal extents (Poiani et al. 2000; Sala & Knowlton 2006; Urban et al. 1987). For brevity throughout this thesis I collectively refer to the landscape and seascape scales as the meso-scale.

1.2. IMPACTS OF ENVIRONMENTAL CHANGE ON COMMUNITIES

Species are expected to respond individualistically to environmental change through shifts in distributional range (Bush 2002; Huntley 1991). At the community level, these range shifts will be observed as emigration or local extinction of an existing species, or immigration and colonisation of a new species (Benning et al. 2002; Gritti et al. 2006; Hansen et al. 2001; Killengreen et al. 2007; Olden et al. 2004; Stachowicz et al. 2002; Truong et al. 2007; Ward & Masters 2007). Such changes subsequently impact upon community composition, structure and partitioning (Table 1). As a result, biodiversity loss is leading to changes in the composition and structure of communities (Poiani et al. 2000; Sala & Knowlton 2006; Walther et al. 2002).

Community composition can be regarded as mediated by four processes: speciation, dispersal, selection, and drift (Vellend 2010). The processes of dispersal and speciation add species to the community, whereas selection and drift shape the relative abundance of those species (Vellend 2010). Although exceptions exist (Skelly et al. 2007), speciation and selection tend to occur over larger temporal scales than those examined within this thesis. Therefore, these processes will not be considered further here. Also important are processes of species loss from a community, which can occur through emigration and extinction.

Table 1. Examples of observed impacts of environmental change on communities

Ecosystem & Community Impact	Environmental correlate	Reference
Ocean		
Reef fish assemblage composition: ↑ southern-adapted species ↓ northern-adapted species	Increase in SST and nutrient upwelling	(Holbrook et al. 1997)
Arid vegetation		
↑ shrub cover ↓ in some previously abundant species ↑ in new species ↑ in some rare species Some species no change	↑ average winter rainfall	(Brown et al. 1997)
Hawaiian forest		
↑ risk of avian malaria contraction for Hawaiian honeycreepers (Drepanidae)	↑ air temperature = ↑ access for malaria vectors to higher altitudes	(Benning et al. 2002)
Old-growth tropical forests		
↑ biomass in old-growth tropical forests	↑ atmospheric CO ₂	(Phillips et al. 2002)
Marine invertebrates		
↑ recruitment of introduced species ↓ recruitment of native species	↑ water temperature	(Stachowicz et al. 2002)
Mature tropical forests		
↑ tree recruitment, growth, mortality	10 drivers	(Lewis et al. 2004)
Tropical forests (synthesis)		
↑ turnover rates, biomass, stem number, mortality and growth in the Amazon	↑ atmospheric CO ₂ , solar radiation and/or air temperature	(Malhi & Phillips 2004)
Ex-arable grassland		
↑ in summer precipitation led to ↑ total cover abundance the following summer	↑/↓ summer precipitation (experimental)	(Morecroft et al. 2004)
Northern Swedish forests		
Range of mountain birch (<i>Betula pubescens</i>) is expanding to higher altitudes, altering treeline and associated communities	↑ air temperature	(Truong et al. 2007)

Owing to the large body of research that suggests many species have or are expected to shift distributional range in response to environmental change (McCarty 2001; Parmesan et al. 1999; Root et al. 2003; Walther et al. 2005), dispersal, and local extinction are two sides of the same coin and are central to a thorough understanding of the effects of environmental change on communities.

Different forms of environmental change affect biodiversity through impacting upon different ecological processes. Habitat loss is well associated with the process of local extinction because species-area curves suggest that a reduction in habitat area will reduce the carrying capacity and thus species richness will inevitably decrease (Koh & Ghazoul 2010; MacArthur & Wilson 1967), creating a depauperate community. Such extinctions often involve a time lag, occurring as sub-lethal effects reduce the survival probability and fecundity of individuals within a population (Kuussaari et al. 2009). These lags, during which time the patch owes an extinction debt, have been identified in response to habitat loss after 70 years for calcareous grasslands (Helm et al. 2006) and 75 years for butterflies (Sang et al. 2010). Smaller areas of habitat at the meso-scale will normally result in larger gaps between habitat patches and therefore can be associated with reduced connectivity. This reduced connectivity is also a symptom of habitat fragmentation that can impact biodiversity through a compromised process of dispersal (Bennett 2003).

Dispersal and associated immigration are frequently documented processes in the context of climate-induced range shifts (e.g. Mieszkowska et al. 2006) and result in biodiversity change at higher organizational levels. Differential species dispersal traits (Chapter 6) can lead to the development of non-analogous communities or biotic homogenization as some species continue to be capable of dispersal, whilst others are inhibited. In temperate regions of the northern hemisphere, warm-adapted southern species are shifting their ranges northwards towards higher latitudes (Hawkins et al. 2009). Far less evidence has been accumulated for retreat from low latitude range boundaries, although this has been clearly demonstrated for three

species of British butterfly (Franco et al. 2006). In some cases, contraction of species from the low latitude edge of their boundaries may be masked by a compensating upwards shift in elevation to maintain environmental temperature (Wilson et al. 2005).

A recent horizon scanning exercise of future threats and opportunities for biodiversity identified the need to “...facilitate species range change in the face of climate change” and listed “understanding range shifts” as a research requirement to enable the issue to be addressed (Sutherland et al. 2008). Range shifts can only be facilitated if we understand the constraints imposed on species dispersal and how an area can remain uncolonised despite suitable climatic conditions, due to inaccessibility of that area to propagules (Crisp & Southward 1953). This idea is captured within the dispersal barrier hypothesis for maintenance of range boundaries, which suggests that propagules are physically prevented from crossing the boundary (Gaines et al. 2009). An alternative mortality hypothesis suggests boundaries are maintained because although individuals of a species can disperse beyond the boundary, those individuals are not adapted to the conditions and cannot survive (Gaines et al. 2009).

Hodgson et al. (2009) urge caution of over-reliance upon connectivity to deliver effective conservation. Uncertainty surrounding estimation of connectivity and its effects suggest that increased habitat area would be a less risky conservation action that is easy to quantify and demonstrates clear effects, however, connectivity remains a potentially useful tool (Hodgson et al. 2009).

1.2.1. Community constraints on species responses

The community can also constrain species responses as competition, pollination, predator-prey interactions, parasitism and mutualism create complex interdependencies (Montoya et al. 2006). One would therefore expect a diminished capability for some species to respond individualistically to climate change. For example, a species could be an obligate mutualist (Anstett et al. 1997), constrained by a competitor

(Morecroft & Paterson 2006; Southward & Crisp 1956) or constrained by requirements for habitat structure (Hansen et al. 2001). In such situations, a change in inter-specific interactions can cascade to produce a wider change in community composition, processes and functioning (Brooker et al. 2008; Gilman et al. 2010; Walther 2010).

The loss of a species from a community can induce a trophic cascade, causing disruption of entire food webs. This effect has been documented in marine systems as over-exploitation has resulted in the ecological extinction of a trophic level, whereby the species is at such a low abundance it no longer has meaningful interaction within the ecosystem (Casini et al. 2008; Daskalov 2002; Frank et al. 2005; Jackson 2008; Myers & Worm 2003; Worm et al. 2006). Striking inverse abundance trends of predatory and planktivorous fishes in the Black Sea demonstrate well the effect of predator removal and subsequent trophic cascades on community structure (Daskalov 2002). Trophic interactions are also impacted by environmental change through altered phenology that is variable across trophic levels and can result in trophic mismatch (Both et al. 2006; Post & Forchhammer 2008; Walther 2010). Thompson et al. (2002) suggested that climatic warming impacts the biodiversity of intertidal communities by altering competitive relationships at species' range boundaries. Similarly, facultative interactions can be affected by changes in environmental conditions (Brooker et al. 2008). Facilitation is also a potential factor in species invasions, which can be facilitated by other exotic or native species (Brooker et al. 2008). Temperature is also expected to have a more subtle effect through altering metabolic rate and subsequent activity levels, thus affecting encounter rates of species (Woodward et al. 2010).

Therefore, evidence suggests that although species respond individually to environmental change, they do so within the bounds imposed by community interactions. For example, generalist species with many weak inter-specific connections are less likely to be constrained by the community due to a high redundancy of interaction. One would therefore expect the strength of individualistic response to vary amongst species

within the ecological community, producing more complex responses to environmental change than those projected by models that consider species in isolation from the community e.g. bioclimatic envelope models (see Appendix III). As a consequence of such responses to environmental change it is expected that recent climate change will trigger the formation of non-analogous communities (Stewart 2009; Williams & Jackson 2007). The concept is based on palaeoecological ideas and describes novel assemblages that form as a consequence of individualistic species responses to environmental change (Chapter 2). However, the concept has only recently begun to filter through to modern ecology and its application is uncertain.

1.2.2. Diversity of multiple communities

Inter-community diversity is often referred to as beta-diversity, a scale in between that of alpha-diversity (intra-community diversity e.g. species richness) and gamma-diversity (regional species richness). However, the definition and measurement of beta-diversity is debateable (Jurasinski et al. 2009; Tuomisto 2010a; Tuomisto 2010b; Whittaker et al. 2001). Recent reviews suggest that ‘true beta-diversity’ should measure the richness of compositional units to ensure it is in line with alpha- and gamma-diversity (Tuomisto 2010a; Tuomisto 2010b). However, the term is more commonly used to refer to the pairwise similarity amongst communities within a given area (Jurasinski et al. 2009), also called effective species turnover (Tuomisto 2010b). Owing to this commonality of use, I follow the latter definition throughout this thesis and apply it to communities or assemblages at the meso-scale (Jurasinski et al. 2009).

The impacts of environmental change on beta-diversity are particularly neglected. The reason for the comparative lack of analyses on the impacts of environmental change at this scale is most likely because these impacts remain relatively hidden without the attainment of data at the appropriate scale, as alpha-diversity may not be altered (Hillebrand et al. 2010). However, in recent years analyses at this scale have increased in frequency (e.g. Beck & Khen 2007; Devictor et al. 2008; Hobbs et al. 2006;

Olden & Poff 2004). Intra-community responses can collectively alter beta-diversity. One of the simplest impacts of environmental change on beta-diversity is biotic homogenization and convergence (Chapters 3 & 4; McKinney & Lockwood 1999; Olden et al. 2004). This is a pattern of increased similarity between assemblages or communities over time and therefore is not detectable with single site analyses. Increased similarity is caused by the differing responses of ‘winner’ (positively impacted) and ‘loser’ (negatively impacted) species following environmental change or the introduction of exotic species (McKinney & Lockwood 1999).

1.2.3. Metacommunities

A useful framework within which to explore inter-community diversity is the metacommunity concept, within which a metacommunity is “..a set of local communities that are linked by dispersal of multiple potentially interacting species.” (Leibold et al. 2004). The concept of the metacommunity incorporates spatial dynamics within community ecology and describes a level of ecological organisation. It builds upon the idea of metapopulations whereby local populations of a single species are linked through the potential for dispersal between patches (Levins 1969). The spatial aspect acts at a regional scale and can be implicit (e.g. assuming global dispersal) or explicit (e.g. parameterisation of specific distances of dispersal) (Holyoak et al. 2005; Leibold et al. 2004).

In a metacommunity, local and regional processes act jointly to explain dynamics that control community assembly and structure. This metacommunity concept has been successfully used as a framework for empirical analyses on, *inter alia*, plant-butterfly-parasitoid assemblages (Van Nouhuys & Hanski 2005); pitcher plant inquiline communities (Miller & Kneitel 2005); and bryophyte-based communities (Gonzalez 2005). Such studies suggest that spatial scales beyond the local may be best viewed as a hierarchical nested structure of different scales and are appropriate to the operation of different species (Kolasa & Romanuk 2005; Miller & Kneitel 2005; Van Nouhuys & Hanski 2005). This notion demonstrates the

importance of exploring impacts of environmental change at organizational levels above that of the species and supports the focus on communities within this thesis.

In a literature search on ISI Web of Knowledge with “metacommunit*” in the title, “metacommunity” was often used to describe an organisational level (Burns & Neufeld 2009; Questad & Foster 2007), with no invocation of dynamics or structures that are central to the concept. The concept appears, therefore, to be generally accepted for describing scale, however, it requires further empirical testing of its central assumptions before its unquestioned use is fully appropriate. Although the concept can describe an organisational level, the explicit spatial scale of metacommunity studies is highly variable ranging from microcosm test tube communities (Cadotte et al. 2006), to an area of interconnected rock pools with a radius of just 30 m (Azeria & Kolasa 2008), to landscape and national scales (Brooks et al. 2008).

A central issue in the metacommunity concept is whether community level environmental factors or regional dispersal have the most influence on structure and dynamics. As a result of this, much work in the area focuses on only one of these aspects suggesting a false dichotomy (Boudell & Stromberg 2008). In fact, it is likely that metacommunities express a combination of local environmental and regional dispersal processes. For example, a microcosm approach suggested that dispersal maintains greater species richness on a local scale but has little effect on a regional scale; a more localised predation effect reduces species richness and an environmental resource amount is positively correlated with predation (Cadotte et al. 2006). Modelling has suggested that dispersal is a regional process capable of homogenizing a metacommunity because greater connectedness was associated with increased synchronicity of local communities (Koelle & Vandermeer 2005).

The dynamics of metacommunities are described under four paradigms or models, two of which are strongly influenced by local environmental heterogeneity within patches and two of which are strongly

influenced by more regional spatial parameters. The paradigms describe the dynamics that determine the composition and spatial distribution of communities. The paradigms are species sorting, patch dynamics, mass effects, and neutral (Table 2). The four paradigms are not mutually exclusive but rather vary in relative importance (Mouillot 2007). There are also six metacommunity structures proposed that are indicative of various species distributional patterns. These structures are discussed fully within Chapter 5 and as such will not be discussed further here.

The paradigms in the literature that most often conform to observed dynamics in natural systems are species sorting (Cottenie & De Meester 2005; Kolasa & Romanuk 2005) and mass effects, therefore suggesting that local environmental factors are more important than inter-specific interactions and random dispersal. Analyses of freshwater interconnected ponds specifically support the importance of local environmental factors (Cottenie & De Meester 2003; Debout et al. 2009). For example, local fish predation pressure and macrophyte cover are key to the structure of communities (Cottenie & De Meester 2004). For more vagile assemblages it is likely that dispersal contributes more to the explanation of dynamics. For example, mass effects was the most important paradigm within a bat assemblage and bats are highly mobile species (Stevens et al. 2007).

The patch dynamics paradigm (Leibold et al. 2004) builds on the ideas of Tilman (1982) who suggested a competition-colonisation trade-off as a mechanism for species co-existence. Species that compete with high success are slow to colonise uninhabited patches, whereas species that are relatively unsuccessful competitors colonise uninhabited patches much more quickly (Leibold et al. 2004). This means that even though poor competitor species cannot maintain a population in the presence of a superior competitor, the metapopulation of those species can be maintained by a high incidence of dispersal. This is supported by a modelling exercise that simulated the trade-off with the additional consideration of asymmetric dispersal (Salomon et al. 2010).

Table 2. The paradigms of metacommunity dynamics and implications for conservation (adapted from Leibold et al. 2004; Moullot 2007)

Characteristics (adapted from Leibold et al. 2004)	Conservation Requirements (adapted from Moullot 2007)
Neutral paradigm	
<ul style="list-style-type: none"> • Species are equivalent • Communities are dispersal-assembled • Compositional drift maintains heterogeneity of metacommunity • Built on foundation of the null hypothesis (Hubbell 2001) 	<ul style="list-style-type: none"> • Moderate connectivity of local communities should be maintained. • High connectivity may lead to biotic homogenisation.
Species sorting paradigm	
<ul style="list-style-type: none"> • Local community composition jointly affected by patch quality and dispersal • Spatial niche separation emphasised above spatial dynamics • Dispersal allows compositional changes to track changes in local environment 	<ul style="list-style-type: none"> • Maintenance of heterogeneity within patches. • Connectivity within patches vital, connectivity between local communities can be low to moderate.
Patch dynamics paradigm	
<ul style="list-style-type: none"> • Patches are equivalent • Each patch is capable of containing populations • Patches may be unoccupied or occupied • Local species diversity is limited by dispersal • Spatial dynamics are dominated by local extinction and colonisation • Competition-colonisation trade-off 	<ul style="list-style-type: none"> • Ensure moderate to high connectivity of local communities is maintained. • Maintain abiotic variability. • Permit high turnover of individuals.
Mass effects paradigm	
<ul style="list-style-type: none"> • Focus on the effects of immigration and emigration on local population dynamics • Species can be rescued from local competitive exclusion in communities where they are bad competitors, by immigration from communities where they are good competitors • Source-sink communities • Emphasises role of spatial dynamics 	<ul style="list-style-type: none"> • Maintain regional abundance of species, not just local abundance. • Ensure moderate connectivity of local communities is maintained. • Maintain heterogeneity of local communities to prevent biotic homogenization.

However, there is only limited empirical support for the patch dynamics paradigm (Driscoll 2008). Many other studies use the paradigm in order to set the context for an analysis of co-existence (Noda 2009). This limits the analysis to one aspect of metacommunity dynamics. However, as it can become highly complicated it is worthy of separate exploration that can later improve an integrated approach. The neutral paradigm is generally accepted as only applicable for use as a null hypothesis, however, a recent analysis of fish metacommunities in the US supported its use as a predictor of diversity (Muneepeerakul et al. 2008).

In addition to its effect on the capability of species to track climate, changes in dispersal between habitat patches can also impact metacommunity dynamics at the meso-scale. Metacommunity dispersal can be described in terms of internal and external dispersal whereby external dispersal is from a regional pool, and internal dispersal is between local communities (Fig. 1, Fukami 2005). Dispersal has been suggested as a process capable of reducing heterogeneity, and subsequently biodiversity, within a metacommunity. This would produce a pattern of biotic homogenization. Modelling analyses demonstrated that highly connected local communities create more synchronous local communities than those that are less connected (Koelle & Vandermeer 2005). However, the model was highly simplified, simulating only two habitat patches and therefore may not be representative of a multi-patch system. Fukami (2005) established through computer simulations of dispersal from the two sources that infrequent external dispersal led to a homogenization of the metacommunity. Alternatively, frequent external dispersal could also lead to a species rich metacommunity that was saturated and thus resistant to species invasions (Fukami 2005).

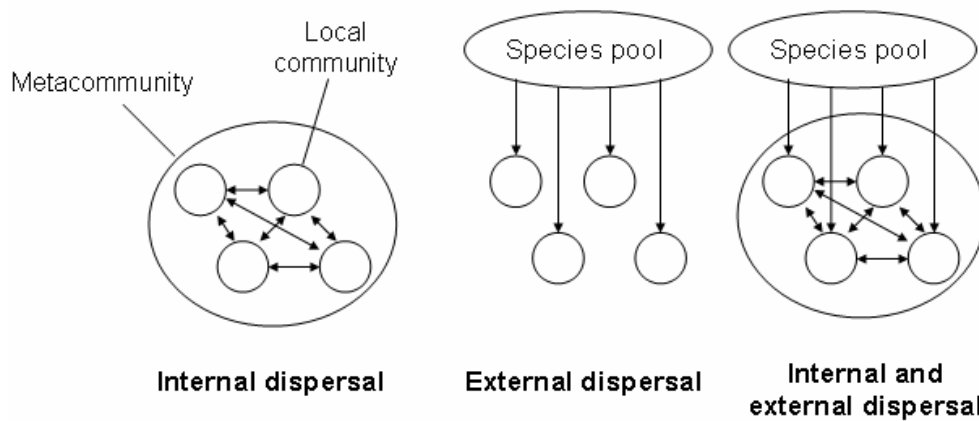


Fig.1. Internal and external dispersal of metacommunities (Fukami 2005)

Furthermore, metacommunities can demonstrate specific competitive and mutualistic relationships that affect local and regional processes. This can be in terms of extinction rate, establishment, and propagule production either being increased or decreased in co-occupied patches (Klausmeier 2001). These relationships can differ from local community relationships, for example, mutualists may be facultative at the local level whilst being obligate at the metacommunity level owing to the effects discussed above, specifically in terms of colonisation ability (Klausmeier 2001).

1.2.4. Long-term impacts

Data on multi-decadal time scales are extremely useful for exploration of the impacts of environmental change on communities because these time scales better encompass the temporal extent of community dynamics, and by definition are necessary for long-term studies (MacArthur & Wilson 1967; Urban et al. 1987; Willis et al. 2007). The time scale of community interactions can be constrained by the generation time of the longest-lived species within the community or the variability of the environmental factors acting upon it. Furthermore, time lags can occur between the point of disturbance and an observable impact, referred to as a relaxation time (Diamond 1972) or an extinction debt (Jackson & Sax 2010; Kuussaari et al.

2009). Failure to consider potential lags can lead to an underestimation of impacts.

Time scales over which the impacts of environmental change in modern ecology are analysed rarely exceed 20 years, in part because most ecological monitoring programs have started since the 1970s (Morecroft & Keith 2009). This has hindered accumulation of evidence for the impacts of environmental change on higher organizational levels as a paucity of suitable long-term data inhibit the potential for multi-decadal analyses (Pullin & Salafsky 2010), particularly when multi-species assemblage data are required. This is reflected in the evidence base for biotic homogenization. Although it has rapidly gained empirical support over recent years (Devictor et al. 2008; Olden & Poff 2004; Rooney et al. 2004), the majority of analyses infer homogenization over time using environmental gradients (Devictor et al. 2007) or comparisons of exotic and non-exotic species at a single point in time (Castro & Jaksic 2008; Qian & Ricklefs 2006). These methods are used over the comparison of the same collection of sites at two points in time (Rahel 2000; Rooney et al. 2004) because suitable historical data are often unavailable (Olden & Rooney 2006). Therefore, the evidence for this concept must be strengthened by direct comparison of communities at different points in time over relevant time scales. For further discussion of this point, see Chapter 3.

Towards the other extreme of scale, palaeoecological time scales can be highly informative (see Chapter 2). However, the resolution of such data are coarse owing to time-averaged compositions (Jackson & Williams 2004; Roy et al. 1996) and poor taxonomic resolution of fossils (Bennett 1997). This means composition of assemblages using such data does not match up with the hypothesis of individualistic species responses. Furthermore, whilst the breadth of paleoecological evidence provides robust evidence for the impacts of climate change on communities in the past and strong suggestions for the future, the effect of other anthropogenic influences may confound extrapolations from palaeoecological evidence. For example, habitat fragmentation and loss will restrict the ability of species to respond

individualistically through the process of dispersal. Therefore, evidence from palaeoecological research must be supported by additional recent evidence.

1.3. COMPARISON OF TERRESTRIAL AND MARINE ENVIRONMENTS

Few papers discuss the comparisons between marine and terrestrial systems (Chase 2000; Steele 1985; Stergiou & Browman 2005), and even fewer compare multiple ecosystems with empirical data (Gray et al. 2006). A lack of multi-disciplinarity thus far is more widely revealed in an asymmetry in cross-citation, and thus perhaps in information exchange, between the disciplines – aquatic authors cite terrestrial papers ten times more often than the reverse (Menge et al. 2009). However, ecological theories and concepts are often applicable across the disciplines (e.g. Paine 1969). Analyses of the impacts of environmental change on biodiversity use data from a single ecosystem (i.e. terrestrial, freshwater, or marine). Therefore, this divide between the three broad environments is reducing our ability to fully understand environmental change because it is a universal phenomenon that requires assessment across ecological taxa. Comparing between different ecosystems may allow us to identify common processes and principles.

Although findings from multiple environments have been combined within review papers (e.g. Parmesan 2006), analyses are from different geographical areas and, therefore, comparisons available as a result are likely to differ in the environmental change experienced. In contrast, comparisons of impacts on multiple environments in the same geographical area would determine whether we can expect to observe similar responses to environmental change. If similar changes are observed, this would suggest a common response of species to environmental change, regardless of the environment it inhabits. To the best of my knowledge, this has not been attempted prior to this thesis. Within this thesis I use data from the terrestrial and marine environments to explore biodiversity change and

permit a comparison of pattern, process and driver for impacts of environmental change on ecological communities (Cole 2005).

There are known similarities between the two environments. For example, Gray et al. (2006) contrasted the assemblage structure of marine benthos and fish with terrestrial microfauna and ants and found that assemblages from both demonstrated lognormal species abundance distributions. Conversely, the differences in variability allude to the possibility that these structural distributions may become disparate over time as a result of responses to environmental change.

1.4. THESIS FOCUS, OBJECTIVES AND STRUCTURE

1.4.1. Knowledge gaps

The preceding literature review identifies the lack of a substantial evidence base for the impacts of environmental change on diversity at the level of ecological communities, specifically: (i) focused on the meso-scale with specific reference to beta-diversity and metacommunities, (ii) focused on multi-decadal temporal scales, and (iii) comparisons of multiple biomes in the same geographical area. Therefore, within this thesis I focus on these knowledge gaps using a multidisciplinary approach. The exploration of the metacommunity concept focuses on metacommunity structure only because mutually exclusive hypotheses could not be formulated for the paradigms.

1.4.2. Aim and Objectives

My thesis aims to assess the impacts of environmental change on the diversity of ecological communities over multi-decadal temporal scales, using the spatial meso-scale. I will assess these changes in a terrestrial and a marine habitat, allowing cross-biome comparison. Furthermore, I will attempt to elucidate the relative importance of individualistic species response and community constraints. Specifically, my objectives are to:

1. Apply the palaeoecological concept of non-analogous community formation to intra-community impacts of environmental change

- a. Has this been addressed in conservation legislation?
 - b. Is there evidence for its recent occurrence?
- 2. Assess the extent of change in inter-community (or assemblage) diversity in southern England over multiple decades as a result of environmental change.
 - a. Has inter-community diversity of woodland plant communities in southern England changed over 70 years?
 - b. Has inter-assemblage diversity of temperature-sensitive intertidal rocky shore invertebrates in southern England changed over 50 years?

For 2a & 2b:

- i. Is this reflected by intra-community diversity?
 - ii. What are the environmental drivers of the observed change?
- 3. Identify the metacommunity structure of woodland plants at two points in time, seventy years apart and determine how much the structure had changed.
 - a. Does metacommunity structural change reflect community level changes?
- 4. Determine whether the climatic tracking response can be individualistically limited by the presence of physical barriers to dispersal.
 - a. Will the individualistic limitations alter under scenarios of future environmental change?

1.4.3. Thesis Structure

Chapter 2 addresses the first objective through discussion of the implications of the individualistic species responses on community

composition. I discuss the likelihood of non-analogous community (NAC) formation in the first direct adaptation of the concept to modern ecology (Keith et al. 2009). Within the following two chapters (3 & 4), I explore observed change in biodiversity within and between communities (objective 2) with data obtained from surveys of the same sites at two points in time. Such data provides inevitable limitations, for example, comparability of the two surveys, 'snap-shot' data with no time series with which to assess variability on shorter timescales, and missing or sparse data (Peterken 1992). Whilst these limitations are important considerations within my thesis they do not preclude the ability to achieve my objectives and provide valuable historical information. Specific limitations of each dataset are addressed within the relevant chapters. In Chapter 5 I address objective three through an exploration of whether the observed community changes (Chapter 3) have translated to changes in the metacommunity. Chapter 6 will focus on the process of community level biodiversity change through species level responses, specifically on the role of dispersal in establishment and maintenance of beta-diversity. The final chapter discusses the findings of each previous chapter in the context of the impact of species responses to environmental change on communities, and compares findings in marine and terrestrial habitats.

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Chapter 2

Non-Analogous Community Formation in Response to Climate Change

2.1. ABSTRACT

Palaeoecological and current ecological evidence suggests that species will respond individualistically to future climate change. This is likely to lead to the formation of Non-Analogous Communities (NACs), which may be defined as communities that are different in species composition from any communities that can be recognised at a selected reference point in time. I explore the process of NAC formation, with reference to the key processes of immigration and extinction and the potential influence of landscape pattern, in the context of a metacommunity framework. NAC formation has considerable implications for the development and implementation of conservation policies, which frequently refer to the maintenance of current communities. The achievement of such an objective represents a substantial challenge in an era of rapid environmental change, and fails to accept the dynamic nature of communities. The discussion suggests that conservation policies should identify potential responses to community change based on an understanding of the processes of NAC formation.

2.2. INTRODUCTION

The complex and rapid environmental changes that characterise the modern era represent a major challenge to conservation management. Research evidence indicates that climate change is already having a major impact on global biodiversity (McCarty 2001; Parmesan & Yohe 2003; Root et al. 2003; Rosenzweig et al. 2007; Thuiller 2007) but the implications of such impacts for conservation, and how best to address them, remain uncertain. Given the nature of the changes that are occurring, and are likely to occur in the future, the potential policy implications are profound. This is

exemplified by a recent horizon scanning exercise, which suggests that “nature conservation policy and practice will not keep pace with environmental change” (Sutherland et al. 2008).

Palaeoecological evidence suggests that ‘non-analogous’ climates, different from any currently found, occurred in the past and are likely to occur in the future (Fox 2007; Jackson & Williams 2004; Williams et al. 2007; Williams et al. 2001). Some currently recognised climates and environmental domains are also projected to disappear (Saxon et al. 2005; Williams et al. 2007). Based upon two Intergovernmental Panel on Climate Change (IPCC) emissions scenarios (Nakicenovic & Swart 2000), it has been estimated that by 2100, 17-100 % of global land area will experience novel climate (Williams et al. 2007). In the US, 53.6–63.1 % of environmental domains, defined by edaphic, topographic and climatic factors, are projected to have become non-analogous during the same period, and are considered to be at greatest risk of biodiversity loss (Saxon et al. 2005).

Available evidence suggests that range shifts of individual species are likely to result in changes in community composition, as a result of local extinction and dispersal/migration (Benning et al. 2002; Hansen et al. 2001). Climate change would therefore be expected to cause changes in community composition and this is consistent with palaeoecological observations of previous climate change events (Williams & Jackson 2007).

Maintenance of ecological communities is a central objective of many conservation policies. For example, the European Union Habitats Directive (HD) promotes conservation of habitat features, which are based upon the CORINE community classification system (Devillers et al. 1991) and consist of a list of expected species occurrences (DG Environment 2007). Other national and international conservation strategies similarly focus on maintaining areas with a particular species composition, including the UK Habitat Action Plans (UK Biodiversity Group 1999), the US National Wildlife Refuges System (US Fish and Wildlife Service 2004), the National Strategy for the Conservation of Australia's Biological Diversity

(Department of the Environment Sport and Territories 1996) and the WWF ‘Ecoregions’ (Olson et al. 2001). In this chapter I question whether maintenance of ecological communities, defined in terms of their species composition, may be possible or desirable in an era of rapid environmental change. I explore the topic through application and enhancement of ideas embedded in the palaeoecological literature to modern conservation ecology. I focus on climate change, as potentially the most important element of environmental change for global biodiversity.

2.3. NON-ANALOGOUS COMMUNITIES

Evidence from palaeoecology suggests that the majority of species will respond individualistically to changes in climate (e.g. Bush 2002; Huntley 1991). This may result from contrasting physiological tolerances of different species, or climatic effects on interactions between species or with the physical environment. Where non-analogous climates develop, the formation of communities that are different from anything currently recognised is likely. Such communities can be referred to as ‘non-analogous communities’ (NACs), a designation which may be applied at global or regional scales (Bennett 1997). The fossil record of the Quaternary period, most specifically during the Pleistocene Epoch, contains much evidence of individualistic species responses to climate change from a range of taxa including plants (e.g. Huntley 1991), insects (e.g. Coope 1987) and mammals (e.g. Graham et al. 1996). Furthermore, evidence from analysis of Quaternary fossil and palynological assemblages indicates non-analogy to assemblages observed in modern ecology (Williams & Jackson 2007), as in the case of European and North American plant communities from the late glacial period (e.g. Williams et al. 2001).

Methods of detecting NACs are important for understanding climate change impacts and developing appropriate policy and management responses. Such detection depends critically on how NACs are defined.

Two explanations (the second providing an explicit definition) were identified for the NAC concept in the palaeoecological literature:

- (1) “Communities emerge as temporary assemblages of taxa whose components will dissociate as they respond individualistically to environmental change, and will form new associations under new environmental conditions. ...some past assemblages of taxa must be expected to differ from any that we can find today. This is manifested by so-called ‘no-analogue’ assemblages of fossils...” (Huntley 1991, p.18)
- (2) “No analog communities consist of species that are extant today, but in combinations not found at present. “No-analog” is therefore shorthand for “no present analog” and can refer to both past and potential future communities.” (Williams & Jackson 2007, p.477)

In these explanations, present communities provide the point of reference. This is exemplified by the use of the term “no analogue” as shorthand for communities with “no modern analogue”, and applies to comparisons of past and future communities with those occurring currently (Williams & Jackson 2007). However, this takes no account of changes in community composition that may have already occurred in response to recent climate change, which could potentially be revealed by long-term monitoring studies. Given this, I propose the following definition of NACs: *“Non-analogous communities differ in species composition from any communities that can be recognised at a selected reference point in time.”* This more flexible definition permits comparison of current communities with those that have occurred at any selected reference point in the past, which should be made explicit. The magnitude of difference required to qualify as an NAC is discussed in the following section.

NACs may be usefully differentiated from other related concepts in the scientific literature, such as ‘recombinant communities’ (Angold et al. 2006), ‘invasive communities’ (Sutherland et al. 2008), the ‘highly modified community’ (Masters & Ward 2005), ‘emerging ecosystems’ (Milton 2003)

and ‘novel ecosystems’ (Hobbs et al. 2006) (Table 3). The proposed definition provides a concept that is not habitat specific, recognises all species and has practical applicability to conservation management.

Two different types of NACs can be recognised based on the hypotheses proposed by Williams (2000). One type can be considered transitional, resulting from differential time-lags in response to the changing environment arising from differences between species in, for example, dispersal ability, reliance on mutualistic or facilitative relationships with other species, or abiotic requirements (Coope 1987). This idea focuses on the concept that NACs are communities that are at disequilibrium with their environment. Alternatively, Williams & Jackson (2007) propose a type of NACs that are not simply an extended state of transition but communities in which a new equilibrium is established with a non-analogous climate. To some extent all communities are transitional, but there is a meaningful distinction between communities which are developing towards a new, but already recognised, community and those which are developing in a novel direction.

Table 3. Differentiation of Non-Analogous Communities from other apparently related concepts in the scientific literature. Non-analogous communities differ in species composition from any communities that can be recognised at a selected reference point in time.

Concept	Definition/Explanation	Difference from NAC concept
Recombinant communities (Angold et al. 2006)	Referred to in the abstract: "...cities provide habitats for a rich and diverse range of plants and animals, which occur sometimes in unlikely recombinant communities"	These concepts do not impinge on my proposed NAC definition and could be encompassed within the proposed NAC definition as additional aspects for consideration.
Invasive communities (Sutherland et al. 2008)	Identified as a potential future threat and refer to a community where each new invader facilitates invasion by another species and so on, resulting in 'invasional meltdown'	
Highly modified community (Masters & Ward 2005)	An altered community resulting from the <i>Arriver</i> and <i>Leaver</i> conceptual models developed by the MONARCH project	
Emerging ecosystems (Milton 2003)	"An ecosystem whose species composition and relative abundance have not previously occurred within a given biome."	These concepts are close to my proposed definition of NACs, but refer explicitly to community colonisation from a blank starting point as a consequence of human disturbance. Following conventional definitions of the term 'ecosystem' (O'Niell 2001), these concepts would also include biophysical variables and system-level processes, in addition to the species present.
Novel ecosystems (Hobbs et al. 2006)	"An ecosystem whose species composition and relative abundance have not previously occurred within a given biome." (following definition of Milton 2003)	

2.4. DETECTION AND PREDICTION

Detection and prediction of NAC formation would facilitate the adaptation of conservation to climate change in many ways, including the identification of vulnerable habitats, setting of realistic management objectives and development of appropriate measures to increase habitat connectivity (Hannah et al. 2007; Hill et al. 1993; Wilson et al. 2005). The determination of which communities qualify as NACs depends on comparing species composition with a community at a selected reference point in time, then selecting a threshold of similarity. One method with the potential to achieve this is the palaeoecological ‘modern analogue technique’ (MAT; Gavin et al. 2003; Jackson & Williams 2004; Williams & Shuman 2008). The MAT is used in palaeoecology to determine objective thresholds for distinguishing between fossil and modern pollen assemblages (Gavin et al. 2003; Jackson & Williams 2004; Williams & Shuman 2008). The MAT determines this threshold by resolving the optimum resemblance measure to distinguish recognised community (vegetation) types at a single point in time (see Gavin et al. 2003 for further detail). The method is therefore dependent on the reference point that is selected. This resemblance measure could be used to objectively determine the threshold resemblance measure to distinguish NACs. When the resemblance measure is applied in combination with a multivariate statistical technique, NACs can be identified (Fig. 2).

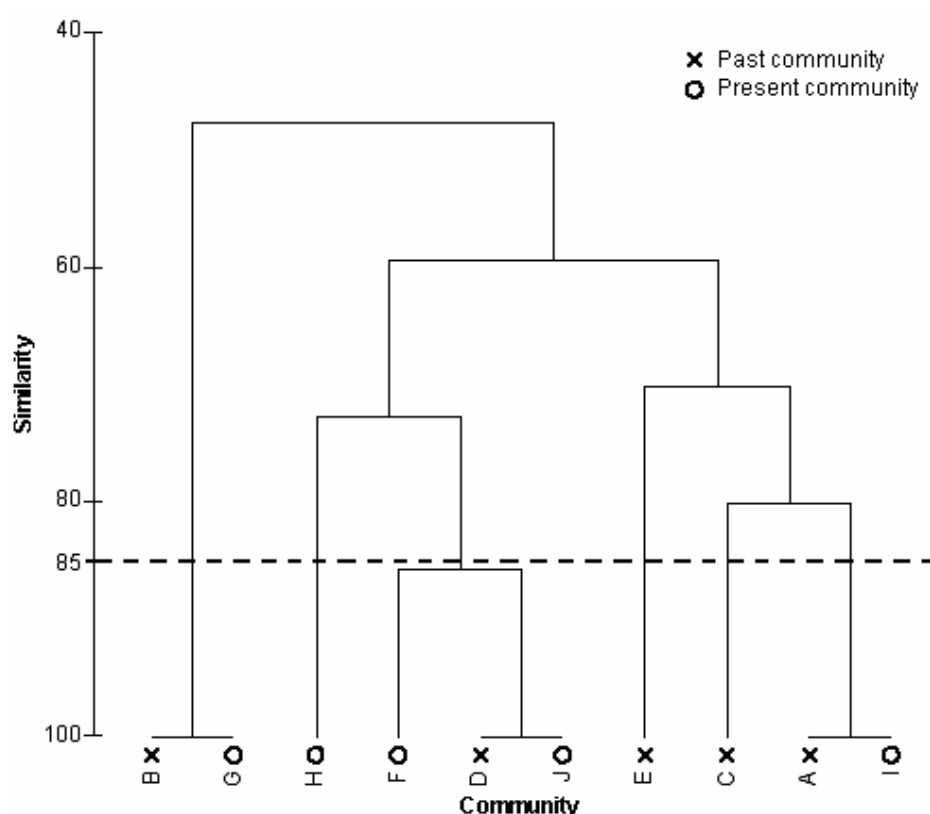


Fig. 2. Example of Non-analogous community (NAC) detection using multivariate analysis in conjunction with adaptation of the 'Modern Analog Technique' (MAT). NACs differ in species composition from any communities that can be recognised at a selected reference point in time. The threshold of similarity (dashed line) is determined by the MAT. The diagram represents a scenario where the MAT has determined the similarity measure as $NAC = <85\%$ similarity. Therefore, communities F, I, J and G are analogous to past communities. Community H is non-analogous.

2.5. PROCESS OF NON-ANALOGOUS COMMUNITY FORMATION

NAC formation could occur through direct or indirect effects of climate change on individual species. Direct effects involve the impacts of changes in the abiotic environment of the species whereas indirect effects involve change in the biotic environment of the species through altering inter-specific interactions. Palaeoecology proposes similar notions regarding

immediate causes of community composition change. Webb (1986) identified an 'Immediate Type A' response that alters the competitive balance within the community, and a 'Full Type B' response that involves range extensions and/or soil development as a necessary prerequisite for community change (Webb 1986).

Knock-on events following such direct or indirect effects may ensue in response to environmental change. There are many documented examples of 'extinction cascades' whereby the extinction of one species leads to secondary extinctions of other species within the same community, a process that is particularly evident following the extinction of a top predator or a keystone species (Borrvall & Ebenman 2006; Frank et al. 2005; Paine 1969). Knock-on events have also been observed for immigration, for example facilitation in the form of soil development or shade provision during succession (Baumeister & Callaway 2006). Research on the effect of extreme climatic events can yield insight into NAC formation in response to climate change. Thibault and Brown (2008) recorded a complete reorganisation of a rodent community following a flood event, and noted the importance of immigration of individuals from surrounding communities in causing dramatic changes in species dominance.

Immigration and local extinction (hereafter referred to as extinction) are key processes governing the species composition of communities within an area and, therefore, NAC formation. These processes are influenced by the spatial characteristics of landscapes such as the size and connectivity of habitat patches and the influence of the landscape matrix on dispersal, as demonstrated through developments in metapopulation theory (Hanski 1998; Hanski 1999) and landscape ecology (Dunford & Freemark 2005; Lindenmayer et al. 2008; Turner 2005). The resistance and resilience of existing communities will also play a critical role (e.g. Grime et al. 2000). Stable inter-specific interactions coupled with low rates of immigration and/or extinction will tend to maintain the same community. Dispersal and subsequent immigration and establishment of a novel species from one community to another will result in either formation of a NAC or an

alternative analogous community. Local extinction will produce a depauperate version of the original community, which may be considered as an NAC if it is sufficiently different from other communities with which it is being compared. However, these situations are simplified; in reality, gains and losses of multiple species are likely to occur from a given community depending on the timescale considered. Immigration and extinction will therefore act in combination to produce NACs, with the balance between the processes shifting under different external influences such as landscape pattern.

The rate of the process of NAC formation also requires consideration. It could be continuously gradual, subject to a threshold or a combination of both of these. Thresholds represent a point at which a small change in environmental variables, such as the spatial configuration of habitat, can cause a large and abrupt change in ecological processes (With & Crist 1995). For example, sea level rise could cause a breach of coastal barriers (e.g. headlands), allowing propagules of intertidal species to rapidly immigrate into previously inaccessible communities. For NAC formation, thresholds might occur in cases where a particular climatic change causes idiosyncratic responses of species to become markedly more evident, or spatial variables influence a switch between immigration and extinction as the primary process of NAC formation.

The recently developed metacommunity concept could provide an appropriate ecological framework for understanding the spatial dynamics of NAC formation at the landscape scale. A metacommunity is defined as “...a set of local communities that are linked by dispersal of multiple potentially interacting species” (Leibold et al. 2004). Metacommunity dynamics have been examined with respect to four paradigms: Species Sorting, Patch Dynamics, Mass Effects, and Neutral (Leibold et al. 2004). The four paradigms are not mutually exclusive, although it is likely that the relative importance of the paradigms will vary in different situations. Depending on which paradigm is dominant, different conservation responses will be required (Mouillot 2007). Identification of metacommunity paradigms

associated with particular landscapes could help identify local communities that are vulnerable to conversion to NACs. For example, the patch dynamics paradigm stresses the necessity of species turnover and fragmentation in the co-existence of competing species. Therefore, one can hypothesise that a reduction in flow of individuals between local communities increases their vulnerability to NAC formation through extinction. Conversely, the species sorting paradigm emphasises the importance of heterogeneity of microhabitats within patches for maintenance of species richness, the patch becoming 'saturated' when all microhabitats are filled. Under this paradigm, if climate change results in production of new microhabitats within a community, that community is vulnerable to immigration and subsequent NAC formation.

The metacommunity concept may therefore assist with identification of communities vulnerable to NAC formation at the landscape scale. Conservation management can be informed by identification of the metacommunity paradigms acting on a focal community (Mouillot 2007). Development of conservation responses at a landscape scale could provide a buffer to local climate change impacts through a functionally networked metacommunity.

2.6. IMPLICATIONS AND FUTURE DIRECTIONS

Evidence suggests that NACs will form in response to climate change and this presents a major challenge to conservation policy and practice. Adaptation of conservation policy to climate change has been the subject of much academic and policy-orientated discussion, over the last 25 years (Heller & Zavaleta 2009). However, this discussion has often been conducted in general terms and led to broad, high-level recommendations. There remains an urgent need to develop and test adaptation strategies that can be applied to specific situations. The NAC concept and metacommunity framework can be used to provide a structured approach to reviewing conservation strategies and management plans addressing community

composition. Where a particular community composition is a stated conservation objective it will initially be necessary to consider the point at which a community is considered to have changed significantly.

If a designated community was to be maintained, changes beyond proposed limits would need to be addressed by appropriate conservation responses, the choice of which depends on understanding the process of NAC formation. For example, NACs formed by immigration might be addressed by species removal, whereas NACs formed by extinction might be addressed by reintroduction or assisted migration (McLachlan et al. 2007). However, prevention of NAC formation may prove to be prohibitively expensive, impossible, or undesirable.

Alternatively, NAC formation may be a positive development for wider conservation objectives, for example, where a species immigrating into a community is experiencing loss of, or decline in, its historical range. In these circumstances amending policy and management objectives to accommodate change would be desirable and necessary. Accommodation of change has been accepted in principle by many conservation organisations. For example, the government conservation agency Natural England states in a position paper on climate change that “...*designations need to become more dynamic to enable species to move to more suitable habitats...*” (Natural England 2008). However, practicalities surrounding the application and implementation of these principles have not been established. Good practice is demonstrated in the management of marine and coastal areas, where identification and classification of marine biological assemblages has the facility to define transitional biotopes, primarily through reducing the detail of classification (Connor et al. 2004; Olenin & Ducrotoy 2006). The development of spatially and temporally appropriate management responses would depend upon adequate monitoring of community composition to detect NAC formation, supported by analysis of its potential causes. In order to determine spatially appropriate responses and to prioritise action, the rate of NAC development must be considered.

Examination of the process of NAC formation provides a broad research agenda, involving a shift in focus from species-specific responses to climate change, to examining the potential impacts of climate change on community composition. Potential lines of enquiry regarding NAC formation include: (1) analysis of immediate effects (e.g. altered inter-specific interactions), (2) analysis of processes responsible for NAC formation (i.e. immigration and extinction), (3) analysis of the rate of NAC formation, i.e. gradual change or rapid transitions (thresholds), (4) analysis of the influence of spatial variables (e.g. habitat configuration), (5) vulnerability analysis, and (6) analysis of the desirability of NACs.

Improved understanding would support the development of tools for detection of NACs for use in environmental monitoring, and for prediction of vulnerability to NAC formation at various spatial and temporal scales. In parallel, it is imperative to consider how to incorporate the concept into conservation policy and practice. Conservation managers require guidance on the degree of community change that might be considered acceptable, in terms of achieving their specific management objectives. This guidance should be provided by appropriate policy. There is therefore an urgent need for dialogue among policy makers and other relevant stakeholders to define the limits of community change that are deemed acceptable. These limits should be based on an understanding of the processes of NAC formation.

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Chapter 3

Taxonomic Homogenization of Woodland Plant Communities over Seventy Years

3.1. ABSTRACT

Taxonomic homogenisation is the increasing similarity of the species composition of ecological communities over time. Such homogenisation represents a form of biodiversity loss and can result from local species turnover. Evidence for taxonomic homogenisation is limited, reflecting a lack of suitable historical datasets, and previous analyses have generated contrasting conclusions. I present an analysis of woodland patches across a southern English county (Dorset) in which I quantified 70 years of change in the composition of vascular plant communities. I tested the hypotheses that over this time patches decreased in species richness; homogenised, or shifted towards novel communities. Although mean species richness at the patch scale did not change, I found increased similarity in species composition among woodlands over time. I concluded that the woodlands have undergone taxonomic homogenisation without experiencing declines in local diversity or shifts towards novel communities. Analysis of species characteristics suggested that these changes were not driven by non-native species invasions or climate change, but instead reflected re-organisation of the native plant communities in response to eutrophication and increasingly shaded conditions. These analyses provide the first direct evidence of taxonomic homogenisation in the UK, and highlight the potential importance of this phenomenon as a contributor to biodiversity loss.

3.2. INTRODUCTION

Biodiversity loss is occurring widely at local and regional scales, leading to changes in the composition of biological communities (Poiani et al. 2000). Altered composition can result from local species loss, which reduces the number of species present within a habitat patch (lower α -diversity), or from immigration, which increases species richness. At larger spatial scales, such processes can lead to biotic homogenisation (BH). BH refers to increasing similarity among communities over time, reflecting changes in species composition caused by local immigration and extinction (Castro & Jaksic 2008b; McKinney & Lockwood 1999). It is generally caused by an increase in the abundance of cosmopolitan or widespread species, which may be accompanied by a decrease in the abundance of more specialist or rare species (Castro & Jaksic 2008a). BH has attracted increasing research interest in the context of understanding the impacts of environmental change on biodiversity because of its potential role in the loss of specific community types and biotic impoverishment (Olden et al. 2004; Rooney et al. 2007). Despite such interest, understanding of BH remains limited.

The evidence for BH is highly variable and sometimes conflicting. Such variation can be attributed partly to the occurrence of different types of BH: genetic, taxonomic and functional (Olden & Rooney 2006). Genetic homogenisation refers to an increased similarity between gene pools as a result of hybridisation or genetic bottlenecks. Functional homogenisation (FH) refers to an increase in the similarity of species' functional 'roles' across communities, and is the most strongly supported by evidence (Olden & Poff 2004; Olden & Rooney 2006). FH has been observed in plant communities in Britain, being attributed to expansion of historically contingent species with 'winning' traits in response to land-use change (Smart et al. 2006).

Taxonomic homogenisation (TH) refers to an increase in similarity of species composition across a set of communities (Olden & Rooney 2006). If TH occurs this will often indicate FH, but also indicates a decrease in species' β -diversity. Most commonly, TH has been documented as the

result of the spread of non-native species across a region, resulting in the loss of native species (McKinney & Lockwood 1999). Evidence for TH comes primarily from regional or national comparisons of the similarity between introduced and native species pools (Castro et al. 2007; Hoagstrom et al. 2007; Magee et al. 2008; McKinney & La Sorte 2007), and community similarities along large-scale spatial gradients (Blair & Johnson 2008; Dormann et al. 2007; Kuhn & Klotz 2006). However, contrasting evidence is also available (Beck & Khen 2007). For example, species invasions were found not to simplify taxonomic composition of Mediterranean floras (Lambdon et al. 2008), and the flora of two US states showed more instances of differentiation than homogenisation (Qian et al. 2008).

Conflicting evidence for TH partly reflects variation in the methods used. The most powerful method for detecting TH involves the comparison of complete species pools from the same sites at different times (Olden & Rooney 2006). This method has rarely been employed because it is dependent on the availability of suitable historical data, which are usually lacking (Olden & Rooney 2006). Application of this approach demonstrated TH over five decades in Wisconsin (USA) woodland plant communities as a result of local extinction (Rooney et al. 2004). In contrast Smart et al. (2006) found no evidence of taxonomic impoverishment in a sample of plant communities throughout Britain over a 20 year period. Different results have therefore been obtained both in terms of the occurrence of TH and the processes responsible. Variation among studies might also be attributable to the contrasting timescales investigated.

In this investigation I analysed changes in the composition of woodland vascular plant communities using surveys undertaken at an interval of seven decades. This represents the longest time period over which TH has been assessed by examining changes in composition at the same sites. Specifically, I tested the following (not mutually exclusive) hypotheses: (1) habitat patches from the two survey times do not differ significantly in species composition (null hypothesis); (2) species richness

of patches has decreased over time; (3) patches have become significantly more similar to each other over time (demonstrating TH); (4) communities present in 2008 are a subset of those present in the 1930s, and therefore novel communities have not developed over this time period. I examined the potential processes responsible for any observed composition changes by testing whether: (5) plant traits indicate that environmental conditions (soil fertility, the degree of shading, soil pH, soil moisture, air temperature) had changed between the two surveys; and (6) the proportion of non-native species had increased over time.

3.3. METHODOLOGY

3.3.1. The “Good” Survey

I used a data set created in the 1930s, which provides a rare opportunity to examine changes in species composition over seven decades. The use of long-term data is imperative if we are to understand changes over time. However, such data should be used with an awareness of the caveats, which in this case concern the snapshot nature of the data (i.e. only two points in time) and differences in sampling effort between the two surveys. For discussion of these points I refer the reader to Chapter 7 of this thesis (section 7.4.1, p.174).

From 1931-1939 Ronald Good undertook a survey of vascular plant species at 7,575 sites throughout the southern English county of Dorset. Good selected sites using what he referred to as the “stand” method. Stands were “...reasonably distinct topographical and ecological entit[ies]...” and were required to be “...as evenly scattered as possible” across Dorset (Good 1937). Stands varied in size from 0.5 to 20 ha and were surveyed by recording all vascular plant species encountered during a survey of approximately one hour. Stand locations were recorded on a series of six inch Ordnance Survey (OS) maps (Webb 1999), which were subsequently digitised by the Dorset Environmental Records Centre (DERC). Each patch

was visited once, generating presence-absence data that are relatively robust to sampling error (Hirst & Jackson 2007).

3.3.2. Resurvey of woodland patches

For clarity, henceforth I refer to Good's stands as 'patches' and the species list for a patch as a 'community'. I resurveyed a selection of the patches classified as woodland by Horsfall (1989). I selected a sample of patches for potential resurvey by determining which were still extant and had not been re-planted, using current maps of woodland habitat provided by DERC. Selected woodlands corresponded to ancient semi-natural woodland habitats (Natural England 2003) and priority habitats of lowland mixed deciduous woodland, lowland beech and yew, wet woodland, and wood-pasture and parkland (BRIG 2008). Of the resulting 592 selected patches, a sample of 86 were randomly selected for resurvey. During the survey process, 21 patches were found to be inaccessible and were replaced by new samples.

Patches were relocated in the field using a Global Positioning System (eTrex venture, Garmin Ltd., Southampton, UK) supported by digital maps of the Good patches derived from DERC and 1:25000 scale raster OS tiles. Each patch was surveyed on a day and month as close as possible to the dates employed by Good in the 1930s, and was searched over approximately two hours to minimise errors of species loss. A single person carried out all surveys. All vascular plant species were identified *in situ* or by removing or photographing specimens for expert determination. A few plants were identified only to genus by Good and were assumed to be the same species as specimens of that genus found in a patch in 2008.

3.3.3. Data Analysis

To identify any bias caused by different sampling dates, changes in species number within each patch between the two surveys were correlated against the number of days between the Good survey date and the resurvey date. I performed Analysis of Similarity (ANOSIM) with 1,000 permutations using the 'vegan' package (Oksanen et al. 2008) in R version 2.8.1 (R

Development Core Team 2008) to determine whether species composition of patches differed between the two surveys. I then used Sørensen similarity indices (S) to assess homogenisation of, and any shift in, community composition within patches between the surveys (Shaw 2003).

$$S = \frac{2a}{2a + b + c} \quad (\text{Equation 1})$$

where a is the total number of species present in both patches being compared, b is the number of species present only in patch 1 and c is the number of species present only in patch 2.

To determine changes in variation among the communities, I calculated the Sørensen index between all community pairs using the Good data. This resulted in 85 indices for each community from which I calculated the mean Sørensen index for each community x , which was designated S_i^x . I repeated these steps for the 2008 resurvey data, which provided measures of the variation among the communities in 2008, S_j^x . To determine the extent of the changes between the Good survey and the resurvey, I calculated the mean of the indices for each 2008 community compared to all 1930s communities S_k^x . In the event of homogenisation, one would expect $S_j^x > S_i^x$. In the event of differentiation, one would expect $S_i^x > S_j^x$. In the event of a shift in community composition, S_k^x would have the lowest value. The non-parametric Kendall's W test for multiple related dependent samples was used to compare S_i^x , S_j^x and S_k^x .

I also assessed community changes by multivariate Detrended Correspondence Analysis (DCA) using the 'vegan' package (Oksanen et al. 2008) in R version 2.8.1 (R Development Core Team 2008). The number of axis rescalings was set at the default of four and segments as 26 (Oksanen 2008). Outliers were detected by the Mahalanobis distance of the four DCA axes on the first run (Tabachnick & Fidell 2001). Communities that

exceeded the critical Mahalanobis value of 18.47 (for $p < 0.001$ d.f.=4) were removed, along with their corresponding patch pair. As a result the number of samples included in the analysis was reduced by five patches and the number of species was reduced by sixteen. The 'ellipse' package (Murdoch et al. 2007) was used to create bivariate standard deviational ellipses for DCA axes 1 and 2 at 90% confidence intervals. Ellipses were created for the Good data and for the resurvey data.

I examined the potential processes behind observed composition changes by using scores of plant traits that indicate tolerance of different environmental conditions. Trait scores for all species were obtained from PLANTATT (Hill et al. 2004) and were used to create a mean value for each trait for each patch in each survey. The traits examined provide an indication of soil fertility (Ellenberg N), the degree of shading (Ellenberg L), soil pH (Ellenberg R), soil moisture (Ellenberg F) and climate (mean January and mean July temperatures; see Hill et al. 2004 for calculation details). In addition, species were classified as either native or non-native (archaeophytes, neophytes and casuals), to determine any changes in the proportion of non-native species between the surveys.

3.4. RESULTS

There was no correlation between the changes in species number within each patch and the number of days (i.e. time of year) between the dates of the two surveys ($r_s = 0.11$; $p = 0.33$), suggesting that any differences in survey date did not bias the results. The ANOSIM suggested a highly significant difference between habitat patches from the two survey times ($R = 0.026$, $p = 0.001$). Comparison of species lists across all sites showed that 117 species were lost and 47 species were gained between the 1930s and 2008 surveys. However, the mean (\pm SE) number of species per patch did not change significantly between the 1930s (57 ± 2.8) and 2008 (53 ± 1.6) ($\chi^2 = 0.145$, d.f. = 1, $p = 0.70$), indicating no significant biotic impoverishment at the patch level. Patches with a relatively high species

number in the 1930s tended to show decreased species number by 2008, but the converse was also true (Fig. 3). As a result, the species number of patches converged between the surveys. This was demonstrated by linear regression which indicated a significant influence of species number per patch on values obtained in the 1930s on that in 2008, with the gradient of the regression line being less than 1 (Fig. 3).

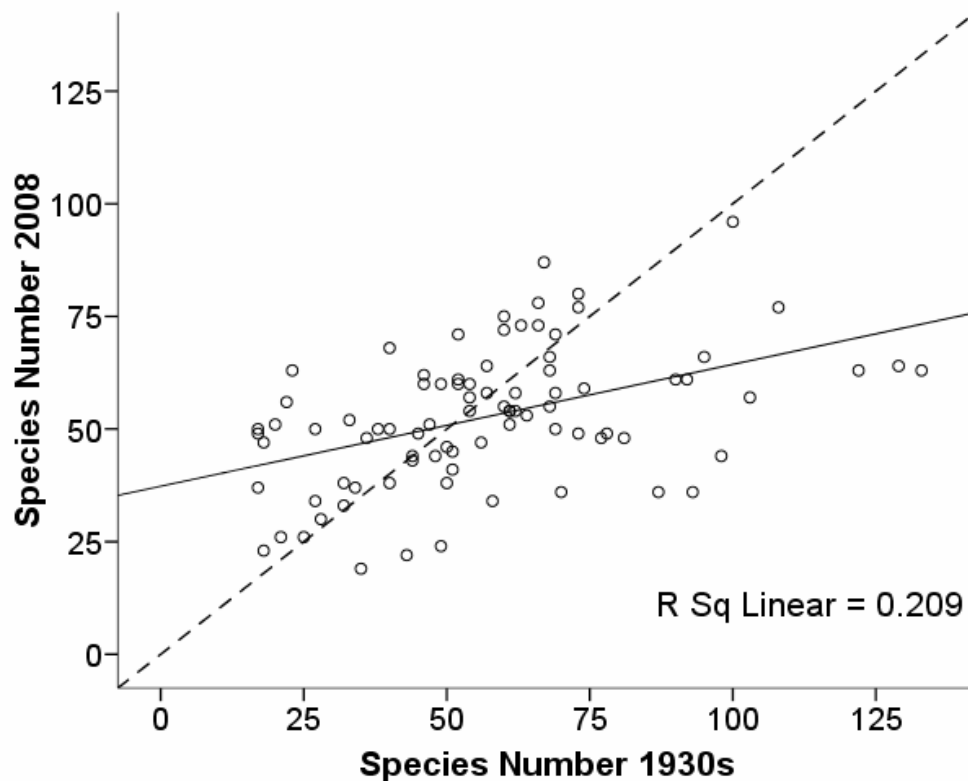


Fig. 3. Species numbers at each survey time. The dashed line represents the null hypothesis of no change in species number of a community between the two surveys. The solid line represents the fitted relationship ($r^2 = 0.209$; d.f. = 85; $p < 0.001$), which suggests that sites with communities with high species number in the 1930s have tended to decrease over time and those with a low species number in the 1930s have increased over time. The gradient of the regression was significantly different to 1 (gradient 0.27; 95% confidence intervals 0.16, 0.39).

The Sørensen indices for the 1930s (mean across all x patches, $\bar{S}_i = 32.8$), for 2008 ($\bar{S}_j = 46.6$) and for the 1930s vs. 2008 ($\bar{S}_k = 35.1$) were significantly different from each other ($W = 0.728$, d.f. = 2, $p < 0.001$). This suggests greater taxonomic homogeneity in 2008 than in the 1930s, a finding supported by the DCA, which indicated both a reduction in variation and a shift in composition between the surveys (Fig. 3). Eigenvalues for the DCA were 0.25 and 0.17 for axes 1 and 2 respectively. Wilcoxon tests showed that the difference between the median sample scores for the 1930s and 2008 surveys were significant for axis one ($T = 159$, $p < 0.001$) and axis two ($T = 542$, $p < 0.001$). The 90% confidence interval ellipses for axes 1 and 2 showed strong overlap of the 1930s and 2008 communities, indicating that novel communities have not developed over this time period (Fig. 4).

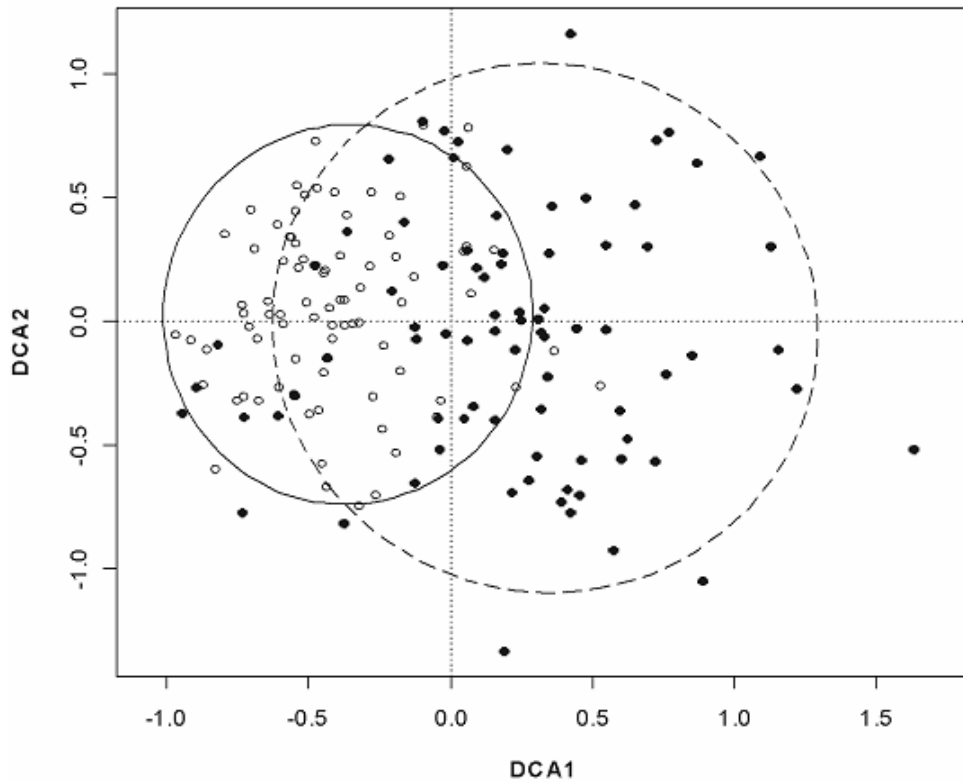


Fig. 4. Detrended correspondence analysis (DCA) bi-plot for samples. Filled circles are 1930s samples, open circles are 2008 samples. The plot depicts bivariate standard deviational ellipses for axes 1 and 2 at a confidence interval of 90% for each survey time. The ellipse to the right is for 1930s communities and to the left is for 2008 communities. The ellipses overlap and show a shift of communities to the left of the plot over time.

Changes in the mean plant trait values per patch between the two surveys suggested highly significant ($p < 0.001$, Wilcoxon matched pairs tests) increases in soil fertility and in shading (Table 4), but there were no significant differences in traits relating to air temperature, soil pH or soil moisture. The proportion of non-native species within a patch increased significantly over time ($p = 0.019$, Wilcoxon matched pairs test), but the proportion was extremely low in both surveys (≤ 0.03).

Table 4. Wilcoxon's matched pairs test on mean trait scores for patches. Overall mean patch scores for each survey are provided to indicate the direction of change in traits.

Trait	Mean 1930s patch score	Mean 2008 patch score	<i>T</i>	<i>p</i>
Ellenberg L (Light)	5.80	5.44	465	< 0.001
Ellenberg N (Fertility)	5.02	5.44	229	< 0.001
Ellenberg R (pH)	5.87	5.93	1434	0.060
Ellenberg F (Moisture)	5.57	5.55	1814	0.808
Mean January temperature (°C)	3.52	3.52	1787	0.719
Mean July temperature (°C)	14.51	14.52	1779	0.694
Proportion of non-native species	0.02	0.03	981	0.019

3.5. DISCUSSION

This study provides clear evidence of changed community species composition of the woodland flora over a 70-year period. The effect of this change has been taxonomic homogenisation (TH), as indicated by the increase in Sørensen indices over time and the reduction in variation detected by DCA. I therefore accept the hypothesis that patches have increased in similarity in terms of their species composition, demonstrating TH. To our knowledge, this is the first time that taxonomic homogenisation has been documented in the UK. Our result contrasts with the analysis of Smart et al. (2006), which found no evidence for TH among a large number of habitats throughout Britain over 20 years, but did find evidence for functional homogenisation, which was attributed to the expansion of species with similar ‘winning’ traits. The contrasting results obtained here may reflect the different time spans over which the comparison was made, with the current study being longer than that of any previous study using the same method.

Contrary to previous studies where TH has been identified (Rooney et al. 2004), the observed TH was not associated with a decline in mean number of species per habitat patch. However, there was a decline in species number at the landscape-scale between the surveys. While losses of α -diversity have been detected in some previous studies of changes in British plant communities (e.g. Stevens et al. 2004), others have not. Smart et al. (2006) observed increased floristic species richness in some habitat patches over two decades in Britain, which was attributed to initial habitat productivity and disturbance. Within the Dorset woodland patches, the spread of species with traits more suited to the changed environment appears to have been matched by declines in other species, leading to a balance between the number of colonisations and extinctions.

The large overlap of DCA ellipses and the relatively high similarity of communities between the two surveys (\bar{S}_k) supports the hypothesis that the woodland communities have not shifted towards novel compositions, an

expected response to climate change (Keith et al. in press; Williams & Jackson 2007), and that those communities found in 2008 were a sub-set of those occurring in the 1930s. This result suggests that the Dorset woodlands are not yet showing any response to recent climate change, a conclusion supported by the lack of climate-related changes in the plant trait analyses.

Analysis of plant traits suggested that the TH observed reflected re-organisation of the native plant communities in response to eutrophication (Ellenberg N) and increasingly shaded conditions (Ellenberg L). Eutrophication has previously been associated with local extinctions (Walker & Preston 2006) and changes in communities of native plant species (Portejoie et al. 2002) in the UK, and Smart et al. (2006) implicated eutrophication and changes in anthropogenic disturbance in the functional homogenisation of British plant communities. The increasingly shaded conditions of woodlands in the UK can be attributed to the widespread decline in traditional woodland management since the 1930s (Kirby et al. 2005). Van Calster et al. (2007) showed similar management-driven TH within a Belgian forest in a comparison of coppice-with-standards forest with high forest.

The results of the current investigation therefore indicate that TH can be caused by environmental change without contribution from non-native species. While the proportion of non-native species increased significantly between the surveys, it was extremely low in both. Much previous research into different types of BH has focused on invasion by non-native species as a principal cause (Castro et al. 2007; Hoagstrom et al. 2007; Magee et al. 2008; McKinney & La Sorte 2007). Whilst non-native species can cause large losses of native species in some circumstances (Maskell et al. 2006a), national surveys accord with the results of this study in showing that non-natives are minor components of many British plant communities (Maskell et al. 2006b).

In conclusion, Dorset woodlands have undergone taxonomic homogenisation over the last 70 years with no floristic impoverishment at the patch scale, nor any shift towards new community compositions.

Changes are attributable to a re-organisation of native plant communities, possibly in response to increasing eutrophication and more shaded conditions. The contrast between scales of measurement illustrates the value of landscape-scale (β -diversity) analyses in detecting biodiversity loss that might otherwise go unnoticed. Our findings also highlight the importance of changes in native species distributions, which is a more subtle floristic change than invasion of non-natives, but is of equal consequence to biodiversity loss at higher levels of organisation (Cassey et al. 2008).

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Chapter 4

Reduced thermal gradient as a possible driver of invertebrate assemblage convergence at a biogeographic boundary zone

4.1. ABSTRACT

Evidence is rapidly mounting for the loss of beta-diversity. I provide one of the first empirical attempts to elucidate the mechanisms and drivers of the process. The assessment of a role of temperature in beta-diversity loss was optimized through use of a model rocky shore assemblage composed of temperature-sensitive invertebrate species situated at a biogeographic boundary zone between warm temperate and cold temperate waters. Long-term change in relative abundance and composition of the model assemblage surveyed at two discrete times, five decades apart, at 28 sites was assessed with Analysis of Similarity (ANOSIM) and mean Bray-Curtis similarity indices (B). Indices were tested for assemblage conversion. Analyses were repeated on inter-annual (2002-04) data. Mean change in annual sea surface temperature range over time was tested with a Spearman's Rho correlation. Non-metric multi-dimensional scaling determined the spatial pattern of change in assemblage similarity. McNemar's test determined whether there was significant change in the site occupation of individual species and a Wilcoxon's matched pairs test assessed change in the site abundance of species. Model assemblage relative abundance significantly changed and spatially converged over time, whilst the inter-annual (2002-04) difference did not. Mean annual sea surface temperature range had a significant negative correlation with time ($r^s = -0.516$; $p < 0.001$). Species site occupation did not significantly change between survey times and species abundance changed significantly for two species. Convergence of the assemblage over time was linked with the mechanistic responses of individual species to greater similarity in thermal

regime among sites. I hypothesise that reduced thermal gradient has led to improved winter survival, higher fecundity and consequential increase in larval supply of southern species, as the biogeographic boundary zone has become more diffuse. Future research should test whether the mechanisms and driver of beta-diversity loss in this model assemblage can be applied to higher organizational levels that experience biotic homogenization.

4.2. INTRODUCTION

Biodiversity loss is a global phenomenon in terrestrial, freshwater and marine environments. Throughout the world's oceanic and coastal habitats, which represent some of the most species-rich areas, this loss is a cause for great concern (Spence et al., 1990; Stokstad, 2006; Worm et al., 2006). Altered locality and extent of species distributional ranges in response to environmental change have been implicated in biodiversity loss (Ling, 2008) and have been documented in numerous habitats (Holbrook et al., 1997; Thompson et al., 2002; Herbert et al., 2003; Mieszkowska et al., 2005; Mieszkowska et al., 2006; Lima et al., 2007; Mieszkowska et al., 2007; Hawkins et al., 2008; Parmesan 2006; Walther et al. 2002; Wethey & Woodin, 2008). Changes in the abundance and distribution of individual species can lead to changes in assemblage composition (Poiani et al. 2000; Holbrook et al., 1997). Although species richness within assemblages can remain stable during species flux, large-scale patterns of biodiversity can be dramatically altered through changes in the degree of similarity between assemblages. Inter-assemblage variability is referred to as beta-diversity and, relative to intra-community (α -) diversity, is a cryptic aspect of biodiversity. The change in beta-diversity is best observed with multi-species assemblages surveyed at two discrete points in time (Olden & Rooney 2006). Unfortunately, availability of such datasets is scarce, thereby imposing a limit on current knowledge in this area (Olden & Rooney 2006).

The most commonly discussed form of beta-diversity loss is biotic homogenization whereby inter-community similarity increases over time (Castro & Jaksic, 2008a). Biotic homogenization is a process of

conservation concern because it often indicates large-scale biodiversity loss through reduced species richness and the demise of unique assemblages (Olden et al. 2004; Rooney et al. 2007). It can be defined “..as an increase in the spatial similarity of a particular biological variable over time...” (Olden et al. 2004). The most common biological variable to be analysed in the context of biotic homogenization is the ecological community (e.g. Rooney et al., 2004; Britton et al., 2009; Keith et al., 2009), however, analysis of functional groups (e.g. Smart et al., 2006; Devictor et al., 2007; Winter et al., 2008), assemblages (e.g. La Sorte & McKinney, 2006; Beck & Khen, 2007) and population genetic units (e.g. Oliveras et al., 2005; Puillandre et al., 2008) can also provide useful insight (Olden & Rooney, 2006). Evidence is rapidly mounting for homogenization, however, knowledge would be improved if empirical studies were expanded to a greater variety of ecological environments. Existing analyses have disproportionately focused on plant (Rooney et al., 2004; Kuhn & Klotz, 2006; La Sorte & McKinney, 2006; Smart et al., 2006; Castro & Jaksic, 2008a, b; Britton et al., 2009; Keith et al., 2009), bird (Devictor et al., 2008) and freshwater fish communities (Radomski & Goeman, 1995; Rahel, 2000; Marchetti et al., 2006; Hoagstrom et al., 2007; Leprieur et al., 2008). In the marine environment biotic homogenization has been largely overlooked (Airoidi et al., 2008) and is yet to be quantitatively assessed.

Many previous analyses in other environments have identified the driver of beta-diversity loss as non-native species immigration and this was the origin of the concept of biotic homogenization (La Sorte & McKinney, 2006; Schaffelke et al., 2006; McKinney & La Sorte, 2007; Castro & Jaksic, 2008a; Manor et al., 2008). However, recent evidence within woodland and alpine plant communities has shown that changing environmental conditions can also drive the process, with non-native species having little effect (Britton et al., 2009; Keith et al., 2009). If changing environmental conditions can drive biotic homogenization, it is possible that the current rapid climate change event (Solomon et al., 2007) will contribute to an

increasing incidence of beta-diversity loss, through both immigration of non-native species and reorganisation of native species.

Despite the rapidly accumulating evidence for the occurrence of beta-diversity loss through biotic homogenization, understanding of underlying causes and mechanisms remains limited (Olden, 2006). To predict future consequences of beta-diversity loss the process must be better understood. Advancement of understanding and assessment of ecological processes is often best achieved through the use of variables (e.g. species, assemblages) that are well-studied, easily identifiable, cost effective to measure and sufficiently sensitive to provide an early warning system for wider change (Noss 1990). In combination with the necessity of suitable historical datasets, finding suitable model assemblages is difficult. However, a rare dataset for intertidal rocky shore invertebrate assemblages along the south coast of the UK, surveyed at two discrete times 50 years apart (Crisp & Southward, 1958; Mieszkowska et al., 2005), fulfil these demands and provide the data for this analysis paper. Unfortunately, the cost of such data is that the historical survey is incomplete in its coverage of rocky shore species and so cannot provide a baseline with which to assess homogenization of the entire community. The model assemblage comprises ten native temperature-sensitive animal species, including those with key structural and functional roles in rocky shore ecosystems such as barnacles and limpets (Hawkins et al., 2009). The sensitivity of the assemblage increases the possibility of detecting the role of temperature in the process.

Analyses further optimize the elucidation of process because the model assemblage straddles a biogeographic boundary zone between western warm temperate and eastern cold temperate waters on the south coast of the UK (Forbes, 1858; Fischer-Piette, 1936; Crisp & Southward, 1958; Herbert et al., 2009). The impacts of climate change on assemblages are more readily detected at biogeographic boundary zones, where groups of co-occurring species reach their range limits (Blanchette & Gaines, 2007; How & Kitchener, 1997; Gaston, 2009). Such zones provide a sensitive system within which to evaluate the impacts of climate change events on

groups of species. In the marine environment, surface isotherms describe a gradient of temperature change with latitude and have long been recognised as a key factor in the maintenance of biogeographic boundaries (Forbes, 1858; Crisp & Southward, 1958; Lewis, 1964). In light of this, sea surface temperature would be expected to be an important driver of beta-diversity loss in the coastal marine environment. In single species studies, warm-temperate species within the model assemblage have demonstrated eastwards range expansions, including *Osilinus lineatus* (Mieszkowska et al., 2006; Mieszkowska et al., 2007) and *Perforatus perforatus* (Herbert et al., 2003).

The aim was to investigate evidence for convergence of a temperature sensitive suite of species (referred to as the model assemblage), containing those with key functional roles, during a period of climatic change, and seek to elucidate mechanisms that enable such change. I addressed the following hypotheses: (1) assemblages from the two discrete times do not differ significantly in species relative abundance along the south coast (null hypothesis), (2) inter-assemblage similarity has significantly increased, demonstrating assemblage convergence in the study region, (3) there was a significant change in number and location of sites where species were present, and in their relative abundance, and (4) sea surface temperature change indicates a convergence in thermal regime in the study region.

4.3. METHODOLOGY

4.3.1. Study Area

The study area on the south coast of Great Britain extends from Cape Cornwall in the west (50.1284°N, 05.7070°W) to Dover in the east (51.1558°N, 01.3937°E), a distance of approximately 1,000 km along the coast. For 2008, HadISST data (Rayner et al., 2003) showed minimum and maximum mean monthly sea surface temperature (SST) of 7.4 °C and 17.8 °C respectively for the western English Channel and 5.2 °C and 18.6 °C respectively for the eastern English Channel, demonstrating wider SST

variation in the east. The area is characterised by a complex coastline with strong prevailing winds from the west and south-west (Barne et al., 1996a; Barne et al., 1996b, c; Barne et al., 1998a; Barne et al., 1998b).

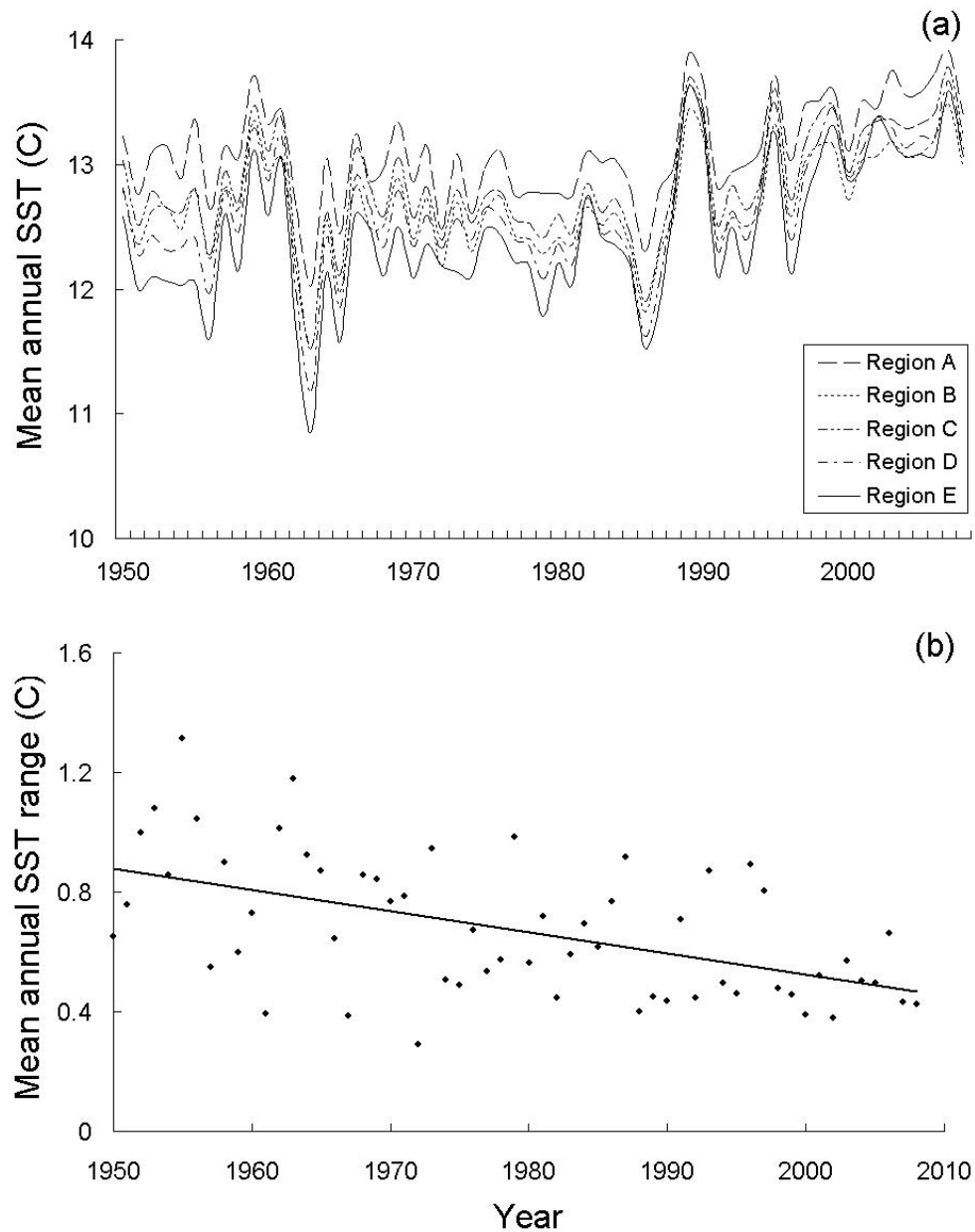


Fig. 5. (a) Annual mean sea surface temperatures (SST) from 1950 – 2008, and (b) annual mean SST range, along the south coast of England, $r = -0.525$; $p < 0.001$; [data sourced from HadISST (Rayner *et al.*, 2003)]. Region A = Land's End to Lizard Point; Region B = Lizard Point to Start Point; Region C = Start Point to Portland Bill; Region D = Portland Bill to Selsey Bill; Region E = Selsey Bill to Dover.

In the English Channel SST has fluctuated considerably since 1950, with a particularly cold period from the early 1960s to the mid 1980s followed by a rapid increase over the last decade (Hawkins et al. 2009; Fig. 5a). The coastline of the English Channel has been assigned to coastal cells based upon movement and retention of sediment (Motyka & Brampton, 1993). There is also increasing evidence for hydrodynamic barriers to larval dispersal along the English Channel caused by headlands that form the boundaries of these cells (Gilg & Hilbish, 2004; Herbert et al 2007). I use these coastal separations as a basis for spatial analysis.

4.3.2. The Historical Survey and Re-survey Data

The dispersal phase of rocky shore species is predominantly pelagic causing the continued survival of populations to be dependent upon open sea, therefore, rocky shore species are useful indicators for the wider marine environment (Hawkins et al. 2009). Crisp & Southward (1958) recorded the abundance of 23 intertidal animal species at over 200 sites along the south coast of Britain, the Channel Isles and the French coast from 1949-1957. A mean of 9.5 species were sampled per site, ranging from 3 to 23 species, although absence was not always recorded. The Marine Biodiversity and Climate Change (MarClim) project (www.mba.ac.uk/marclim; Mieszkowska et al., 2005) revisited a selection of the sites in 2002-2005, to record the abundance of 59 species, including the 23 species in the base-line survey.

Use and resurvey of historical datasets must be accompanied by appropriate caveats. In this case there are three potential issues: (i) snapshot data i.e. only two points in time, (ii) difference in sampling effort and comparability of the method, and (iii) missing values. The methodology was not an issue here because it was comparable with the historical survey. Furthermore, it used the ACFORN abundance scale devised by Crisp & Southward (1958), which increases by orders of magnitude making it less susceptible to error. For full discussion of these long-term data issues I refer

the reader to section 7.4.1 of Chapter 7 (p. 174). Inter-surveyor reliability was greatly facilitated by the fact that one surveyor (Alan Southward) was involved in the historical survey and resurvey, and actively taught his methodology to the re-survey team. Four sites in the eastern region sampled in 2006 by Roger Herbert using the same sampling protocol were included to increase the site replicates in region E.

4.3.3. Data Selection

Historical survey and resurvey data from 28 sites were selected along the entire south coast of Britain between Lands End and Dover (Fig 6). Sites were selected on the basis of maximum number of species sampled. Low, mid and high water barnacle data for sites were merged. Species were excluded from the original list if ≥ 25 % of records were missing within the sample of 28 sites. This resulted in a final assemblage of ten consistently surveyed invertebrate species (Table 5). Prior to 1976, *Chthamalus* was regarded as a single taxon (Southward, 1976), therefore, *C. montagui* and *C. stellatus* records have been combined in the resurvey data. Coastal regions were delineated by headlands *sensu* Motyka & Brampton (1993; Fig. 6) for consideration of spatial patterns of change in the analyses.

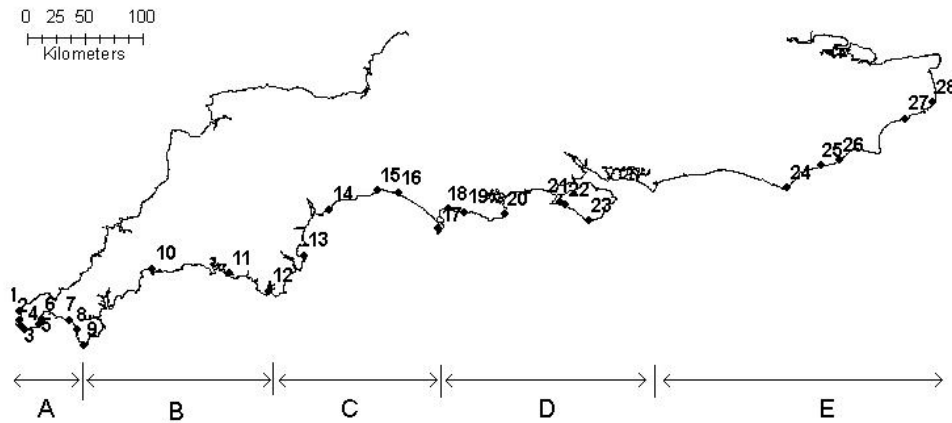


Fig. 6. The south coast of England (coastline data source: National Geophysical Data Center, 2009) indicating extent of coastal regions delineated by major headlands (A-E). Site locations are numbered and marked with closed circles. Region A: 1 = Cape Cornwall, 2 = Nanjizal, 3 = Sennen Cove, 4 = Porthgwarra, 5 = Lamorna Cove, 6 = Mousehole, 7 = Porthleven Harbour, 8 = Poldhu Cove, 9 = Lizard Point. Region B: 10 = Polkerris, 11 = Wembury, 12 = Salcombe, South Sands. Region C: 13 = Brixham, 14 = Budleigh Salterton, 15 = Lyme Regis, 16 = West Bay. Region D: 17 = Portland Bill, 18 = Osmington Mills, 19 = Lulworth Cove, 20 = Peveril Point, 21 = Freshwater Bay, 22 = Brook (Hanover Point), 23 = St. Catherine's Point. Region E: 24 = Eastbourne, Beachy Head, 25 = Bexhill, 26 = Fairlight, 27 = Folkestone, 28 = Dover. Projected on the British National Grid (GCS_OSGB_1936).

Table 5. Biome association of species included within the temperature sensitive assemblage.

Species	Nomenclature authority	Biome association
<i>Actinia equina</i>	Linnaeus	Boreal
<i>Chthamalus</i> spp.	Southward	Lusitanian
<i>Semibalanus balanoides</i>	Linnaeus	Boreal
<i>Perforatus perforatus</i>	Poli	Lusitanian
<i>Patella ulyssiponensis</i>	Gmelin	Lusitanian
<i>Patella depressa</i>	Pennant	Lusitanian
<i>Patella vulgata</i>	Linnaeus	Boreal
<i>Gibbula umbilicalis</i>	da Costa	Lusitanian
<i>Osilinus lineatus</i>	da Costa	Lusitanian
<i>Melarhaphe neritoides</i>	Linnaeus	Lusitanian

4.3.4. Data Analysis

The species data were ordinal categories from the ACFORN abundance scale (Crisp and Southward 1958), ranging from 0 = ‘not found’ to 5 = ‘abundant’. Unless specified otherwise, analyses were performed with PRIMER v.6 (Clarke & Gorley, 2006). I tested for significant differences in inter-annual variability within a three year sample (2002-04) to compare with inter-decadal variation. Thirty-three assemblage samples from twenty different sites were used. Analysis of Similarity (ANOSIM) with a one-way design was employed to compare year of survey.

The dataset for inter-decadal analyses included 80 records of missing values, imputed using multiple imputation (Schafer, 1999) with NORM v. 2.03 (Schafer, 2000), which employs a Markov Chain Monte Carlo (MCMC) method to create a small number of independent draws and is suitable for ordinal data. One thousand iterations were run to obtain ten simulated datasets (Barnard & Meng, 1999) and rounded to the nearest observed value. Each simulated dataset was subjected to all analyses and mean values across simulated datasets with 95 % confidence intervals (CI)

where possible, and standard errors where C.I. was not possible, were reported.

ANOSIM was performed to compare surveys and determine whether assemblages differed significantly in relative abundance between the two surveys. I followed the methodology of Chapter 3 to calculate mean (with 95 % C.I.) Bray-Curtis indices (i.e. similarity) amongst assemblages at each survey time for each of the 10 simulated datasets, to determine whether assemblages had converged and/or shifted. The mean Bray-Curtis index for the historical survey is referred to as B_{1950} and for the resurvey as B_{2000} . In the event of beta-diversity loss (i.e. convergence), one would expect $B_{1950} < B_{2000}$. Non-metric multi-dimensional scaling (NMMDS) was used to determine the spatial pattern of change. NMMDS used the rounded mean of the ten simulated datasets. Fifty restarts were used to create a 2-dimensional bi-plot of all assemblages.

4.4. RESULTS

The ANOSIM of the inter-annual variability from 2002-2004 suggested there was no significant inter-annual difference (Global $R = -0.115$, $p = 0.80$). The series plots for the worst linear function parameter created as an output of the multiple imputation confirmed that the value set for k was appropriate and highly conservative. The ANOSIM of the two survey times demonstrated a highly significant difference between the two surveys (mean Global $R = 0.32 (\pm 0.014)$, mean $p = 0.001 (\pm 0)$). The Bray-Curtis indices for the historic survey ($B_{1950} = 68.26$; C.I. lower 65.36, upper 71.15) and for the resurvey ($B_{2000} = 72.96$; C.I. lower 71.03, upper 74.89) showed increased similarity, and therefore beta-diversity loss over time ($B_{1950} < B_{2000}$), although there was a very slight overlap of 0.12 in confidence intervals. I repeated this analysis with the inter-annual (2002-04) dataset and found no evidence for beta-diversity loss.

The non-metric multi-dimensional scaling (2D stress 0.07) demonstrated far western assemblages and central assemblages had become more similar to other mid-western regions (Fig. 7). The eastern Channel

sites varied in their response from convergence to differentiation. Only one site significantly decreased in similarity (Site 13 – Brixham; $p = 0.025 (\pm 0.008)$) to all other sites, whilst ten sites (Sites 4, 5, 7, 9, 19, 22-26) increased significantly ($p < 0.05$). Sites 4 and 22-26 experienced a high influx of new species relative to other sites.

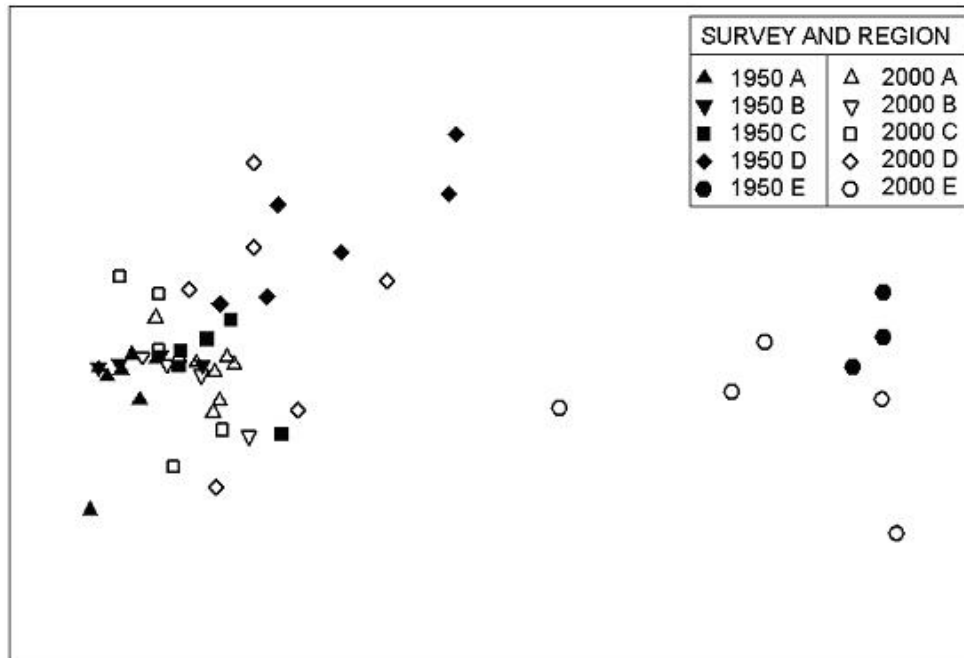


Fig. 7. NMMDS bi-plot (2D stress: 0.07) depicting similarity between assemblages (rounded mean of 10 simulated datasets). Assemblages are labelled by survey (filled = 1950s; open = 2000s) and by coastal region.

Species site turnover across different coastal regions was not significant for any of the species within the assemblage in McNemar's tests (Table 6), however, the majority of species experienced an increase in the number of sites occupied over time. The exceptions were *Actinia equina*, which experienced a decrease; and *Chthamalus* spp. and *Patella vulgata*, which showed no change in site occupation. *Perforatus perforatus* was the only species to demonstrate turnover in sites occupied, with five gains and two no longer found. There was much change in the abundance of species at different sites (Fig. 8), including significant change in the abundance of

Semibalanus balanoides ($T = 42.50$; $p = 0.033$) and *P. vulgata* ($T = 10.00$; $p = 0.018$), demonstrated by a Wilcoxon matched pairs test. The other species did not change significantly in their abundance, however, the patterns of change warrant description.

Table 6. Change in the number of sites occupied for each species with McNemar's test for significance of change in sites occupied. Numbers are means of 10 simulated datasets, standard errors are included where datasets did not agree.

n1950	n2000	Sites gained	Sites lost	p
<i>Actinia equina</i>				
27.7 (± 0.15)	26.0	0.3 (± 0.15)	2.0	0.650 (± 0.076)
<i>Chthamalus</i> spp.				
23.0	23.0	0.0	0.0	1.000
<i>Semibalanus balanoides</i>				
23.0	28.0	5.0	0.0	0.063
<i>Perforatus perforatus</i>				
21.0	24.0	5.0	2.0	0.453
<i>Patella ulyssiponensis</i>				
22.9 (± 0.10)	24.0	1.1 (± 0.10)	0.0	0.950 (± 0.13)
<i>Patella depressa</i>				
22.0	23.0	1.0	0.0	1.000
<i>Patella vulgata</i>				
28.0	28.0	0.0	0.0	1.000 (± 0.16)
<i>Gibbula umbilicalis</i>				
21.0	23.9 (± 0.10)	3.0	0.1 (± 0.10)	0.288 (± 0.04)
<i>Osilinus lineatus</i>				
15.0	19.0	4.0	0.0	0.125
<i>Melarhaphe neritoides</i>				
21.7 (± 0.15)	23.3 (± 0.30)	3.6 (± 0.31)	0.0	0.797 (± 0.07)

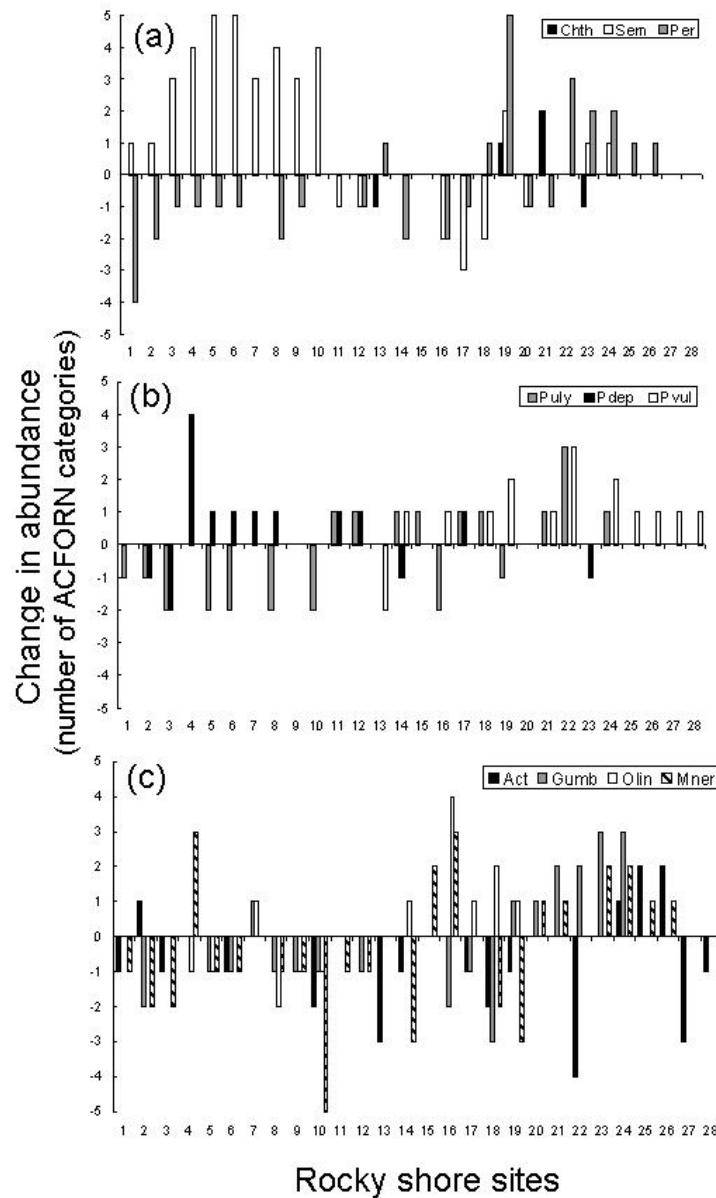


Fig. 8. Change in the abundance of rocky shore intertidal invertebrate species of (a) barnacles, (b) limpets, (c) anemone and molluscs, along sites in the English Channel. Sites are organised from west to east along the x axis. Change in abundance is represented by the difference in ACFORN (A = abundant, C = common, F = frequent, O = occasional, R = rare, N = not found) abundance scale category between the historic 1950s survey and 2000s resurvey. The ACFORN abundance scale is semi-logarithmic. Species key: 'Chth' = *Chthamalus* spp.; 'Sem' = *Semibalanus balanoides*; 'Per' = *Perforatus perforatus*; 'Puly' = *Patella ulyssiponensis*; 'Pdep' = *P. depressa*; 'Pvul' = *P. vulgate*; 'Act' = *Actinia equina*; 'Gumb' = *Gibbula umbilicalis*; 'Olin' = *Osilinus lineatus*; 'Mner' = *Melarhaphe neritoides*.

The barnacles (Fig. 8a) overall showed an increase in abundance, particularly the boreal *Semibalanus balanoides*, which increased in the eleven most westerly sites whilst slightly decreasing in abundance within Lyme Bay and maintaining abundance at eastern sites. The boreal limpet species, *Patella vulgata*, increased in eleven sites whilst only decreasing in one site. The southern *Chthamalus* spp. barnacles remained abundant in the western Channel and occasional at its range boundary on the Isle of Wight. *Perforatus perforatus*, a warm-water barnacle, decreased in abundance in the west and became locally extinct in the furthest western site, whilst colonising four eastern sites. *Patella depressa* increased in abundance at eight sites and decreased in four sites, with most changes occurring in the western regions (Fig. 8b). *P. ulyssiponensis* abundance increased and decreased in a similar number of sites, however, the magnitude of decreases was slightly higher, and eastern sites remained uncolonised. The sea anemone, *Actinia equina*, decreased in abundance in three times as many sites as those in which it increased, with no obvious spatial pattern (Fig. 8c). *Gibbula umbilicalis* colonised three eastern sites and increased in abundance at sites on the Isle of Wight - the location of its range boundary. However, the species showed decreases in abundance at a higher number of sites overall along the coast. *Osilinus lineatus* colonised some sites east of Portland Bill, previously the location of the species' range boundary. Finally, *Melarhaphe neritoides* changed in abundance at many sites but with no obvious pattern.

There was a highly significant negative correlation between the annual mean sea surface temperature range along the south coast of England and time over the last five decades, tested with a Pearson's correlation ($r = -0.525$; $p < 0.001$; Fig. 5b).

4.5. DISCUSSION

4.5.1. Beta-diversity

Assemblages from the two discrete times differed significantly in relative abundance, indicated by the ANOSIM, therefore, the null hypothesis can be rejected. There was no significant recent inter-annual (2002-04) difference in relative abundance, increasing confidence that the difference found between the historical survey and the resurvey represents a long-term trend. I accept the hypothesis that inter-assemblage similarity has increased, demonstrating beta-diversity loss through assemblage convergence for this model assemblage; a conclusion that is supported by the comparison of mean Bray-Curtis indices and the NMDS. No convergence was found within the inter-annual analyses.

Biotic homogenization is generally recognised as convergence amongst entire communities (i.e. all species that share geographical space and potentially interact), despite the definition (see introduction) simply referring to increased similarity between “biological variables” (Olden et al. 2004). Therefore, I recognise that the results do not permit a claim to the occurrence of biotic homogenization of the wider community because data was unavailable for some key species, such as canopy forming macroalgae. Rather, I only claim to provide evidence for a more specific case of beta-diversity loss. However, the results provide empirically testable hypotheses regarding whether the same mechanisms and drivers that here influence assemblage convergence can be applied to explain the process of biotic homogenization.

4.5.2. Drivers of assemblage convergence

Sea surface temperature (SST) range along the south coast of England has decreased over time indicating a convergence in thermal regime (Fig. 5). The reduction in the SST gradient has caused the biogeographic boundary zone, which is primarily delineated by isotherms, to become more diffuse. Such a shift in boundary zone conditions explains the convergence of assemblages as warm-temperate species increased in abundance, potentially

leading to increased connectivity with the eastern Channel. I suggest that sites that were previously population sinks for southern species due to inhibition of reproduction by unsuitable temperatures were enabled as source populations as temperatures became more suitable over time. In essence, the decreased SST gradient across the Channel is liable to have reduced variability in thermal regime and, in doing so, reduced variation in reproductive success across sites, thus driving convergence of assemblages. The association between SST and beta-diversity is highly suggestive, although, as it is not possible to unequivocally establish cause and effect, I now explore other possible drivers.

Over the past 50 years, other environmental changes have affected species and assemblages of rocky shores in our study area and may have also contributed to assemblage convergence. For example, pollution from tributyltin (TBT) has caused depletion of populations of the predatory dogwhelk *Nucella lapillus* (Bryan et al., 1986; Gibbs et al., 1987, 1990; Langston et al., 1990; Spence et al., 1990; Bryan et al., 1993; Smith et al., 2008), a predator of limpets, potentially releasing some species from predation. However, evidence suggests that for inherently stable exposed and sheltered shores on the south coast of England, dogwhelk predation has little impact (Spence et al. 1990). Severe oil spills seriously impacted some shores close to the wreck of the Torrey Canyon in the west of the region, made worse by application of dispersants (Smith, 1968; Southward & Southward, 1978) with recovery taking over ten years (Hawkins & Southward, 1992; Hawkins et al., 2002; Southward et al., 2005). More recent research has demonstrated that for some species the recovery period from TBT was much longer (Smith et al., 2008). Eventual recovery means that oil spills are unlikely to have contributed to assemblage convergence. In contrast, TBT pollution may be a contributing factor, but would require consideration of individual species responses that lie outside the scope of this paper.

The severe winter of 1962-63 seriously curtailed the distribution and abundance of southern species including *Osilinus lineatus* and *Perforatus*

perforatus in the eastern Channel (Crisp 1964). Eastern sites in our study have tended to gain species over time, suggesting the recovery from curtailment of ranges in the 1960s. The recovery from all of the above environmental changes infers that these can be largely ruled out as the cause of assemblage convergence, although equilibrium may still not have been reached at some of the most disturbed sites. Therefore, the reduction in SST gradient across the Channel, reflected in convergence of thermal regime across sites provides the most parsimonious explanation for assemblage convergence, particularly in this case because our model assemblage is temperature sensitive. Furthermore, SST is strongly implicated in range shifts of individual species, including some within our subset (Holbrook et al., 1997; Thompson et al., 2002; Mieszkowska et al., 2006; Lima et al., 2007; Wethey & Woodin, 2008; Hawkins et al. 2009), therefore, explaining the colonisation of eastern sites by some species. Although I did not detect significant changes in site occupation, such changes could be anticipated for the future (Hawkins et al 2009; Mieszkowska et al. 2005).

I emphasize that the model assemblage does not include any non-native species, which could have had an effect on wider community similarity, and has been inferred as the driver of community-wide convergence (biotic homogenization) in previous analyses (La Sorte & McKinney, 2006; Schaffelke et al., 2006; McKinney & La Sorte, 2007; Castro & Jaksic, 2008a; Manor et al., 2008). Localised introductions of species can initially lead to biotic differentiation. However, fast-spreading, dominant species have the capacity to progress to rapid colonisation and establishment throughout a region and cause convergence (McKinney & Lockwood, 1999). The warm-temperate barnacle *Elminius modestus* is an example of localised introduction followed by prevalent spread in our study area (Crisp, 1958), and has an indirect effect on native barnacles.

4.5.3. Mechanism of assemblage convergence

The increased SST and reduced gradient would be expected to drive assemblage convergence through increased reproductive success of the southern species. In addition, the colonisation of eastern sites may have occurred due to increased larval supply and connectivity, facilitated by exploitation of the increasing number of artificial coastal structures as ‘stepping stones’, uniting previously separated sites and making it possible for species to track changing environmental conditions such as increased SST (Mieszkowska et al., 2005). Observed changes in species abundance are strongly supported by analyses of some individual species from our model assemblage (Kendall et al. 2004; Southward 1991; Wethey & Woodin 2008), as are eastward range shifts of warm temperate species (Herbert et al., 2003; Mieszkowska et al., 2006; Mieszkowska et al., 2007), therefore, I will not discuss this in depth but refer the reader to the cited literature for further information.

The non-metric multi-dimensional scaling bi-plot suggests the far west of the Channel and region D became more similar to the area between Lizard Point (site 9) and Portland Bill (site 17). This area has extensive rocky shores and large populations, making it potentially a critical source of larvae for communities throughout the English Channel (Herbert et al. 2007). Increased temperatures would permit warm temperate species to achieve greater reproductive success, increasing larval output from established sites, enabling colonisation of new sites. Increased SST could simultaneously create competitive release from cold temperate species (Southward 1991). The cold-temperate barnacle *Semibalanus balanoides* is a competitor of warm temperate *Chthamalus* spp. and the abundance of both barnacles is primarily determined by an interaction between temperature and competition (Connell 1961; Wethey 1984). Increased SST is predicted to lead to a decreased *S. balanoides* population and increased *Chthamalus* spp. populations (Hawkins et al. 2009; Poloczanska et al. 2008; Southward 1991). Our data demonstrates a significant increase in *S. balanoides* and continued abundance of *Chthamalus* spp. in the western English Channel,

where SST has increased. Time series data for these species demonstrate annual fluctuations concurrent with SST and are consistent with our results (Mieszkowska et al., 2005).

I reject the hypothesis that there was a significant change in the number and location of sites in which species of the model assemblage were present, indicated by the McNemar's tests. Despite the lack of significance at the individual species level, over half of the sites that experienced significant change were the sites that had the highest influx of new species, suggesting that eastwards range expansions of individual species did contribute to the assemblage convergence. Range expansions, driven by an increase in SST in the eastern Channel, can be attributed to increased reproductive success that provided greater numbers of larvae with the potential to colonise new sites, together with reduced winter mortality. Hutchins (1947) notes that the ability of propagules to reach suitable sites and successfully recruit as an important factor in the ecological limits of species at range edges.

4.5.4. Conclusion

Assemblage convergence in the intertidal animal community has occurred in a comparison of two points in time 50 years apart amongst our model assemblage of ten native temperature-sensitive intertidal invertebrate species on the south coast of England. The use of a temperature sensitive model assemblage has enabled detection of a link for convergence with the responses of individual species to greater similarity in thermal regime across sites, regionally demonstrated by a reduced gradient of SST throughout the English Channel. Therefore, SST change is the most parsimonious underlying cause of the convergence and indicates a diffusion of the biogeographic boundary zone as Lusitanian elements previously characteristic of the western Channel now prevail throughout the English Channel. The mechanism is concordant with changed reproductive success influencing larval supply of southern species, altering abundance at established sites and, in some cases, enabling colonisation of eastern sites.

Sites that experienced the greatest change in similarity tended to have an increased number of species, therefore, despite beta-diversity loss, local species richness was not dramatically reduced. I suggest that future research empirically test whether the same mechanisms and driver can explain the process of biotic homogenization at a higher hierarchical scale of ecological organization. Furthermore, it would be extremely useful to explore the role of connectivity between rocky shore sites to gain greater understanding of the mechanisms of beta-diversity loss. This would improve our predictions of future threats to biodiversity.

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Chapter 5

Plant metacommunity structure remains unchanged during biodiversity loss in English woodlands

5.1. ABSTRACT

The metacommunity concept provides important insights into large-scale patterns and dynamics of distributions of interacting species. However, temporal change of metacommunity structure is little studied and has not been previously analysed in the context of biodiversity change. As metacommunity structure is determined by multiple species distributions, it is expected to change as a result of biodiversity loss. To examine this process, I analysed structural change of a southern English woodland metacommunity at two points in time, seven decades apart. During this interval, the metacommunity lost β -diversity through taxonomic homogenization. I performed an Elements of Metacommunity Structure (EMS) analysis (Leibold & Mikkelsen 2002) to examine metacommunity structure, based upon three structural elements: coherence (i.e. gaps in species range along a structuring gradient), spatial turnover (replacements), and species range boundary clumping. I predicted that metacommunity structure would decrease in spatial turnover and thus become more nested over time. I tested for change in individual structural elements with z scores and examined the role of spatial and environmental variables as potential structuring mechanisms through correlation with EMS ordination axes. The results demonstrated that the metacommunity had a Clementsian structure that was maintained over time. Despite no change in broad structure, coherence and species range boundary clumping increased. Spatial turnover increased along the first structuring gradient but decreased on the second gradient. I hypothesise that this difference between gradients may reflect the

presence of competing processes affecting spatial turnover. The mechanisms of biological structuring involved both environmental and spatial factors at the scale of the individual woodland. Therefore, the results suggest that broad metacommunity structure would not be a good landscape-scale indicator for conservation status. Conversely, knowledge that metacommunity structure does not change over time could assist in long-term conservation strategy because fundamental metacommunity structural processes are resistant to environmental change.

5.2. INTRODUCTION

The metacommunity concept is an important theoretical advance that has unified spatial and community ecology (Holyoak et al. 2005; Leibold et al. 2004; Presley et al. 2010), and has attracted much research interest over the last decade (e.g. Cadotte et al. 2006; Cottenie & De Meester 2005; Kolasa & Romanuk 2005; Miller & Kneitel 2005). As a result, a strong empirical foundation for the concept is emerging. A metacommunities is defined as “..a set of local communities that is linked by dispersal of multiple potentially interacting species” (Leibold et al. 2004) and are relevant to understanding large-scale patterns of multiple species distributions and their dynamics.

Spatial structure of a metacommunity is dependent upon three structural elements: coherence, species turnover in space (replacements), and species range boundary clumping (Leibold & Mikkelsen 2002; Fig. 9). An Elements of Metacommunity Structure (EMS) analysis simultaneously tests multiple hypotheses of idealised structural patterns based on consideration of these elements (Leibold & Mikkelsen 2002). Within EMS, the coherence element is the degree to which species occurrence, and therefore community composition, is structured by dominant axes of variation (Leibold & Mikkelsen 2002). Axes of variation reflect structuring factors, for example climatic variables or geographic distance. Species turnover, in the context of EMS analysis, is a spatial property that describes replacement, or swapping, of one species with another between

communities. Throughout I will refer to this element as spatial turnover to clearly distinguish it from temporal species turnover. The converse of spatial turnover is when species richness changes amongst sites, negating replacements. This situation would create a pattern of nestedness amongst communities. The third element is species range boundary clumping and represents coincidence of species' range boundaries in space and thus degree to which sets of species co-occur. EMS analysis has been successfully applied to animal metacommunities, specifically invertebrates and bats (Azeria & Kolasa 2008; Bloch et al. 2007; Ellis et al. 2006; Heino 2005; McCauley et al. 2008; Presley et al. 2009; Presley & Willig 2010).

The combined state of each of these three elements has been interpreted in terms of six metacommunity structures that represent idealised patterns of species distributions among communities (Leibold & Mikkelsen 2002; Fig. 9). Previous analyses of animal metacommunities have indicated a Clementsian structure for larval odonates (McCauley et al. 2008), a Gleasonian structure for stream midges (Heino 2005) and largely Clementsian distributions for Paraguayan (Presley et al. 2009) and Caribbean bats (Presley & Willig 2010). Clementsian communities are strongly delineated into specific community types because species are constrained by inter-specific interactions (Clements 1916). In contrast, Gleasonian communities represent a situation whereby species respond individualistically to environmental gradients and, as a result, community composition falls along a continuum (Gleason 1926). These concepts are highly applicable to metacommunity structure because both describe spatial organisation of multiple communities.

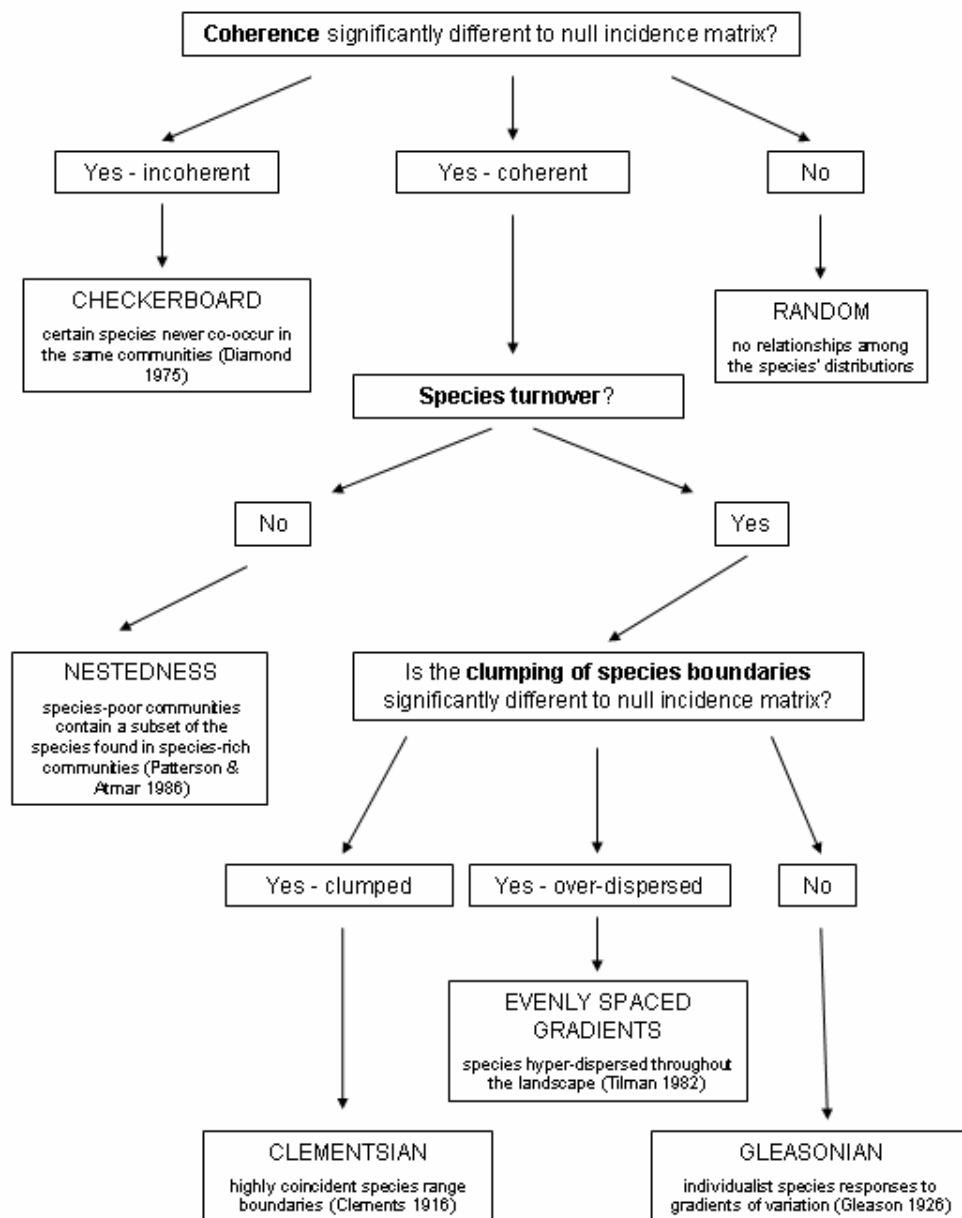


Fig. 9. Elements of the analytical approach examining metacommunity structure. The flow chart depicts the steps of the method and the conclusions (capitalised) associated with each outcome. The outcome depends upon three structural elements of coherence, species turnover and range boundary clumping (Leibold & Mikkelsen 2002). Species distributions within the metacommunity can be structured by dominant axes of variation, and the amount of structuring is termed coherence. Species turnover refers to spatial replacement, or swapping, of one species with another between communities. Within the text, I refer to this element as spatial turnover to distinguish from temporal turnover. Range boundary clumping is the coincidence of species' range boundaries in space.

Because the three structural elements describe aspects of species' distributions one would expect changes in biodiversity to impact metacommunity structure. Biodiversity loss is occurring widely at multiple scales (Mace et al. 2005; Rosenzweig et al. 2007) and the rate of loss is expected to accelerate in the current era of rapid environmental change (Botkin et al. 2007; Thomas et al. 2004; Thuiller 2007). Incidences of large-scale biodiversity loss (β -diversity and γ -diversity) are most appropriately explored at a large scale of organisation with due consideration of spatial organisation (Whittaker et al. 2005).

Furthermore, use of landscape-scale strategies in conservation is growing, stimulating research into large-scale biodiversity patterns and processes. Biodiversity loss would be expected to elicit different impacts on different metacommunity structures. Idiosyncratic species loss within a Clementsian structure could reduce delineation between specific community types, whereas a Gleasonian structure would be unaffected. On the other hand, systematic species loss could increase community delineation within a Clementsian structure and perhaps drive a Gleasonian structure towards increased range boundary clumping and a more Clementsian configuration.

Few analyses have explicitly investigated impact of biodiversity loss on metacommunity structure, and none have done so using the EMS approach, despite its considerable advantages (Presley & Willig, 2010). In addition, to my knowledge, only two previous analyses have assessed change of metacommunity structure over time: in terrestrial gastropod metacommunities over 13 years (Bloch et al. 2007); and in tree hole mosquitoes over 26 years (Ellis et al. 2006). Bloch et al. (2007) state that comparison of temporal dynamics of structural elements in EMS analysis cannot be compared at different times owing to methodological limitations and therefore focus on only a comparison of nestedness. Here I introduce new methodology to permit such comparisons.

An understanding of metacommunity structural change could contribute to prediction of wider impacts of biodiversity loss in response to environmental change because different metacommunity structures vary in

dynamic stability of the community and in reliance on local or regional processes to maintain biodiversity (Leibold et al. 2004). For example, a metacommunity structured by individualistic species responses to environmental gradients (e.g. Gleasonian) may be predicted to respond to environmental change through individualistic species range shifts. In contrast, a structure defined by species co-occurrence may be more likely to respond to environmental change through loss of species or coincident range shifts because species occurrence is constrained by inter-specific interactions or common environmental limitations, such as particular range of soil acidities or shade tolerance.

In this study I aimed to determine change in metacommunity structure over time. I applied EMS analysis to a dataset comprised of species presence-absence data for 86 sample communities from a southern English woodland metacommunity surveyed at two time periods, 70 years apart. During this time the metacommunity lost β -diversity through taxonomic homogenization, which was probably caused by increased nitrogen availability and increased shade (Chapter 3; Keith et al. 2009a). Biodiversity loss was also reflected by reduced γ -diversity, with a reduction from a total of 391 species in the 1930s to 324 species in 2008 (Chapter 3; Keith et al. 2009a). It was expected that this pattern of biodiversity loss would result in a metacommunity structure of nested subsets. Whilst there was loss of diversity overall, some species became more widespread. Therefore, I hypothesised that there were two possible impacts on coherence. If species that increased in patch occupation over time were not woodland specialists (i.e. generalists) one would expect coherence to have decreased because influence of the dominant axes of variation would be reduced. In contrast, if increasing species were woodland specialists, one would expect an increase in coherence as gaps in species occurrences were filled. Therefore, in the assessment of coherence I tested the hypothesis that (1) species that increased in patch occupation over time were generalists, and therefore that (2) metacommunity coherence decreased. Generalist species were those that were not species associated with only the

‘Broadleaved, mixed and yew woodland’ broad habitat type on the PLANTATT database (Hill et al. 2004). I predicted that (3) species replacements between patches, and therefore turnover through space, decreased because there was greater similarity in species composition between patches, resulting in fewer inter-patch species replacements. This scenario would cause structure to become one of nested subsets. I also expected (4) species range boundary clumping to decrease because number of different community types decreased over time (Keith et al. 2009a). Finally, I aimed to determine structuring factors represented by dominant axes of variation. I therefore tested hypotheses that metacommunity structure was ordered by (5) spatial variables (patch area, patch perimeter, patch shape, patch isolation) and (6) local environmental variables (soil acidity, soil texture, soil fertility, drainage and elevation).

5.3. METHODOLOGY

Please refer to Chapter three (3.3.1 and 3.3.2) for details of the “Good” survey and resurvey (Fig. 10). Owing to the potential influence of patch size on temporal species turnover, I tested whether there was a correlation between temporal species turnover and patch area using Spearman’s rank correlation. I tested for spatial autocorrelation of community composition with a mantel test using Pearson’s method and 1,000 permutations in R software ver. 2.9.2 (R Development Core Team 2009). The difference in the proportions of woodland specialist species at each survey was assessed with a Mann Whitney U test.

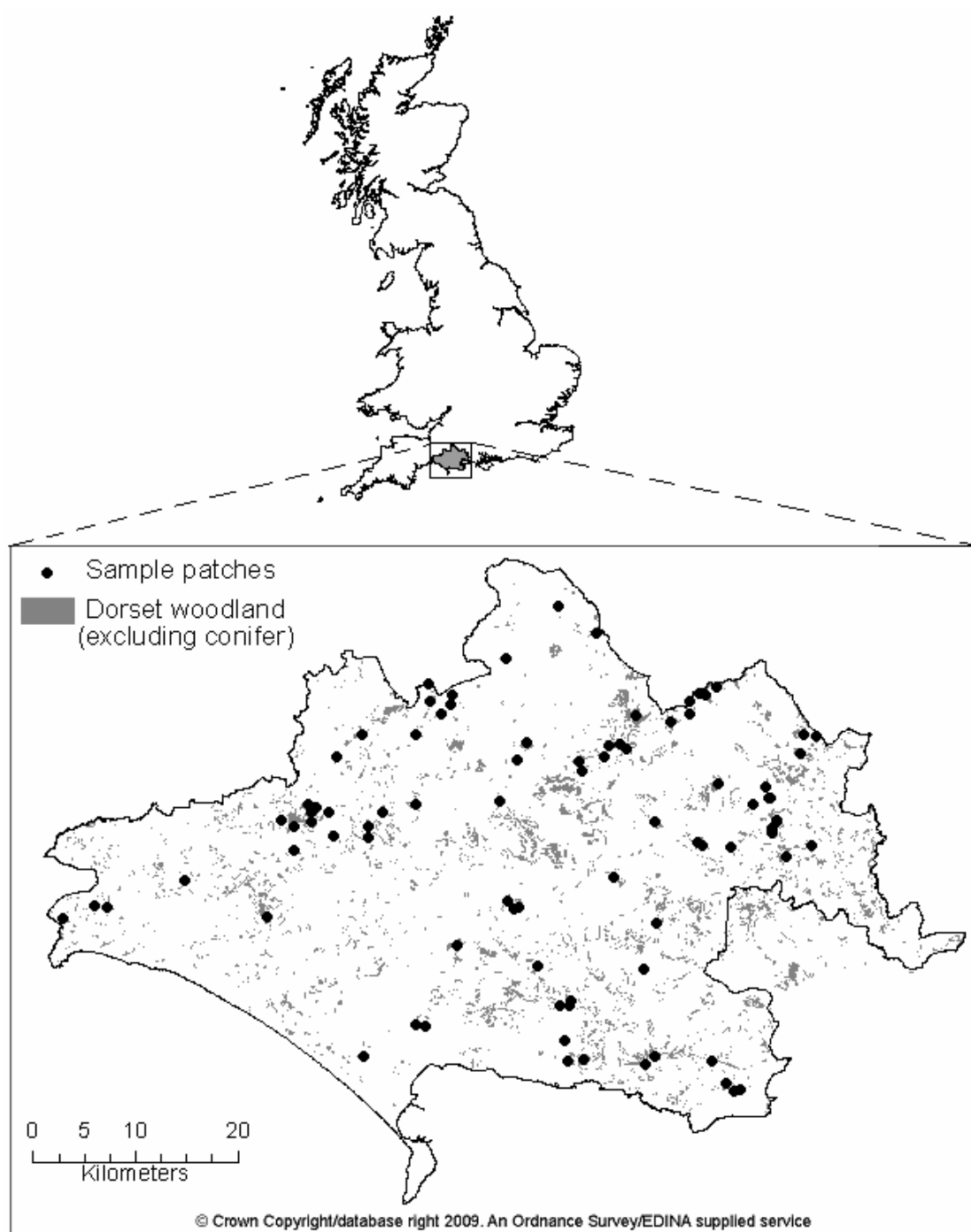


Fig. 10. Location of resurveyed patches (closed circles) within Great Britain and Dorset (adapted from Ordnance Survey 2009a, b). Woodland (excluding coniferous) throughout Dorset (grey patches) is from the National of Woodland and Trees - Interpreted Forest Type (NIWT-IFT; Forestry Commission 2009) and Ancient Woodland Priority Habitat data (English Nature 2003). County boundary excludes the boroughs of Poole and Bournemouth, which were not part of Dorset in the 1930s.

5.3.1. Metacommunity Structure

The metacommunity structure analysis included all species found at more than one patch ($n_{1930} = 311$, $n_{2008} = 235$). Two species-by-site incidence (presence-absence) matrices were created, one for the 1930s and one for 2008. Species that occurred only at one site were excluded because these have a strong positive effect on coherence and boundary clumping, which can bias the EMS result (Presley et al. 2009). I used the methodology described in Leibold & Mikkleson (2002), modified by Presley et al. (2009), to determine the idealised patterns of distribution within the woodland plant metacommunity in the 1930s and in 2008. The method tests multiple metacommunity structure hypotheses representing six spatial distribution patterns within a single analysis of coherence, spatial turnover and species boundary clumping (Fig. 9). I compared data from the 1930s and 2008 to assess temporal change of metacommunity structure. To perform the analysis, I ran a MATLAB v. 2008b Student (Mathworks 2008) script designed by Presley et al. (2009) (<http://www.tarleton.edu/~higgins/EMS.htm>). The null model used to generate a random null matrix treated species richness per site as fixed and species occurrence as fixed – EMS model 9 - with 1,000 iterations. Boundary clumping was assessed by species ranges rather than communities, following the recommendations of Presley et al. (2009).

The first step of the MATLAB analysis ordered the matrix using reciprocal averaging (RA; Hill 1973), which reflected the dominant axes of variation. RA achieves an objective order of sites and species that are maximally packed by placing the species with the most similar distributions, and sites with the most similar compositions, near to each other and so striving for maximum correspondence between species scores and samples scores. The original Leibold & Mikkleson (2002) methodology advocates using only the first ordination axis of the RA. However, I followed Presley et al. (2009), who found that the second axis can also represent significant biological structuring.

5.3.2. Structural elements

Whilst comparison of individual structural elements is appropriate for assessment of differences over time, it is not appropriate to compare magnitude of these elements between axis 1 and 2 because of the nature of RA. This is because one would expect a randomly-generated null matrix to have little internal structure, so the majority of structure that does exist by chance will be captured by the primary axis. On creation of the second axis, which is orthogonal and therefore constrained to be uncorrelated with the first axis, there is less structure left to capture. Therefore it is likely that the second axis will show lower coherence than axis 1. In contrast, matrices generated from biological data are likely to be structured by multiple biologically important gradients. As axes generated from the observed matrix are compared to axes generated from the corresponding null matrix, the second biological gradient will appear much stronger in comparison to the second null axis, generating a much higher z score.

Coherence is measured by the number of gaps (absences) in species occurrence across and within communities when the metacommunity is ordered along the RA axes (Leibold & Mikkleson 2002). If this number of embedded absences was significantly different from that expected by chance (i.e. the mean number in the null incidence matrices), the distributions would be coherent, and otherwise the distributions would be random. I then used the results of the ordination to determine whether distributions showed spatial turnover (with species replacement throughout the matrix) or nestedness (with no replacement). It should be noted that the observed β -diversity loss does not equate to spatial turnover, as utilised within EMS analysis, which refers to turnover in space, *not* over time. Finally, boundary clumping was assessed with a chi-squared test of the difference between the observed Morisita's Index (Morisita 1959) and that from the expected distribution. A value that was significant and >1 would indicate clumped boundaries while <1 would indicate unclumped boundaries.

Results for each structural element of the two surveys are based on different null models because each null model is generated from a different

sized starting matrix. To enable comparison, I converted the embedded absences and species replacements for each survey into z scores. A z score ($z = (X - \mu) / \sigma$; where X = observed value, μ = mean, σ = standard deviation) represents the number of standard deviations from the mean and is the standard way of normalising variables to allow comparison (Shaw 2003). For my purposes, the experimental value is the actual number of embedded absences or species replacements, and the mean and standard deviations are the embedded absences and species replacements obtained from the 1,000 null matrix simulations. The difference in z scores was deemed significant if scores were separated by twice the standard deviation (i.e. $2 \times 1.96 = 3.92$). Although the z scores for the secondary axes were much further from the mean, this does not invalidate the comparison between z scores on that axis between surveys. Unfortunately, this technique for comparison was not possible for use on Morisita's index because the index is not based on null matrices. Therefore I could not assess significance of change for this structural element.

5.3.3. Structuring mechanisms

To determine the structuring mechanism of the 2008 metacommunity I performed Spearman's rank correlations between RA sample scores for axes 1 and 2 (i.e. the order of community arrangement along the dominant axes of variation) of the 2008 metacommunity, and environmental and spatial predictor variables. The necessary spatial and environmental data were not available for the 1930s. Because the analyses involved multiple correlation tests on the same data sets, significance levels were assessed in light of a Dunn-Šidák correction for experiment-wise error ($\alpha_e = 1 - (1 - \alpha_r)^{1/k}$; where α_e = new significance value, α_r = the required significance value, and k = number of independent tests).

Environmental and spatial independent variables were calculated using ArcGIS v. 9.2 (ESRI 2006). Good's patches were often part of a larger woodland, therefore, I used the characteristics of that encompassing woodland. Woodland distribution was based on current maps from the

National Inventory of Woodland and Trees provided by the Forestry Commission (www.forestry.gov.uk/inventory). A point layer was created with a centroid for each woodland patch polygon and used the intersect tool to obtain soil and topographic data for community environmental variables. Variables used were soil acidity, soil texture, soil fertility, drainage (all obtained from the National Soil Resources Institute 1:250,000 NATMAP data) and elevation (as a proxy for multiple climatic variables). Elevation was determined for each patch centroid with OS map contours, taking the lowest contour if the patch centroid fell between contour lines. I used Hawth's Analysis Tools (Beyer 2004) to calculate woodland area, perimeter, and isolation (i.e. distance to the nearest woodland), and from these calculated the perimeter:area ratio to represent shape (the smaller the ratio, the more compact the shape).

5.4. RESULTS

There was no significant correlation between temporal species turnover and woodland area ($r_s = 0.099$, $p = 0.365$). The geographic distance between patch centroids and pair-wise community similarity were not significantly autocorrelated in the 1930s ($r = -0.038$; $p = 0.802$) or in 2008 ($r = -0.136$; $p = 0.990$). The proportion of species that were woodland specialists in the 1930s was 0.13 and in 2008 was 0.15. Of those species that became significantly more widespread (McNemar's test, $p < 0.05$), 40% were woodland specialists. There was no significant difference in the number of patches occupied by woodland specialist species during each survey ($U = 2327.5$; $p = 0.730$).

Table 7. Elements of metacommunity structure in the 1930s and 2008 on primary and secondary ordinated (reciprocal averaging) axes. Means and standard deviations (S.D.) are calculated from 1,000 iterations of a null matrix created with a conservative fixed-fixed approach. *P* values represent the significance of the difference between actual number of embedded absences and mean number of embedded absences in the null matrices. EA = embedded absences; R = species replacements; MI = Morisita's Index. Significant *p* values (<0.05) are in bold. Z scores are only supplied for the primary axis.

		1930s		2008	
		Axis 1	Axis 2	Axis 1	Axis 2
Coherence	EA	16,794	17,071	12,069	11,875
	Mean	18,159	20,639	12,617	15,162
	<i>p</i>	< 0.001	< 0.001	< 0.001	< 0.001
	S.D.	370.5	160.8	245.3	96.4
	z	-3.68	-22.19	-2.23	-34.10
Spatial turnover	R	4,862,634	5,136,554	3,019,872	2,334,853
	Mean	4,204,400	3,386,600	1,865,900	1,879,900
	<i>p</i>	0.017	< 0.001	< 0.001	0.004
	S.D.	316,320	269,030	165,770	169,990
	z	2.08	6.50	6.96	2.68
Boundary clumping	MI	2.25	2.60	3.31	3.06
	<i>p</i>	< 0.001	< 0.001	< 0.001	< 0.001
Best fit structure		Clementsian	Clementsian	Clementsian	Clementsian

5.4.1. Metacommunity structure

The EMS analysis suggested that woodland metacommunity structure was Clementsian at both survey times, demonstrated by significant coherence, spatial turnover in space and species range boundary clumping (Table 7). Coherence was indicated by a significantly lower number of embedded absences than the mean of the null simulations. Spatial turnover was significantly more than the null simulations, indicating that structure was not nested. In all cases Morisita's index was significantly different from the

expected distribution of boundaries and the direction of the value suggested clumping of species range boundaries.

5.4.2. Structural elements

Although metacommunity structure maintained a Clementsian gradient, there were changes in magnitude of individual structural elements indicated by the change in z scores (Table 7). There was no significant change in the number of embedded absences on the primary axis over time, indicating no change in coherence. In contrast, the secondary axis showed fewer embedded absences, indicating significantly increased coherence, changing by > 6 standard deviations from a z score of -22.19 to -34.10. Despite this, lack of change on the primary axis suggests this may be due to a statistical artefact. Number of species replacements between communities was significantly higher in the resurvey than in the historical survey on the primary axis according to the change in z scores, indicating an increase in spatial turnover along the first structuring gradient. However, the secondary axis demonstrated the opposite pattern whereby spatial turnover significantly decreased along the second structuring gradient. Morisita's index demonstrated highly significant species range boundary clumping within both surveys.

5.4.3. Structuring mechanisms

The primary axis for the 2008 survey was not correlated with any of the spatial variables, but of the five environmental variables, the axis was significantly correlated with soil drainage ($r_s = 0.422$, $p < 0.001$) and soil fertility ($r_s = -0.443$, $p < 0.001$) (Table 8). In contrast, the secondary axis was not correlated with any of the environmental variables, but was correlated with two spatial variables, namely woodland area ($r_s = 0.347$, $p = 0.001$) and perimeter:area ratio ($r_s = -0.381$, $p < 0.001$).

Table 8. Spearman's rank correlations for RA axes scores, and spatial and environmental variables. Significant p values (Dunn-Šidák correction indicates p value of 0.006 required for original significance of 0.05) are in bold.

	Axis 1		Axis 2	
	r_s	p	r_s	p
Spatial variables				
Area	0.130	0.233	0.347	0.001
Perimeter	0.203	0.060	0.267	0.013
Perimeter:Area	0.108	0.321	-0.381	< 0.001
Nearest patch distance	0.082	0.451	0.192	0.076
Environmental variables				
Acidity	-0.278	0.009	0.090	0.412
Texture	0.004	0.974	-0.134	0.217
Drainage	0.422	< 0.001	-0.142	0.192
Fertility	-0.443	< 0.001	-0.013	0.906
Elevation	-0.219	0.043	0.039	0.721

5.5. DISCUSSION

5.5.1. Metacommunity structure

The woodland vascular plant metacommunity maintained a Clementsian structure at two discrete points in time 70 years apart, despite significant β -diversity loss through taxonomic homogenization (Keith et al. 2009a). This is the first time temporal change in metacommunity structure has been assessed in plants. Lack of a significant relationship between temporal species turnover and patch area suggested that the results were not attributable to sampling effort differences where larger patches were searched for longer periods. The longer searching times during the re-survey in comparison with the historical survey could have led to sampling bias which might have led to increased coherence and decreased spatial turnover as a greater number of species may have been discovered and recorded. However, the results indicate that coherence did not change and spatial turnover increased over time, which suggests that the difference in sampling

effort did not bias the results. In addition, woodland specialist species did not greatly decrease in proportion over time relative to generalist species.

Metacommunity structure was Clementsian on both axes, indicated by significant coherence, spatial turnover and species range boundary clumping. Clementsian structure reveals that the metacommunity is organised into specific community types and species occur together with high fidelity (Clements 1916). A Clementsian structure was similarly identified for Paraguayan bats (Presley et al. 2009) and larval odonates (McCauley et al. 2008) at single points in time, using the same method as that employed here. In contrast, analyses of a tropical rock pool invertebrate metacommunity indicated a nested structure that remained stable over twelve years (Azeria & Kolasa 2008). A terrestrial gastropod metacommunity was also found to have a stable nested structure over thirteen years, however the degree of nestedness was reduced by hurricane disturbance (Bloch et al. 2007). Results from the few studies that have examined metacommunity dynamics over time are therefore consistent with those of the current investigation in that they indicate stability. However, this is the first investigation that has documented unchanged metacommunity structure during biodiversity loss.

A Clementsian structure requires presence of distinct community types as groups of species respond in a similar way to structuring factors. The cause of distinct woodland vascular plant community types throughout the study area (Dorset) is most parsimoniously explained by high geodiversity, in particular, the broad spectrum of acidic to calcareous soils (Dorset County Council 2005). Such soils are associated with particular types of plant communities (Rodwell 1991) and this is supported in this study by significance of soil acidity as a component of the dominant axis of variation. Another explanation is that different woodland management strategies (e.g. coppicing, maintenance of high-forest) have been a more influential factor in generation of different woodland community types. Traditional woodland management has declined across Britain over recent decades (Kirby et al. 2005), potentially explaining loss of a particular subset

of ‘managed’ woodland community types. Although there is no direct support for this hypothesis, lack of autocorrelation amongst woodland communities supports a spatially idiosyncratic mechanism such as this.

5.5.2. Structural elements

I reject the hypothesis for both axes that coherence decreased, as indicated by the z score comparison and consideration of statistical issues. Generalist species did not greatly increase in proportion over time. Of species that significantly increased in patch occupation from the historical dataset, 40% were woodland specialists, despite the fact that proportion of woodland specialists over the whole metacommunity was only 0.15. This may reflect changing management history of woodlands in Dorset. A decrease in frequency of disturbances would benefit woodland specialists that require shaded conditions.

Spatial turnover increased significantly over time causing metacommunity structure to become less nested. Therefore hypothesis 3 must be rejected. In a nested pattern, species are lost or gained from one community to another and so species swapping cannot occur (Leibold & Mikkleson 2002). The reduced species pool and increased inter-community similarity in a situation of taxonomic homogenization would result in less frequent swapping of species. However, a convergence in species richness of communities, also observed for this metacommunity (Chapter 3; Keith et al. 2009a), would simultaneously reduce incidence of species loss or gain from one patch to another because nestedness would be reduced. Therefore, it is feasible that these two changes could interact to produce increased spatial turnover. I reject the hypothesis that species clumping decreased over time, indicated by Morisita’s index.

Continuation of a Clementsian structure in the face of biodiversity loss can therefore be explained by two key points. (1) Homogenization resulted in communities that were a subset of those types represented within the historical data and were not novel, non-analogous communities (Keith et al. 2009a; Keith et al. 2009b). Therefore, distinct community types were

retained within the metacommunity but number of types decreased (Keith et al. 2009a). (2) Species replacements became more frequent in space because a convergence of species richness among patches outweighed reduced number of replacements as a result of a smaller species pool and greater similarity between communities. Therefore, metacommunity structure is not simply a function of the species pool but is the outcome of inter-patch relationships and multiple ecological processes (Hillebrand & Matthiessen 2009).

5.5.3. Structuring mechanisms

Factors contributing to structure of the 2008 metacommunity differed on primary and secondary axes, but both were coherent and indicated multiple biologically-important gradients. Primary axis sample scores were correlated with environmental variables of soil drainage and soil fertility. Therefore, environmental factors contribute to Clementsian structure of the metacommunity. Environmental factors were also found to have a significant structuring effect on: a zooplankton metacommunity subjected to experimental manipulations of macroalgal cover and fish predation (Cottenie & De Meester 2004); a bat metacommunity that was influenced by temperature and precipitation (Presley et al. 2009); and at multiple spatial scales in a reef-fish metacommunity (MacNeil et al. 2009). In contrast, the secondary axis was correlated with spatial variables; namely area and shape (area:perimeter), whilst sharing no correlation with environment. This opposing result is not unexpected because RA axes are orthogonal (Hill 1973). Lack of significance in distance to nearest woodland patch is consistent with lack of autocorrelation, and indicates that spatial configuration at the scale of individual woodlands rather than the entire metacommunity is the important factor.

Significant coherence demonstrated on both axes therefore suggests that both environmental and spatial factors contribute to metacommunity structure. Multiple structuring mechanisms of environmental and spatial factors were also observed in freshwater diatom (Verleyen et al. 2009) and

pond snail (Zealand & Jeffries 2009) metacommunities. In the diatom metacommunity, the importance of spatial factors increased as spatial scale was extended (Verleyen et al. 2009), a pattern that could usefully be explored in other metacommunities such as that described here. The results also provide evidence that large-scale biodiversity patterns are influenced by multiple local factors and that EMS methodology permits rigorous description of these features.

5.5.4. Conclusion

This analysis has demonstrated that a woodland metacommunity has a Clementsian structure at two points in time 70 years apart, despite significant γ - and β -diversity loss. This suggests that broad Clementsian metacommunity structure is robust to diversity loss, however, individual structural elements did change. Difference in spatial turnover demonstrated on axes one and two highlights that multiple processes can simultaneously contribute to metacommunity structure. This complexity is further accentuated by association of axes 1 and 2 with different structuring mechanisms and suggests that future metacommunity analyses would be strengthened by consideration of multiple structural and mechanistic hypotheses.

Lack of change over time in metacommunity structure reveals that it may not be a useful indicator for broad conservation status. On the other hand, continuity of structure suggests that knowledge of structural type could assist in long-term conservation planning because it provides insights into fundamental processes that influence landscape-scale community organization.

For a broader critique of the metacommunity concept I refer the reader to section 7.4.2. within Chapter 7 (p. 176).

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Chapter 6

Larval dispersal of rocky shore invertebrates

Part I. Individualistic species limitations of climate-induced range expansions generated by meso-scale dispersal barriers

6.1. ABSTRACT

Evidence indicates that species are responding to climate change through distributional range shifts that track suitable climatic conditions. I aim to elucidate the role of meso-scale dispersal barriers in climate tracking responses. Historical distributional data were obtained for five intertidal invertebrate species on the south coast of England (the English Channel). I logistically regressed these data on sea surface temperature to determine a climate envelope. This envelope was used to estimate the expected climate tracking response since 1990 along the coast and this was compared with observed range expansions. A hydrodynamic modelling approach was used to identify dispersal barriers and explain disparities in expected and observed climate tracking. Range shifts detected by field survey over the past 20 years were less than those predicted by the changes that have occurred in sea surface temperature. Hydrodynamic model simulations indicated that physical barriers produced by oceanic circulation have variably restricted dispersal of pelagic larvae among the five species. I provide the first evidence that meso-scale hydrodynamic barriers have limited climate-induced range shifts, and demonstrate that life history traits affect the ability of species to overcome such barriers. This suggests that current forecasts may be underestimating the potential impacts of climate change on global biodiversity.

6.2. INTRODUCTION

Climate change is widely recognised as presenting a major threat to global biodiversity that is expected to intensify over time (Rosenzweig et al. 2007). Evidence indicates that species are responding to this threat through changes in behaviour (Post et al. 1999), phenology (Sims et al. 2001) and abundance (Barbraud & Weimerskirch 2001), with consequences for community composition (Hiddink & ter Hofstede 2008; Holbrook et al. 1997; Walther et al. 2002). The distributional range of many species also appear to be shifting to track suitable climatic conditions through space and time (Mieszkowska et al. 2006; Walther et al. 2005). Future projections of climate-induced range shifts indicate massive potential biodiversity loss as suitable climatic envelopes for many species decreases (Thomas et al. 2004; Thuiller et al. 2005). Forecasts suggest that 21–52% of species will be “committed to extinction” owing to non-viable populations by 2050 on a global scale (Thomas et al. 2004).

Such projections are based on bioclimatic envelope modelling approaches that predict distributions of species based on the concurrent distribution of suitable climatic conditions. Such approaches do not realistically incorporate dispersal, which is a process fundamental to shifts of range boundaries (Gaylord & Gaines 2000; Southward 1967; Wetthey & Woodin 2008). Although bioclimatic envelope models are beginning to incorporate more realistic dispersal in terms of maximum dispersal distance (Midgley et al. 2006), information is lacking on the potential role of physical barriers in impeding dispersal. I am unaware of any previous studies that have demonstrated the inhibitory nature of physical dispersal barriers on climate-induced range shifts of species, although the remarkable stability of range edges of some species of barnacles in the focal area of study, the eastern English Channel, has been demonstrated (Herbert et al. 2009). I address this critical knowledge gap through a field-based analysis of five intertidal invertebrate species, supported by a hydrodynamic modelling approach.

Until the last decade, marine environments were considered to have unrestricted or ‘open’ exchange of propagules amongst populations. In

contrast, recent evidence has suggested that this assumption is simplistic and often inaccurate as there is a continuum from fully open to fully closed populations (Cowen et al. 2007; Cowen et al. 2000; Hill 1990; James et al. 2002; Jessopp & McAllen 2008; Largier 2003; Lefebvre et al. 2003; Mitarai et al. 2008). This has served to highlight the importance of connectivity, which can be defined as representing “..the dynamic interactions between geographically separated populations via the movement of individuals” (North et al. 2009). Many marine species achieve propagule dispersal through pelagic larvae that are exchanged with other populations by water movements on a variety of scales from local tidally mediated flow up to oceanic currents (Nybakken & Bertness 2005). Some larvae, for example, those of crustacea and fish, are capable of active swimming and hence vertical positioning behaviour in the water column (Sponaugle et al. 2002). Even for swimming larvae, however, when currents exceed the swimming speed, advection and diffusion become the prominent factors controlling larval transport. Therefore, hydrographic features are of great consequence to the connectivity of populations for species with a planktonic larval phase.

Attention has focused in recent years on larval transport (Gaines et al. 2007; Kinlan & Gaines 2003; Pineda et al. 2007), building on earlier studies (Crisp 1985; Scheltema 1968). Most research has relied on the use of hydrodynamic models within which one can introduce particles from areas of suitable habitat and track their movement. To date, such research has focused on model development and the creation of marine protected areas (e.g. Colby 1988; James et al. 2002; Mitarai et al. 2008); few analyses have applied such models to ecological questions related to climate change. I begin to address this gap by utilising a hydrodynamic modelling approach to elucidate observed range expansions of intertidal invertebrate species in the English Channel along the south coast of England.

I combined historical and recent species distribution data to examine range expansions of intertidal invertebrate species along the south coast of England. The area is highly suitable for this analysis because it is a biogeographic boundary zone between warm-temperate and cold-temperate waters (Crisp & Southward 1958; Herbert et al. 2009). The region has a sea surface temperature (SST) gradient that declines from the western to eastern

Channel. Over the last two decades SST has increased along this gradient as a result of climate change (Joyce 2006), resulting in previously unsuitable eastern sites becoming climatically suitable for warm-temperate species. As a consequence, eastward range expansions of southern intertidal invertebrate species have been observed (Herbert et al. 2003; Mieszkowska et al. 2006; Mieszkowska et al. 2005; Wethey & Woodin 2008), whereas northern species have stayed constant (Herbert et al. 2009). I used this information to assess whether physical barriers have limited climate-induced range shifts, by testing the following hypotheses: (1) species ranges have not expanded to all areas that are climatically suitable and therefore have not fully tracked SST change; (2) connectivity amongst suitable rocky shore habitat patches is interrupted by barriers to larval transport and; (3) these barriers coincide with 2009 species range boundaries, indicating hydrographic features have posed significant barriers to larval transport.

6.3. METHODOLOGY

6.3.1. Study area

The study area on the south coast of Great Britain extends from Start Point in the west (50.2139°N, 03.6936°W) to Dover in the east (51.1558°N, 01.3937°E), a coastline distance of approximately 720 km. The area is characterised by a complex coastline with strong prevailing winds from the west and south-west (Barne et al. 1996a; Barne et al. 1998a; Barne et al. 1996b; Barne et al. 1996c; Barne et al. 1998b; Southward et al. 1995). In the English Channel, sea surface temperature (SST) has been highly variable since 1950, with a cool period from the early 1960s to the mid 1980s and a clear increase over the last decade (Hawkins et al. 2009; Joyce 2006). Although North West European waters can be highly stratified (Austin et al. 2006), SST represents water column temperatures because neritic waters are well-mixed. This region also encompasses the northern range boundary for southern warm temperate species at the edge of their thermotolerance (Crisp & Southward 1958; Lewis 1964; Southward et al. 1995).

6.3.2. Species distribution data and temperature envelopes

Species range boundary location data before and after 1990 were collated for five species that were known to have range boundaries eastwards of Lyme Regis (50.7080°N, 02.9764°W) along the south coast (Fig. 11) and to represent different pelagic larval durations (MarLIN 2008).

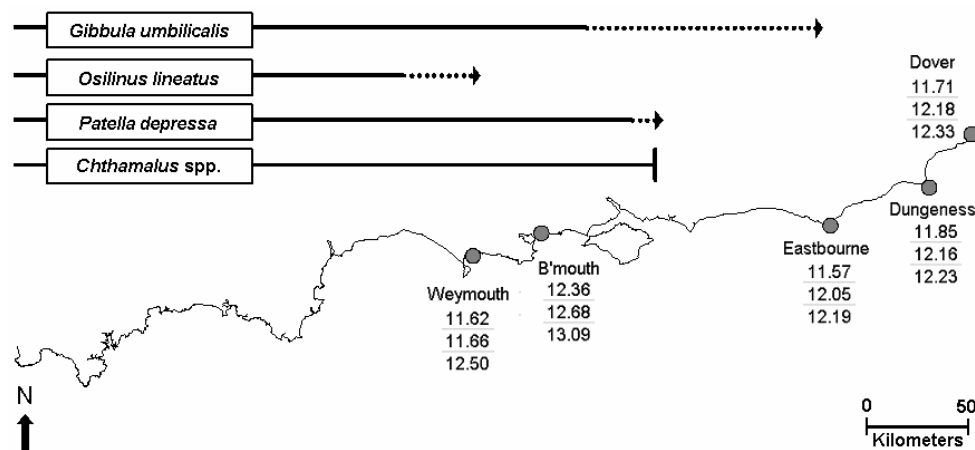


Fig. 11. Range extent of four warm temperate intertidal rocky shore invertebrate species along the south coast of England (Hawkins et al. 2009; Herbert et al. 2009; Mieszkowska et al. 2006). Solid line = range extent to before 1990; dotted line = eastwards range expansion 1990-2009. *Chthamalus* spp. experienced no range expansion during this period. Grey circles are locations of CEFAS monitoring stations along the south coast used to predict expected range boundaries. Numbers listed below the locations are annual mean sea surface temperatures (SST) in degrees centigrade for, from top to bottom, time-averaged periods of 1991-1995, 1996-2000, 2001-2004. Frequency and length of monitoring varies amongst stations.

These species were the molluscs *Gibbula umbilicalis* (larval duration ≤ 7 days), *Osilinus lineatus* (larval duration ≤ 7 days) and *Patella depressa* (larval duration ≤ 14 days) and barnacles *Chthamalus montagui* and *C. stellatus* (larval duration ≤ 28 days). The barnacles have similar range boundaries and have been combined. Despite differences in the estimated pelagic larval duration of the barnacles (Burrows et al. 1999), both represent an extended larval phase relative to the other three species. Range boundary data were collated from published literature (Hawkins et al. 2009; Mieszkowska et al. 2006) and field surveys conducted in 2008-2009 that involved 5 x 3 minute searches for *Osilinus* and *Gibbula* and quadrat surveys for *Patella* and *Chthamalus montagui* and *C. stellatus*. I defined the edge of the range as the most easterly breeding population. Range expansion was examined from 1990 for two reasons: (1) 1961-1990 baseline climate data is a widely accepted time average (Jenkins et al. 2009) because the constant trend of rising SST began after 1990, supported by the use of these data as a baseline for all UKCP09 future forecasts (Murphy et al. 2009) and, (2) recent SST data were only available up to 2004.

Temperature boundaries were determined for each of the four species based on the pre-1990 distribution and UKCP09-derived SST data time-averaged for 1961-1990 at a resolution of 12 km (Lowe et al. 2009). Shapefiles were interpolated using nearest neighbour to produce a continuous surface of SST, and rocky shore centroids were intersected with this layer to determine SST at each shore during the historical time-averaged period. I tested which of three SST variables (mean annual SST, mean winter SST and mean summer SST) was the best indicator of historical species presence-absence with a point-biserial correlation (Tate 1954). This method is appropriate when one variable is dichotomous and the other variable is continuous. Only one of these variables was used to indicate distribution because there was very high multi-collinearity amongst them. Logistic regression was performed for species presence-absence regressed on the best indicator using the 'glm' function with binomial family in R (R Development Core Team 2008). The regression result was used to obtain the SST at a 0.5 probability of occurrence (where $SST_{0.5} = -\alpha/\beta$), which is a typical cut value (Pampel 2000). Using this cut value, here representing SST

tolerance, for southern species I predicted that species will be present at SST above the tolerance value and absent below.

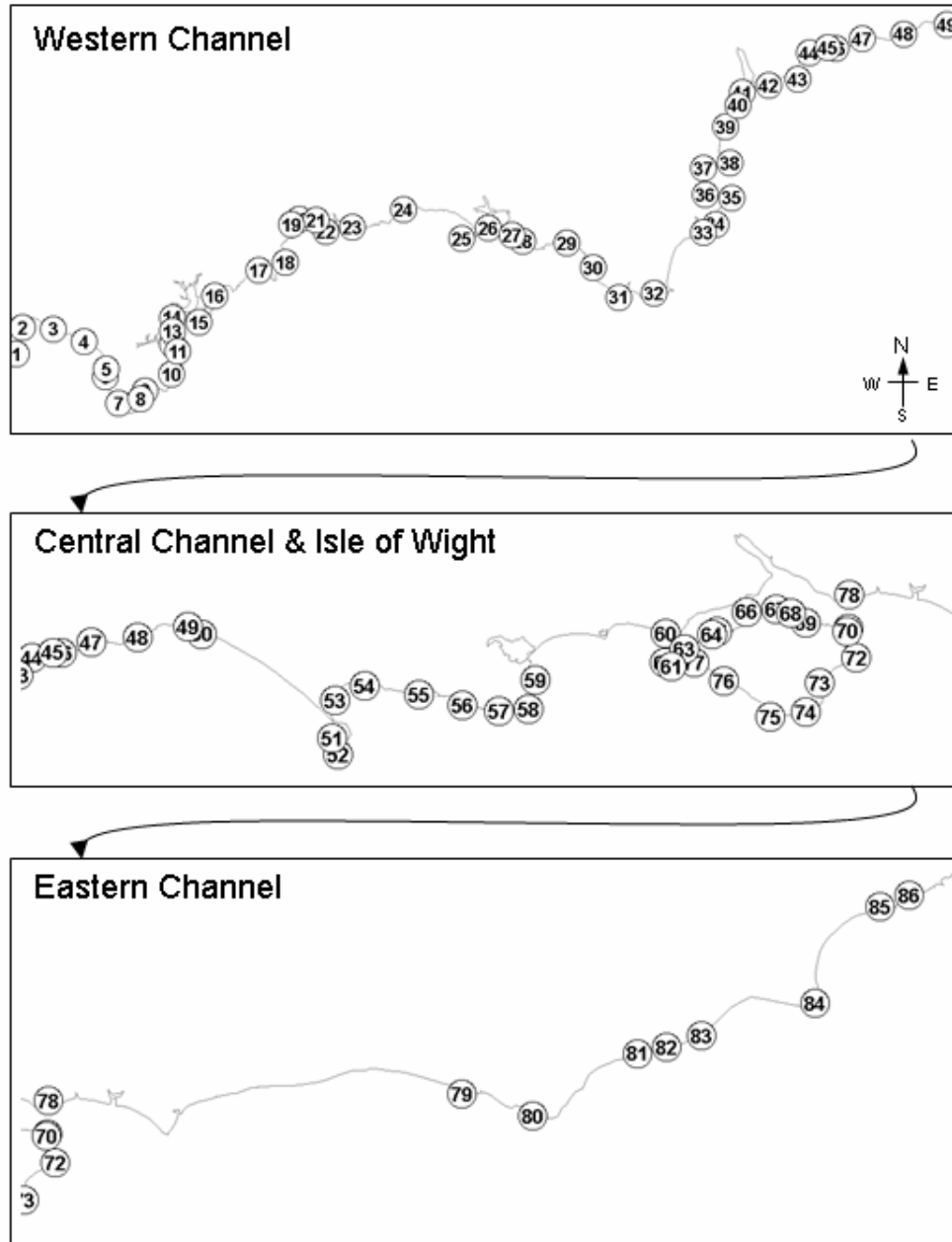


Fig. 12. Centroid locations of 86 rocky shore patches along the south coast of England from the western, central and eastern Channel. The centroid for each of these 86 patches were larval release locations within the particle tracking model simulations. Patches represented in panels overlap to provide full representation of the coastline.

To determine the expected distribution if species had effectively tracked the change in SST, I first calculated shortest geographic distance through water between all rocky shore patches digitally mapped within ArcGIS v.9.2 (Fig. 12; ESRI 2006). Mean speed of water flow was calculated from the hydrodynamic model (see below) and was combined with the shortest geographic distance and pelagic larval duration to establish potential connectivity of rocky shore populations in the absence of barriers. Finally, these tolerance values were combined with SST data for 1990 – 2004 to determine the expected distribution for three time-averaged periods: 1991-1995; 1996-2000; 2001-2004. Current SST was obtained from CEFAS (Joyce 2006). These point data are used by UKCP09 reports when exploring trends since the 1961-1990 baseline, and represent the best available for the area. The CEFAS SST data was obtained from five monitoring stations in the study region (Fig. 11), which from west to east were Weymouth; Bournemouth; Eastbourne; Dungeness and Dover.

6.3.3. Hydrodynamic model and particle tracking module

Hydrodynamics were simulated with a well validated and calibrated hydrodynamic model (ABP Marine Environmental Research 2008) supplied by ABP Marine Environmental Research Ltd (ABPmer) MIKE21 Flow Model version 2008 from the MIKE Zero software, as developed by the Danish Hydraulic Institute (DHI). Model bounds were 51°33'N 05°35'W, 51°15'N 03°00'E, 48°23'N 05°34'W, and 48°60'N 02°28'E. The resolution of the model was 1200 m x 1200 m. Model parameters included a time step of 30 secs and an eddy viscosity (μ) of $0.5 \text{ m}^2 \text{ s}^{-1}$ was used based on a velocity based Smagorinsky formula (Table 9). The projection used was the British National Grid OSGB_1936. The first 12 hours of the simulation were used as a necessary warm-up period. Bathymetry data were compiled from numerous sources and boundary conditions were derived from the Proudman Oceanographic Laboratory's CS3 continental shelf model. Use of the HD simulation offline within the particle-tracking module (PT) ensured standardised hydrodynamics for all PT simulations. Particles were released at a rate of 100 particles per time step (30 secs) for the first 50 minutes, so every time step after this tracked 10,000 particles.

Table 9. Hydrodynamic model parameter settings (ABPmer)

Parameter	Value or Range
Time-step	30 secs
Bed Friction (space varying Manning number)	17-40 m ⁻³ s ⁻¹
Eddy Viscosity (velocity based Smagorinsky formula)	0.5 m ² s ⁻¹
Flooding depth	0.3 m
Drying depth	0.2 m

Larval transport simulation was achieved with the MIKE 21/3 Particle-Tracking module (DHI), which uses a Lagrangian ‘random walk’ technique. The HD simulation was used offline to provide the advection term for the particle tracking module (PT), from a start point of 00:00:00 1st August 2009, coinciding with seasonality of larval production. I simulated release of 10,000 larvae from each of 86 rocky shore patch centroids along the south coast of England (Fig. 11). This model was suitable for studying larval transport because it included the minimal requirements for assessing connectivity, which are an accurate flow field, locations and time of larval release, location of potential settlement sites, pelagic larval duration, pre-competency and competency periods (North et al. 2009; Siegel et al. 2003). Larval mortality rate and specific numbers of larvae released from each site were not included in the model because of the large errors surrounding the estimated values.

Particle (larval) mass and horizontal dispersion coefficient were tested for sensitivity using simulations in which individual parameter values were varied. Sensitivity simulations were based on larval release from eight rocky shore source locations that were the shores used for recruitment surveys (see Appendix IV). The starting value for larval mass was based on 0.75 µg dry mass (minimum wet mass; O’Riordan 1992), which was then converted to wet mass using factor of 9.1 based on wet/dry ratio of zooplankton (Kjelson et al. 1975). This formulation yielded a larval mass of 6.825 µg. The sensitivity test was conducted over five orders of magnitude from 0.0625 µg to 682.5 µg. Initial horizontal dispersion is notoriously

difficult to determine without the use of extensive field-testing with drogues (Gawarkiewicz et al. 2007), therefore the initial value was set to $0.1 \text{ m}^2\text{s}^{-1}$ following expert advice (personal communication, HR Wallingford). The sensitivity test varied the dispersion coefficient over five orders of magnitude, from $0.01 \text{ m}^2\text{s}^{-1}$ to $100 \text{ m}^2\text{s}^{-1}$. This model was suitable for studying larval transport because it included the minimal requirements for assessing connectivity, which are an accurate flow field, locations and time of larval release, location of potential settlement sites, pelagic larval duration, pre-competency and competency periods (North et al. 2009; Siegel et al. 2003). Larval mortality rate and specific numbers of larvae released from each site were not included in the model because of the large errors surrounding the estimated values.

For further critique of the hydrodynamic model and its particle tracking module, I refer the reader to section 7.4.3 within Chapter 7 (p. 178).

6.3.4. Recruitment surveys and particle tracking validation

The particle tracking module was validated with *Chthamalus* spp. recruitment data for eight rocky shore patches. These were visited in June 2009 and 45 areas of 5 cm x 5 cm were cleared of adult barnacles at each of three tidal heights on each shore. On each shore I cleared 45 areas at five locations at each of three tidal heights on each shore. The clearings ensured that adult barnacles did not prevent recruitment through a lack of space – one of the key resources for sessile intertidal invertebrates. These sites were revisited during September and October 2009 following the August breeding season, during which time larvae would have completed the pelagic phase and settled. Cleared areas were digitally photographed within a quadrat and number of *Chthamalus* spp. recruits were later counted from these photographs.

During the validation process the observed recruitment was compared to expected recruitment according to the simulations combined with an estimated larval release for each shore. Such comparisons can provide highly consistent validation of larval transport models without explicit knowledge of larval origin (Werner et al. 2007). Estimated larval

release was calculated by estimating the area (actual length x 50 m), multiplying this by adult density per m², and then multiplying this by an expected brood size per adult of 1,000 larvae (Herbert et al. 2007). The settlement of larvae estimated for each of the eight shores and the recruitment were tested for rank order correlation with a Spearman's test.

6.3.5. Identification of dispersal barriers

The particle tracking simulation results provided the geographical location of each larva at each time step. From these data I extracted the larval locations from time steps for 5 – 7 days, 12 – 14 days and 26 – 28 days from the start of the simulation to represent the competent larval phases of the model species (MarLIN 2008). Larvae were, therefore, only recorded as enabling connectivity between populations if they reached the other rocky shore during the competent phase (Gaylord & Gaines 2000). Settlement on a shore was recorded if a particle moved within a 500 m buffer zone surrounding a rocky shore patch. Only the first patch reached within this competency period was recorded for each particle. Following the recommendation of North et al. (2009) this information was used to populate a matrix where sources (*i*) were across the top of the matrix and endpoints were down the side of the matrix (*j*), with number of larvae from patch *i* that reach patch *j* at a competent larval stage recorded in cell *i,j*.

This matrix was converted to a transition probability matrix (TPM) by dividing the number of particles by 10,000. I created a TPM for each pelagic larval duration (North et al. 2009). The TPMs were used to create three corresponding networks using a combination of Pajek (Batagelj & Mrvar 1998) and the 'igraph' package (Csadri & Nepusz 2006) in R. The use of networks to assess connectivity is increasingly advocated as an appropriate tool for use in ecological studies (Treml et al. 2008; Urban & Keitt 2001). The networks provided a visual representation of connectivity amongst rocky shore patches and were assessed for the number of network components, which are self-contained sections of the network. The number of larval transport barriers equals the number of components minus 1.

6.4. RESULTS

6.4.1. Climate tracking

Point biserial correlation coefficients indicated that time-averaged SST data were highly related to pre-1990 distribution limits (Table 10). Mean annual SST was the best indicator of historical distribution for all species. The two topshells, *Osilinus lineatus* ($r_s = 0.876$, $p < 0.001$) and *Gibbula umbilicalis* ($r_s = 0.833$, $p < 0.001$), showed the highest correlation with mean annual SST, followed in order by *Patella depressa* ($r_s = 0.736$, $p < 0.001$) and *Chthamalus* spp. ($r_s = 0.509$, $p < 0.001$).

Table 10. Point biserial correlation coefficients (r_{pb}) and associated significance values. Significant results at $p < 0.001$ are marked in bold.

	<i>Osilinus lineatus</i>	<i>Gibbula umbilicalis</i>	<i>Patella depressa</i>	<i>Chthamalus spp.</i>
Annual mean SST (°C)				
r_{pb}	0.876	0.833	0.736	0.509
p	<0.001	<0.001	<0.001	<0.001
Winter mean SST (°C)				
r_{pb}	0.873	0.742	0.644	0.415
p	<0.001	<0.001	<0.001*	<0.001
Summer mean SST (°C)				
r_{pb}	-0.086	0.024	0.040	0.113
p	0.429	0.822	0.717	0.302

Logistic regression analysis provided a model with which to predict SST minimum tolerance values for species occurrence along the south coast (Fig. 13; Table 11). When these tolerance values were combined with 1990-2004 SST data, all four species were projected to occur along the entire southern English coast by 1996. The current distributions indicate that this is not the case, therefore, predicted species distributions based on annual mean SST have not been fulfilled.

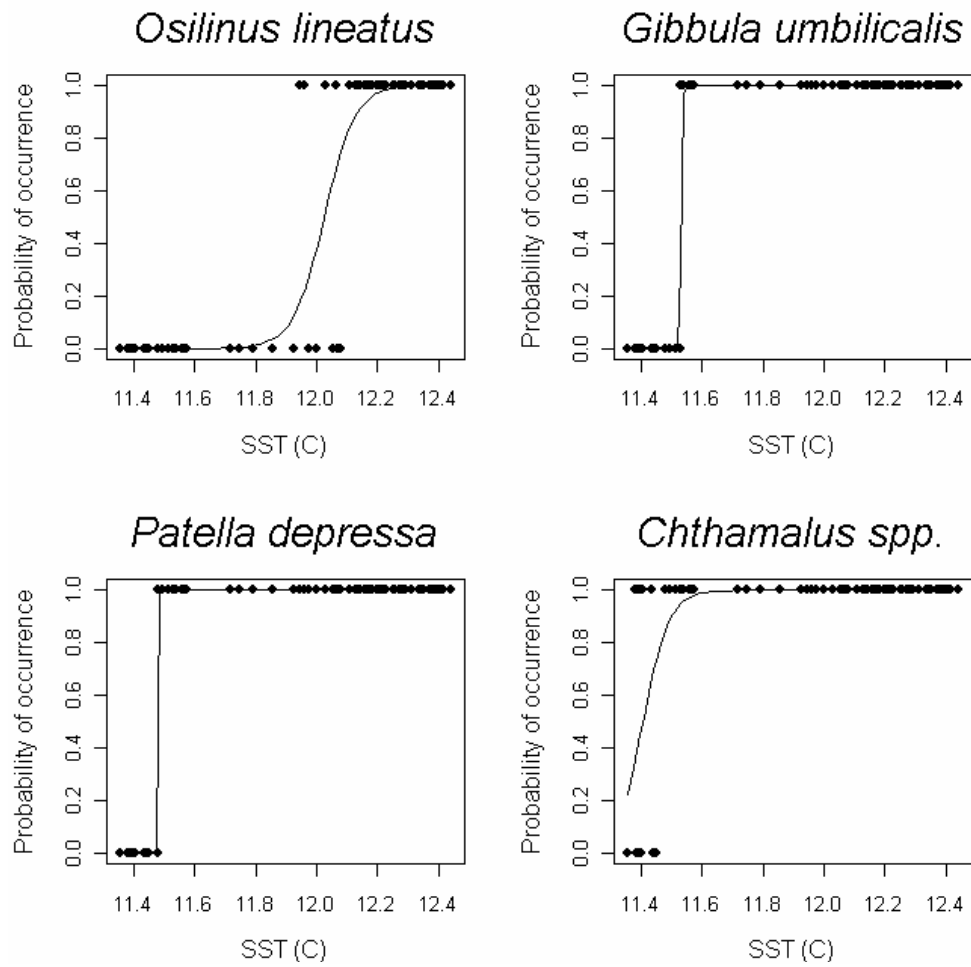


Fig. 13. Logistic Regression plots for all four species. Presence-absence of species is regressed on sea surface temperature (SST). The association of *Osilinus lineatus* with SST is not as clear cut as for *Gibbula umbilicalis* and *Patella depressa*. *Chthamalus* spp. occurs almost ubiquitously, therefore the regression line does not reach a probability of 0.

Table 11. Sea surface temperature (SST) tolerance values for the four study species according to logistic regression results and associated expected range expansions. Range expansion prevented is the percent of the expected range expansion that was not achieved.

Mean annual SST tolerance value (°C)	Expected range expansion (km)	Observed range expansion (km)	Percentage of expected range expansion achieved (%)
<i>Osilinus lineatus</i>			
12.03	384	63	16
<i>Gibbula umbilicalis</i>			
11.53	243	141	58
<i>Patella depressa</i>			
11.48	225	23	10
<i>Chthamalus</i> spp.			
11.41	202	0	0

6.4.2. Dispersal Barriers

Larval settlement of *Chthamalus* spp. predicted by the model was found to be significantly positively correlated with recruitment ($r_s = 0.786$, $p = 0.028$) observed in the field in 2009, providing verification of model output. The simulations indicated that there are hydrodynamic barriers to larval dispersal. The number of barriers reduced as pelagic larval duration increased (Fig. 14), as revealed by network analysis. For species with a PLD of 7 days there were 28 barriers, for 14 days there were 17 barriers and for 28 days there were 8 barriers. A particularly large barrier was found separating the eastern sites from all other sites. Model simulations demonstrate that this is due to a circular hydrodynamic feature (gyre) east of the Isle of Wight causing larvae to be deflected to sea rather than return to shore (Fig. 15). The larval transport barriers suggested by the model all coincided with species range boundaries, which are all located immediately westwards of a barrier.

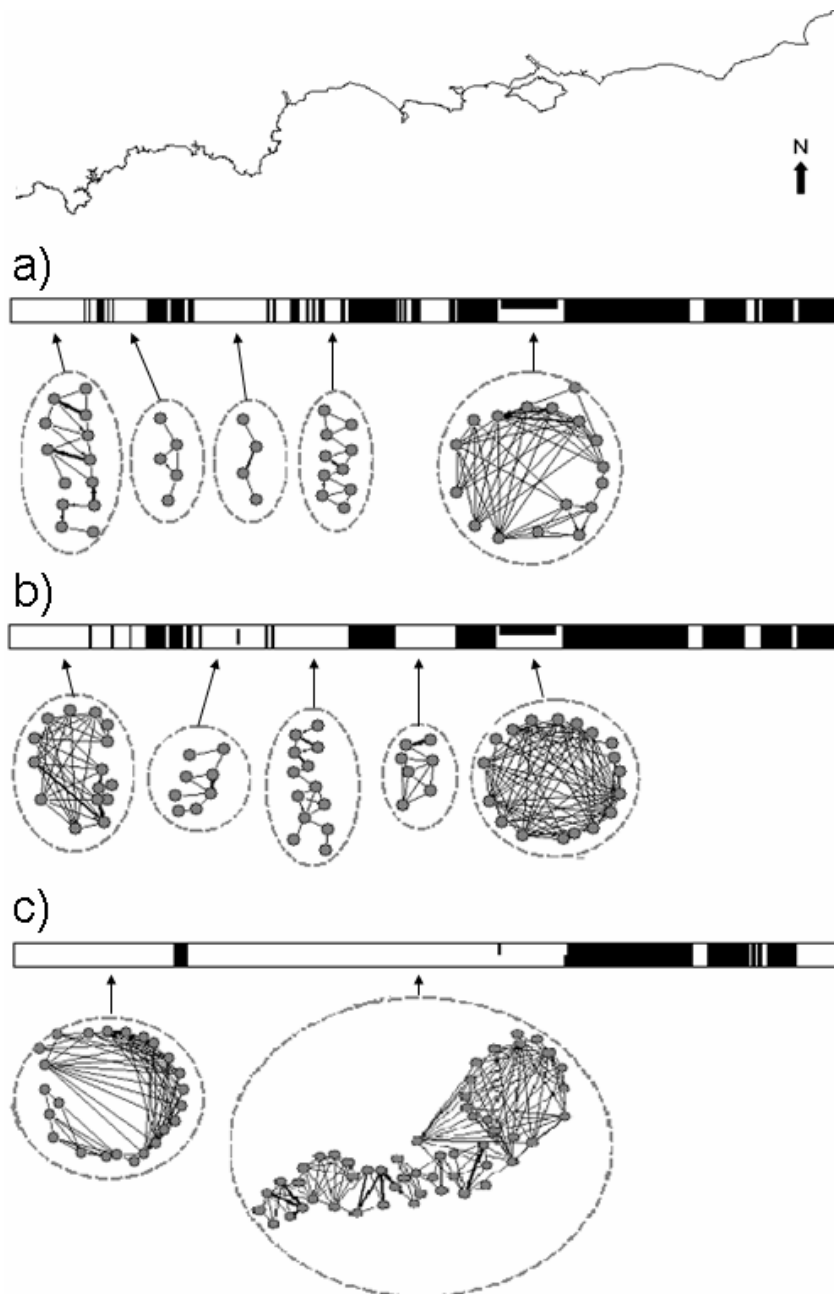


Fig. 14. Locations of larval transport barriers along the south coast of England for species with pelagic larval duration of a) 5-7 days (*Osilinus lineatus*, *Gibbula umbilicalis*), b) 12-14 days (*Patella depressa*) and c) 26-28 days (*Chthamalus* spp.). Barriers are represented in black along a bar that corresponds to the length of the English Channel with the coastline illustrated above. Black barriers that do not reach the top or bottom of the bar are those where one patch is unconnected but patches around it are connected to each other. Within the network, barriers are divisions between network components. Network components with ≥ 4 nodes are illustrated and are enclosed within a dashed line on the seaward side of the coastline with the approximate geographical location indicated with an arrow. The Isle of Wight is shown as a horizontally split section of the bar where the top section represents the coast above the Isle of Wight and the bottom section represents the Isle of Wight and waters to the south. Eastern Channel patches are not connected to any other patches.

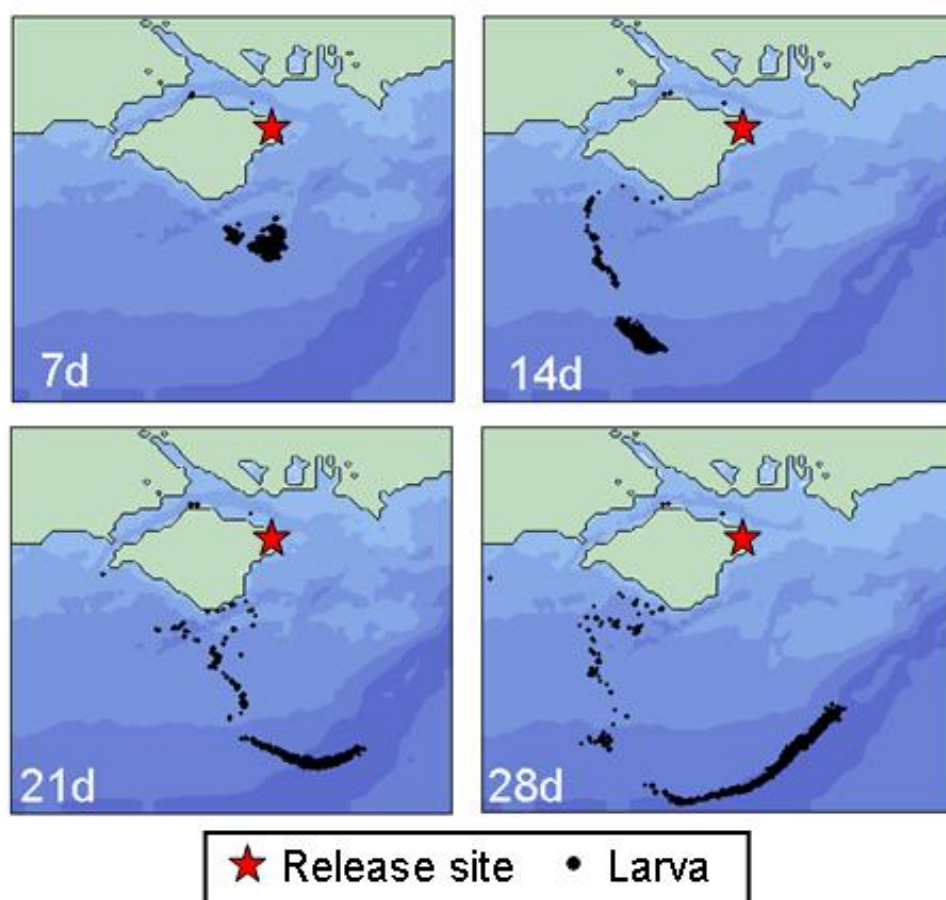


Fig. 15. Model output depicting movement of particles (black circles) at four points in time following release from rocky shore patch 72 (red star; Fig. S1) on the eastern tip of the Isle of Wight. Larval movement is influenced by a hydrodynamic barrier in the form of a gyre to the east of the Isle of Wight, which separates eastern Channel sites from all other sites. Larvae form an arc shape as the gyre creates a circular movement of water. Blue colours indicate water depth (light blue = shallow, dark blue = deep).

6.5. DISCUSSION

This study is the first to explicitly demonstrate long-suspected (Crisp & Southward 1958) limitations imposed by physical barriers to climate-induced range shifts of species, by a combined approach of long-term empirical data and hydrodynamic modelling. The results indicate that bioclimatic envelope models may be currently overestimating climate-induced range shifts by 42% to 100% over the 20 year timescale examined here. Therefore, bioclimatic envelope models are likely to have overestimated the ability of species to track climate change and underestimated the magnitude of the threat to biodiversity (Botkin et al. 2007; Pearson 2006). The potential magnitude of this effect is demonstrated by the analyses presented by Thomas et al. (2004) based on bioclimatic envelope modelling of a wide range of species. Their results suggested species loss of 21-23% when unlimited dispersal was assumed, which rose sharply to 38-52% with the assumption of zero dispersal. The analysis has also demonstrated the individualism of species responses according to differential life history traits, highlighting that connectivity is species specific.

In addition, it could be argued that the presence of dispersal barriers, as demonstrated here, could lead to underestimates of the ability of species to tolerate changing conditions. In the past, a species may have failed to reach a climatically suitable area owing to dispersal barriers preventing spread to all suitable locations from the site of speciation. This issue is routinely considered in the context of species richness gradients and has received much support (Willig et al. 2003). Therefore, climate envelopes based on current distributions without reference to dispersal barriers are likely to underestimate the extent of tolerable conditions.

The study species have not expanded to all climatically suitable areas according to logistic regression modelled on sea surface temperature (SST) and historical distribution. Therefore, I accept the hypothesis that these species have not fully tracked climate change. However, the use of one variable to create an envelope for the climate tracking analysis was not ideal (see section 7.4.3 of Chapter 7, p. 180) and the location of range

boundaries along an established gradient will inevitably lead to a correlation with species distribution, regardless of whether it is causal. Despite this, I am confident that in this case SST was the primary causal factor owing to previous analyses of range boundaries for these species that indicate SST-limited northern and eastern boundaries in Great Britain (Hawkins et al. 2009; Mieszkowska et al. 2006). The strongest evidence comes from the temporal ‘sign-switching’ (i.e. opposite responses to cooling and warming periods) demonstrated during the severe winter of 1962-63 when southern species experienced a southwards and westwards retraction of range boundaries (Crisp 1964) because this is a recognised diagnostic for climate change responses (Parmesan & Yohe 2003).

According to our model simulations, connectivity amongst rocky shore patches is interrupted by barriers to larval transport, indicated by the network analysis of model output. The most prominent barrier to the east of the Isle of Wight also coincides with a lack of suitable rocky shore habitat (Herbert & Hawkins, 2006). The relative importance of hydrodynamic barriers and habitat availability in determining range shifts is difficult to elucidate using the approaches adopted here, although clearly both factors could have been influential. Limitations in habitat availability can have strong effects on the ability of species to shift range distribution (Poyry et al. 2009). A coincidence of limited habitat availability and hydrodynamic features can potentially strengthen the impact of such barriers. However lack of habitat availability does not negate the hydrodynamic basis of this barrier, because animation frames of model output demonstrate that the hydrodynamic impact on the track of larval transport would prevent onshore settlement, even in the presence of suitable habitat.

Larval transport barriers suggested by the hydrodynamic model coincide with 2009 species range boundaries, which are all located immediately westwards of a barrier. This implies that hydrographic features have posed barriers to larval transport over the past 15 years, supporting previous suggestions that range borders can be limited by oceanographic boundaries (Byers & Pringle 2006). However, the strength of these barriers varies amongst species. *Osilinus lineatus* traversed the barrier of Chesil Beach and Portland Bill (patches 50 - 52) and *Gibbula umbilicalis* has

achieved larval transport into the eastern Channel (beyond patch 78). Both of these species have short pelagic phases and have experienced increased reproductive success with increased temperature at the northern range edge (Mieszkowska et al. 2007; Mieszkowska et al. 2006). The range expansion of these trochids may have been facilitated by a short pelagic larval duration. Byers & Pringle (2008) suggest this life history trait increases retention and decreases the influence of prevailing current, which in turn increases the likelihood of range expansions upstream. This is further supported as barriers to connectivity in the ocean are recognised as ‘leaky’ (Gaines et al. 2007; Gaylord & Gaines 2000). Rather than preventing all propagule movement, act by allowing greater flow of propagules in one direction than another (Gaines et al. 2007; Gaylord & Gaines 2000). In contrast, the longer larval durations of the limpet and barnacles experience a greater influence from meso-scale hydrodynamics, which in this case would transport larvae away from the coast and prevent range expansion. Once *G. umbilicalis* overcame the hydrodynamic barrier, the species would have been further inhibited by the lack of suitable rocky shore settlement sites in the vicinity. A possible explanation lies in the recent construction of artificial sea defences along this stretch of coast, which could potentially be used as additional habitat. *G. umbilicalis* has been observed on these structures, which have been previously suggested to facilitate range expansion, acting as stepping stones between rocky shores (Hawkins et al. 2009; Mieszkowska et al. 2006; Mieszkowska et al. 2005).

The limitations on the climate tracking response due to dispersal capability were suggested as a limiting factor in range shifts of Proteaceae in the Cape Floristic Region of South Africa (Midgley et al. 2006), and migration rates of tree species towards the end of the glacial period in Europe (Pearson 2006). Therefore, dispersal limitations based on maximum dispersal distance according to life-history traits have been demonstrated within these analyses. However, in these analyses, environmental barriers were not considered. This paper demonstrates that consideration of this additional factor can lead to the opposite outcome, whereby the species with shortest dispersal distance in fact has the greatest capacity for range expansion. Thus, in addition to consideration of maximum dispersal

distances, explicit consideration of dispersal barriers, and individualistic species responses to these barriers, is crucial to increasing the understanding of range shifts.

The crucial factor determining the number of dispersal barriers appears to be the pelagic duration of the dispersive larval stage of the species. However, increased connectivity with longer larval duration does not account for the influence of life history traits. This is clearly here because the species with the longest pelagic larval duration (*Chthamalus* spp.) was less able to overcome hydrodynamic barriers and track climate than species with short larval durations. Furthermore, other factors are likely to influence the ability of a species to settle successfully, for example, barnacle larvae settle gregariously and as a result may experience Allee effects.

Results suggest that hydrographic features can limit to the ability of species to track climate change and that these limitations are species specific. The widely held assumption that marine species will be able to track climatic change must be rethought and alternatives considered. Connectivity is dynamic and could be altered by climate change, for example, SST is negatively correlated with pelagic larval duration (O'Connor et al. 2007). Future climate change has the potential to modify dynamic barriers further through altered ocean currents, sea level rise and changing weather patterns (Solomon et al. 2007).

Bioclimatic envelope models should be improved through inclusion of physical barriers in addition to maximum dispersal distance, to increase their value for managing future threats to biodiversity. Greater awareness is also needed of the potential limitations of envelope models, which as noted here, could lead to either overestimation or underestimation of future range shifts, given the potential presence of dispersal barriers. In addition, these results demonstrated the individualism of species responses to climate change as a result of differential life history traits. Habitat connectivity is species specific, and this should be borne in mind when developing conservation strategies and plans (Grantham et al., 2003; Hodgson et al., 2009).

Part II. Sea level rise alters population connectivity of marine larvae

6.6. ABSTRACT

I demonstrate that projected sea level rise may alter larval connectivity among marine populations. I used a hydrodynamic modelling approach to simulate larval dispersal and tested the impact of bathymetric changes, comparing low and high scenarios for 2050 to 2009. Bray-Curtis similarity coefficients and network analysis demonstrated that connectivity between populations of rocky shore invertebrates increased with projected sea level rise in the English Channel, dependent on the duration of the pelagic larval phase. Sea level rise is therefore likely to affect patterns of distribution of pelagic species within four decades.

6.7. INTRODUCTION

Impacts of sea level rise on biodiversity have been little explored in comparison with other aspects of climate change. However, estimates of the magnitude of projected sea level rise are being rapidly revised upwards (Rahmstorf 2007), emphasizing the importance of evaluating its potential impacts on biodiversity. Whilst analyses of the impact of sea level on reduction of intertidal habitat area are readily available (Keller et al. 2009; Virah-Sawmy et al. 2009), to my knowledge, no analyses have addressed the potential impacts of forecasted sea level rise on larval transport and the connectivity of marine habitats. This suggests there is a critical knowledge gap regarding projected effects of sea level rise on marine realms beyond the intertidal.

The consequences of sea level rise on marine realms are most likely to be experienced through an impact on connectivity. Recent evidence has demonstrated that species within marine populations lie on a continuum from fully open, connected populations to fully closed, unconnected populations (Cowen et al. 2007). Connectivity is an essential requirement for ensuring continued propagule supply for sink populations and the

persistence of metapopulations (Cowen et al. 2007). Munday *et al.* (2009) suggested that sea level rise could alter local current patterns on reef flats, subsequently affecting larval connectivity. To my knowledge, sea level rise has received no research attention in the context of connectivity.

Here I determine whether sea level rise will alter population connectivity in the English Channel, by testing the hypothesis that simulations of larval connectivity for species with varying pelagic larval durations (time spent in water column prior to settlement) with hydrodynamics modelled with sea level observed in 2009 are different to those modelled on low and high UKCP09 emission scenarios for 2050 sea level rise. I then use network analysis to further quantify differences in connectivity with increasing sea level, to test whether changes would be observed in (i) larval exchange, (ii) the number of connections into and out of rocky shore patches, (iii) the number of larvae supplied and received by each rocky shore patch, and (iv) the number and location of cut-nodes in the network.

6.8. METHODOLOGY

For information on the hydrodynamic modelling approach, including validation and sensitivity analysis, see Chapter six Part I and Appendix IV. Sea level rise projections were incorporated into the model by increasing the bathymetry at all grid cells by the projected value for UKCP09 low (+ 190 mm) and high (+ 270 mm) emissions scenarios (Lowe et al. 2009) for the year 2050 for the south coast of England. Particle tracking simulations were run for the three scenarios, from 86 rocky shore patches, releasing 10,000 particles in each simulation. Mean proportion of larvae exchanged between rocky shore patches during larval competency windows (i.e. larvae capable of settlement) for three pelagic larval durations (PLD; 7 days, 14 days, 28 days) were recorded.

6.8.1. Connectivity and network analysis

Results from the particle tracking simulations were used to complete transition probability matrices (TPM) for each scenario for three pelagic

larval durations, assuming larval competency in the final two days of the larval phase (5-7 days, 12-14 days, 26-28 days). The nine TPMs (2008 x 3 PLDs, 2050 Low x 3 PLDs, 2050 High x 3 PLDs) were tested for any differences by determining the Bray-Curtis similarity coefficient (Clarke et al. 2006), where similarity amongst the three sea level scenarios based on cell values (i,j) were compared for each larval duration.

TPMs were imported to Pajek (Batagelj & Mrvar 1998) and R (R Development Core Team 2009) to create connectivity networks (Treml et al. 2008). Networks consisted of nodes (rocky shore patches) and edges (directed probability of connectivity i.e. proportion of released larvae exchanged). To determine the effect of sea level rise on the network, metrics were calculated for individual nodes on edge strength (mean strength of edges connected to that node), node betweenness (number of edges connected to that node), larvae received and larvae supplied. Wilcoxon tests were used to compare these metrics amongst the networks. Global network metrics were also compared, namely total number of edges (indicating larval exchange between patches), number of network components, proportion of nodes with loops (indicating larval retention), and proportion of reciprocated edges (indicating two-way larval exchange). Cut-nodes, when removed from the network, cause division of a component. I identified cut-nodes that created bi-components of ≥ 3 to ensure that this represented substantial disruption to the network (O'Connor et al. 2007).

6.9. RESULTS

Bray-Curtis similarity measures demonstrate differences between the scenarios for 7, 14 and 28 day pelagic larval durations (Table. 12). The greatest similarity for all larval durations was between the two 2050 scenarios. The greatest difference for all larval durations was between the 2009 sea level and the high 2050 scenario but 2009 and low 2050 scenarios also differed.

Table 12. Bray-Curtis similarity for matrix comparisons based on similarity of proportions within cells (i,j). PLD = pelagic larval duration.

PLD	2009 & Low 2050	2009 & High 2050	Low 2050 & High 2050
7	88.6	84.4	94.4
14	86.5	83.6	94.1
28	92.5	89.4	95.9

The majority of network metrics were not significantly different between scenarios (Table 13). However, edge strength was significantly different between the 2009 sea level and both sea level rise scenarios for the 28d larval duration (2009 vs. low scenario $V = 1232$, $p = 0.030$; 2009 vs. high scenario $V = 1271$ $p = 0.047$). The 2050 sea level rise scenarios both had a greater number of positive ranks than the 2009 sea level, indicating an increase in edge strength with increased sea level. The only other significant node-based difference was the number of larvae received for the 2009 sea level and low 2050 sea level rise scenario for the 7d larval duration ($V = 1145$ $p = 0.049$).

Table 13. Network metrics for individual nodes assessed for difference with Wilcoxon Matched Pairs tests. PLD = pelagic larval duration.

PLD	Edge strength		Betweenness		Received		Supplied	
	V	p	V	p	V	p	V	p
7	2009 & Low 2050							
	1277	0.100	188.5	0.128	1145	0.049	1183	0.886
	2009 & High 2050							
	1362	0.117	167	0.637	1261	0.060	1132	0.654
14	2009 & Low 2050							
	2030	0.277	175	0.483	1237.5	0.860	1666	0.134
	2009 & High 2050							
	1994	0.467	122	0.432	1188	0.929	1515	0.367
28	2009 & Low 2050							
	1232	0.030	239	0.234	924.5	0.130	1184	0.107
	2009 & High 2050							
	1271	0.047	136	0.130	994	0.147	1146	0.071

Global network metrics demonstrated a difference between pelagic larval duration but not between sea level scenarios. As time spent in the pelagic environment increased, model simulations demonstrated an increased number of connections between rocky shores (Fig. 16a), a decreased number of components (Fig. 16b), a decrease in rocky shores with loops (Fig.16c) and an increase in the number of edges that were reciprocated between nodes (Fig. 16d). The proportion of nodes with loops was much higher for the 7d larval duration than for either the 14d or 28d larval duration. In contrast, the edge reciprocity was much higher for the 28d larval duration than for the other two durations.

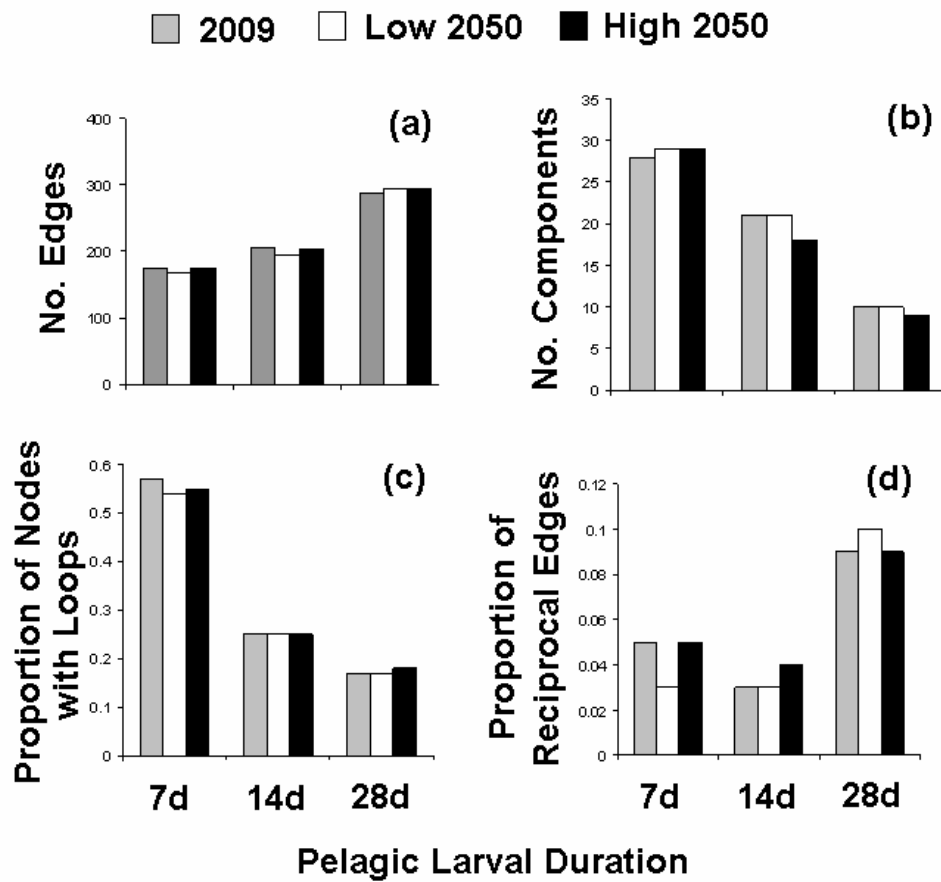


Fig. 16. Network metrics for three pelagic larval durations (7 day = 7d; 14 day = 14d; 28 day = 28d) and three sea levels (2009, Low 2050 scenario, High 2050 scenario). Edges represent exchange of larvae between rocky shore patches, components are stand-alone sections of the network, proportion of nodes with loops represents rocky shore patches that show larval retention, and proportion of reciprocal edges represents those connections that go two ways.

Cut nodes were not present for the 7d or 14d larval duration but were identified for the 28d larval duration (Fig. 17). These cut nodes were centred around the western English Channel and Lyme Bay. No cut nodes occurred on the Isle of Wight or in the eastern Channel.

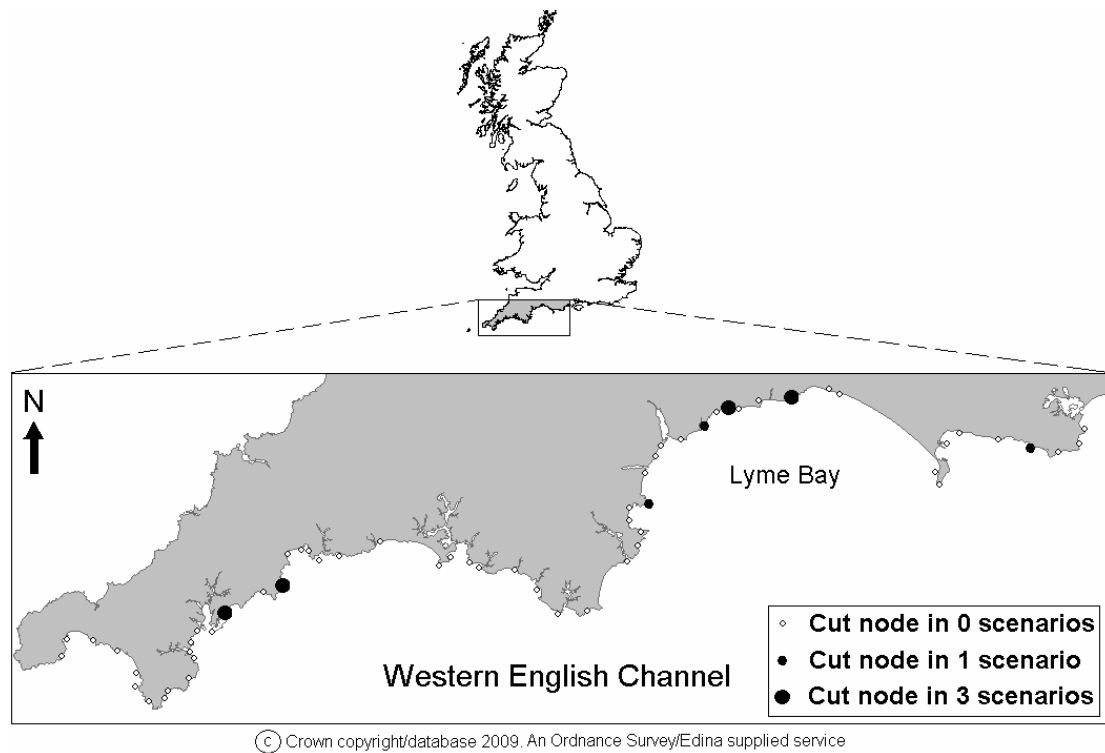


Fig. 17. Cut nodes for bi-components of minimum size 3 nodes for species of 28 day pelagic larval duration. Cut nodes were determined for each sea level rise scenario: 2009, Low 2050, and High 2050. Area of interest is shown in relation to its location within Great Britain (Ordnance Survey 2009).

6.10. DISCUSSION

Sea level rise altered the connectivity of rocky shore patches, suggested by Bray-Curtis similarity coefficients. Although the magnitude of this dissimilarity is small, it is based on bathymetric changes only because the model resolution prevented consideration of coastal morphology change. The addition of this supplementary factor is likely to result in much greater hydrodynamic change because it could lead to breached dispersal barriers. However, this does not invalidate the usefulness of this study because the results demonstrated for the first time that sea level change has the potential to impact on the process of larval dispersal and recruitment of marine organisms.

The increased proportion of exchanged larvae appeared to at least partially explain the difference in connectivity for species with a 28 day pelagic larval duration, as indicated by the Wilcoxon test on edge strength. This suggests that sea level rise will result in increased connectivity for these species. However, the use of graph theory for this analysis did not provide as much insight into connectivity changes as was originally anticipated (see section 7.4.3 of Chapter 7, p. 178). The number of rocky shore patches that were essential to maintain network connectivity was few, indicated by the cut-nodes analysis. Three patches split the network in one scenario and four patches split the network within all three scenarios. This suggests that establishing these shores as protected areas would be conducive to maintenance of connectivity and would be robust to forecasted sea level rise and its effect on bathymetry.

Finally, one must consider the synergistic or additive effects of multiple climate change variables. Sea surface temperature increase has been demonstrated to decrease larval development time and thus decrease the length of pelagic larval duration (O'Connor et al. 2007). The difference suggested here in network metrics between pelagic larval durations suggests that a reduced larval duration combined with sea level rise could have a powerful synergistic effect on connectivity, and therefore the dynamics of metapopulations of pelagic species.

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Chapter 7

Discussion

The impacts of environmental change on ecological communities are poorly understood relative to impacts on species (Gilman et al. 2010; Walther 2010). As a result, our ability to forecast the impacts of environmental change on communities, and on individual species constrained by those communities, is seriously limited (Gilman et al. 2010). This forces the undesirable situation where conservation must act on the basis of limited scientific evidence (Sutherland et al. 2004). In particular, analyses of change in inter-community (beta-) diversity over time have remained elusive owing to a lack of suitable data with which to tackle these questions (Olden & Rooney 2006; Pullin & Salafsky 2010). In turn this has led to a paucity of conservation attention at the inter-community (beta-diversity) level. This thesis aimed to undertake a programme of research on the impact of environmental change on communities to contribute to this required evidence, and was novel in three key areas: (i) focus on long-term change, (ii) parallel investigations of marine and terrestrial ecosystems in same geographical area, and (iii) meso-scale.

Compositional and relative abundance changes were detected in both the marine and terrestrial environment that led to a reduction in beta-diversity revealed through biotic homogenization and assemblage convergence. Identification of these changes was facilitated by the application of a spatial meso-scale approach. I found no evidence for non-analogous community formation from my analyses. The pattern of change was similar within both environments, however, differences were evident in the drivers and processes of the observed change in beta-diversity. In particular, woodland plant community composition was altered by non-climatic environmental change whereas relative abundance of key structural and functional species within a rocky shore assemblage was closely correlated with an increase in sea surface temperature.

Rocky shore species appeared to demonstrate greater individuality of response in contrast to terrestrial species, indicated by the analysis of

community composition and abundance change. Further support for this supposition was obtained from the analysis of woodland metacommunity structure. Unfortunately, metacommunity structure could not be analysed for rocky shores owing to insufficient data. This exemplifies the role of data availability in the lack community level analyses and will be discussed further in a later section. Individualistic responses of rocky shore species were also evident in the analysis of climate tracking as different species tracked the rise in sea surface temperature to different extents owing to varying abilities to traverse potential barriers. These individualistic responses would result in changes in composition and relative abundance within communities. Larval connectivity was also affected by model simulations of sea level rise projected for 2050, adding to the case for a need to understand potential impacts of climate change to ensure robustness of protected area networks and diversity at higher levels of organisation.

In this chapter I will combine findings from across chapters to discuss impacts on environmental change within communities, between communities and within metacommunities. I follow this with a critique of the quality of evidence obtained within this thesis, with particular focus on the use of long-term data. Finally I conclude to what extent the aim of this thesis was achieved and suggest future research directions.

7.1. INTRA-COMMUNITY CHANGE

7.1.1. Objective 1. Apply the palaeoecological concept of non-analogous community formation to intra-community impacts of environmental change

Has this been addressed in conservation legislation?

Following a review of the literature it was clear that although the formation of non-analogous or novel communities had been considered, the concept had not been applied explicitly to modern ecology and its potential consequences for conservation had not been outlined. Despite this, the palaeoecological evidence provided a strong suggestion that such communities would form in the current era of environmental change (Williams & Jackson 2007; Williams et al. 2007). I considered the

consequences of non-analogous communities (NACs) for conservation legislation, which had not been considered previously (Keith et al. 2009b).

Prior to this thesis, NACs had only received brief mention within recent climate change impacts literature (e.g. Berry et al. 2002). However, recent literature appears to have recognised the importance of this consequence as focus on community level impacts of environmental change has increased. A recent forum paper suggested that attempts to maintain existing community composition will inhibit effective conservation (Hodgson et al. 2009). In addition, Walther (2010) reviewed community responses to recent climate change and emphasised the formation of NACs as a result of range shifts and changes in community composition. Finally, Gilman et al. (2010) advocate a community module framework to understand the potential impacts of environmental change on species interactions, and suggest we can expect a ‘re-mixing’ of interactions, which could itself create changes in species distributions and thus NACs. This view of altered interactions as a precursor to altered composition and NACs is extremely interesting and would be enlightening to pursue. Furthermore, novel species combinations would lead to novel interactions between species that have not co-evolved and therefore could have dramatic effects on species fitness (Gilman et al. 2010).

Is there evidence for its recent occurrence?

Despite the expectation for NACs to be detectable after 70 years of environmental change, the analysis of communities within the woodland dataset found no evidence of NAC formation (Chapter 3; Keith et al. 2009a). This was especially unexpected because beta-diversity loss is associated with a reshuffling of communities, although in this case, it occurred within the bounds of existing community types (Keith et al. 2009a). In contrast, a rare analysis identified NACs on Marion Island as plant species individually shifted their altitudinal range in response to warming temperatures since 1966 (le Roux & McGeoch 2008). This suggests that the time-scale of my analysis does not explain the lack of NAC detection. The relative isolation of species in the modern era compared with

during previous climate change episodes could partly explain this result because individualistic responses may be restricted through inhibition of dispersal (e.g. Clark et al. 2010). On Marion Island this was unlikely to be restrictive because the Island is remote.

The Marion Island analysis and Chapter 3 findings are in contradiction and thus highlight the requirement for conservation to be based on a substantial foundation of evidence. Although NAC formation is thought likely in light of palaeoecological evidence, the vulnerability of communities to its occurrence appears to be variable because the results from these two analyses are contrasting. Therefore, a future direction for research may be to determine the factors that contribute to vulnerability of a community to convert to a NAC. An additional area of interest here is the scaling up of NACs to the metacommunity level. It would be interesting to determine whether NACs at the local scale result in a non-analogous metacommunity. The results of Chapter 5 demonstrate robustness of metacommunities to change in community composition and beta-diversity loss, therefore, in the absence of introduced species, one could expect that metacommunities are resistant to non-analogy.

7.2. INTER-COMMUNITY CHANGE

7.2.1. Objective 2. Assess the extent of change in inter-community (or assemblage) diversity in southern England over multiple decades as a result of environmental change.

Comparative to intra-community change, inter-community change has been little considered. Within a recent review of community and ecosystem responses to climate change there was no mention of beta-diversity (Walther 2010), despite increasing support for its loss (Olden 2006). An explanation may be sought in the use of space for time substitutes and comparison of extant species pools for the majority of this evidence. Such methods of analyses are necessary given the lack of suitable data but are not as clear as comparisons of two points in time and therefore may not be as easily assimilated into conservation. Chapter 3 and 4 have contributed to direct evidence for beta-diversity loss.

Has inter-community diversity of woodland plant communities in southern England changed over 70 years? Has inter-assemblage diversity of temperature-sensitive intertidal rocky shore invertebrates in southern England changed over 50 years?

Woodland plant communities (Chapter 3) and intertidal invertebrate assemblages (Chapter 4) experienced a reduction of beta-diversity, demonstrated by biotic homogenization or assemblage convergence. The expectation is that this pattern will be observed across taxa and will be global phenomenon (Olden 2006; Olden et al. 2004), however, there is a need for more supporting evidence from the marine environment before this expectation is shown. Evidence is accumulating across many terrestrial habitats and taxa, including plants (Britton et al. 2009; Castro & Jaksic 2008b; Magee et al. 2008; Van Calster et al. 2007; Vellend et al. 2007), birds (Devictor et al. 2008; Van Turnhout et al. 2007), and freshwater fishes (Olden & Poff 2004), and here I provide a step towards evidence for biotic homogenization in the marine environment. In contrast to the results within this thesis, a substantial proportion of previous analyses demonstrate a pattern of biotic differentiation (Marchetti et al. 2006; Olden et al. 2008; Qian et al. 2008) or no change, known as biotic tracking (Castro & Jaksic 2008a). This highlights the need to test the concept in as many different habitats and with as many different taxa as possible because responses are likely to differ (Dormann et al. 2007).

I hesitate to refer to the convergence of intertidal invertebrates as biotic homogenization because although the definition of biotic homogenization is such that it refers to a “biological variable” (Olden et al. 2004), there was a common misconception that it can only refer to a community. This misconception does make ecological sense, however, because the importance of a selected group of species converging in their presence and relative abundances is most likely to have little significance. However, although the assemblage was comprised of only ten species (owing to data limitations that will be expanded upon in a later section), these species have key structural and functional roles in the rocky shore community, thus their convergence may be indicative of wider biotic

homogenization. Furthermore, these species are temperature sensitive and can therefore be recognised as indicators of species for the community. To avoid unconventional usage I shall continue to refer to the observed change as assemblage convergence but suggest consideration of its wider implications. Despite this, no evidence currently exists for biotic homogenization within the marine environment (although habitat homogenization has been demonstrated; Airoidi et al. 2008; Olden et al. 2004) and therefore this work is a valuable start to the biotic homogenization research agenda (Olden 2006).

Is this reflected by intra-community diversity?

Regardless of this loss of beta-diversity from woodland plant communities and a loss of species from the regional pool (gamma-diversity), the species richness within communities (alpha-diversity) did not significantly change. The analysis of intertidal assemblages demonstrated a pattern of slightly increased alpha-diversity. Gamma-diversity could not be assessed in this case because I did not have data on all species within the pool. Therefore, there was no loss of alpha-diversity in either environment. This is in contrast with other research on biotic homogenization that identified local extinction and reduced alpha-diversity as the process of homogenization (Rooney et al. 2004) and demonstrates that the conservation implications of changes in beta-diversity are unclear.

It has been previously acknowledged that parallel trends are not necessarily indicated by different measures of biodiversity (Sala & Knowlton 2006), and that measures of only point diversity (i.e. alpha) can cause beta-diversity changes to remain unnoticed (Hillebrand et al. 2010). Taken together, this exemplifies the need for meso-scale analyses that consider multiple organisational levels. Whittaker et al. (2001) suggested a hierarchical top-down approach to species diversity that considers alpha, beta and gamma-diversity. However, one could alternatively argue that large-scale patterns are the result of a collection of smaller scale processes and therefore understanding will come from a bottom-up approach. In

criticism, this argument ignores the potential for emergent properties (Gaston & Blackburn 1999; Woodward et al. 2010).

What are the environmental drivers of the observed change?

Although there was similarity in pattern, the drivers and processes behind the loss of beta-diversity demonstrated differences. Homogenization of the woodland communities appeared to be driven by increased nitrogen deposition and decreased light availability, with no discernable impact of climate. This was, however, based on indirect measurements of the environment, i.e. Ellenberg indicator values, suggesting a potentially circular argument. However, the use of indicator species as environmental proxies is a well established practice (Hill et al. 2004). The degradation appeared to be across the majority of communities and therefore environmental gradients were also homogenized. More specifically, the change in environment is indicative of habitat degradation rather than loss, and this is supported by the lack of change in alpha-diversity which would be expected according to species-area relationships if habitat had reduced (MacArthur & Wilson 1967), assuming there was no extinction debt (Jackson & Sax 2010). However, extinction debt is a possibility in this case because it was demonstrated to still be owed after 70 years of habitat fragmentation by a grassland plant community (Helm et al. 2006).

The convergence of intertidal assemblages was correlated with increased sea surface temperature. Use of a temperature sensitive assemblage increased confidence in the attribution of these changes to increased sea surface temperature, however, the attribution is nonetheless based on correlation preventing definitive cause and effect. The changes are affected because the range distributions of southern species have expanded eastwards, appearing to track the gradient of sea surface temperature, which in the English Channel grades from warm waters in the west to colder waters in the east. Evidence is available from single species analyses that support this view (Hawkins et al. 2009; Lima et al. 2007; Mieszkowska et al. 2007; Mieszkowska et al. 2006; Mieszkowska et al. 2005). Therefore, the process and driver in this case is well-supported by previous analyses and

the work within this chapter. The analyses from Chapter 4 of this thesis used data from Crisp & Southward (1958) and the MarClim Project (Mieszkowska et al. 2005) and was therefore was a collaborative effort.

Therefore, homogenization of the woodland communities was correlated with non-climatic changes in the environment, whereas convergence of intertidal assemblages was correlated with increased sea surface temperature, further supported by climate tracking analysis of Chapter 6. Both the gradient of temperature across intertidal assemblages, and differences in inferred nitrogen and shade were reduced, indicating environmental homogenization. This supports the recognition that homogenization of the abiotic environment can be a promoter of biotic simplification (Olden et al. 2004). The abiotic environment, as the driver, differs from the original descriptions of biotic homogenization that were put forward in the context of species introductions as biotic drivers of change (McKinney & Lockwood 1999). Therefore, my thesis offers support to the potential for abiotic, rather than biotic, drivers of beta-diversity loss. Whilst I stress the caveat that direct attribution in both my analyses is not possible because suppositions are based on correlation and indirect evidence, the observation of this relationship in both terrestrial and marine environments adds weight to this support.

A mechanistic consideration of beta-diversity loss in each environment becomes more divergent. The woodland communities lost rare species in tandem with a spread of already common species that were more tolerant of nitrogen and shade, suggesting the involvement of competition whereby new species immigrated and outcompeted the rare species. A contrasting hypothesis is that the rarer species may have become locally extinct due to reduced survival rates in changed environmental conditions, creating an under-saturated environment that then became colonised by species more suited to the conditions. If the latter was true, the situation of community assembly would be a demonstration of the metacommunity species sorting paradigm (see Chapter 5). To test this hypothesis, however, would require time series data or experimental analysis.

In contrast, intertidal assemblages appear to have been altered through increased abundance and colonisation of southern (Lusitanian)

species. However, this does not exclude the possible influence of competition. Two barnacle species within the studied assemblage are known competitors whose interaction is mediated by temperature because one is a cold adapted northern species and the other is warm adapted southern species (Poloczanska et al. 2008; Wethey 1984). Therefore, the process of increased abundance of this particular warm adapted species may have occurred through the mechanism competitive release. A similar pattern was found by A similar pattern was also found in temperate reef fish assemblages, which experienced an increase in southern adapted species (Holbrook et al. 1997). However, the fish assemblage also experienced a loss of northern adapted species (Holbrook et al. 1997) that has not yet been observed within the south coast intertidal assemblage. Therefore, in contrast to the woodland communities, beta-diversity loss was not influenced by extinction.

To summarise, both ecosystems experienced beta-diversity loss without loss of diversity within assemblages (Table 14). This was most likely driven by homogenization of the abiotic environment. In the case of marine assemblages the abiotic variable was sea surface temperature, which drove a process of range expansion and increased abundance of southern species, and in woodland communities were nitrogen concentration and shade, which drove a process of loss of rare species from the regional pool and increased patch occupation by common species.

Table 14. Comparison of meso-scale impacts of environmental change on biodiversity in terrestrial and marine ecosystems based on thesis results

	Terrestrial	Marine
Alpha-diversity	No change	Slight increase
Beta-diversity	Decreased resulting in biotic homogenization	Decreased resulting in assemblage convergence
Gamma-diversity	Decreased through loss of rare species	Unknown, data insufficient
Driver of change	Abiotic homogenization of soil nitrogen concentration and light availability	Abiotic homogenization of sea surface temperature
Process of change	Loss of rare species Increased patch occupation by common species	Increased abundance and range expansion of southern species

7.3. INDIVIDUALISTIC RESPONSES OR COMMUNITY CONSTRAINTS?

7.3.1. Objective 3. Identify the metacommunity structure of woodland plants at two points in time, seventy years apart and determine how much the structure had changed.

Does metacommunity structural change reflect changes in beta-diversity?

Metacommunity structure was identified as Clementsian at both points in time for woodland plants, indicating that communities exist within particular bounds (Chapter 5). The lack of change was unexpected owing to the identification of beta-diversity loss within this metacommunity and did therefore not reflect community level changes. As with the consideration of alpha-diversity, this result supports the lack of parallel trends across levels of organisation (Sala & Knowlton 2006) and that findings from one spatial scale cannot be extrapolated to another (Gaston & Blackburn 1999). On the other hand, the Clementsian structure fits well with the lack of evidence for non-analogous community formation because it suggests that communities are distinct entities owing to high interdependency (Clements 1916), rather than assembled through individualistic species responses to environmental

gradients (Gleason 1926). The latter would create a Gleasonian structure. Although this suggests a constraint on species responses, Appendix II provides evidence for widespread individualistic species responses. Therefore, species seem to be able to respond individually within the bounds of community constraint, analogous to the stretching permitted by an elastic band, which is likely to vary amongst species. This species variation is also suggested by Chapter 6, which will be discussed further below.

Although the broad Elements of Metacommunity Structure (EMS) analysis used an existing method (Leibold & Mikkelsen 2002; Presley et al. 2009), determination of how much the structure had changed required a new way to compare the results from two EMS analyses, which I achieved with the use of z scores. This enabled identification of changes within the individual structural elements, three of which are combined to determine overall structure. Using this analysis I found that although the metacommunity was Clementsian at both times, there was greater spatial turnover of species in 2008 than in the 1930s. This initially seemed to contradict the pattern of homogenization observed within Objective 2a, however, this discrepancy was due to a difference in definition of species turnover (Keith et al. accepted). In a situation of reduced beta-diversity, one would expect there to be less change in species between communities and thus less turnover. However, the definition of turnover in EMS is that species are replaced between communities rather than there being an increase or decrease in species richness between communities. Therefore, the EMS definition of species turnover refers to differences in alpha-diversity between communities and was different in Dorset woodlands because alpha-diversity, represented by species richness, had converged. It would be helpful to rectify this confusion of definition to improve the communication of metacommunity literature.

A further issue with the analysis within Chapter 5 was that there was no control landscape that had not experienced biodiversity loss with which to compare the results of the metacommunity. This means I cannot be sure that the changes in individual structure observed were not a symptom of biodiversity loss but instead represented natural variation. Once more, time

series data would have assisted with this assurance and would have provided unambiguous proof on whether the structure changed in the intervening years.

7.3.2. Objective 4. Determine whether the climatic tracking response can be individualistically limited by the presence of physical barriers to dispersal.

Chapter 4 (Objective 2a) identified assemblage change that was thought to be a consequence of range expansions in response to rising sea surface temperature. Rocky shore species were known to have undergone range expansion in recent decades and this expansion was strongly correlated with an increase in sea surface temperature (Hawkins et al. 2008; Hawkins et al. 2009; Mieszkowska et al. 2007; Mieszkowska et al. 2006). Such range expansions would be dependent upon dispersal to newly suitable areas via larvae. The analysis I conducted in Chapter 6 (Part I) suggested that climate tracking had been limited by meso-scale hydrographic barriers to larval dispersal and that these limitations varied amongst species. Differential species dispersal capabilities are an individualistic species response, indicating the process of assemblage convergence of intertidal invertebrates (Chapter 4). Of particular note was that the species with the shortest pelagic phase was most able to expand its range owing to consolidation of adult populations and reduced hydrodynamic influence (Byers & Pringle 2008). This would be contrary to expectation of previous models that have not considered meso-scale dispersal barriers and rather consider range expansion as a function of maximum dispersal distance (e.g. Midgley et al. 2006).

Together, these findings demonstrate that dispersal as a process of biodiversity change is complex and requires greater understanding if we are to make accurate forecasts. Furthermore, variation in species dispersal capabilities is critical to changes at the community level (Gilman et al. 2010). However, the individualism may be reduced at southern boundaries because theory suggests that while northern boundaries are determined by abiotic factors, southern range boundaries are primarily determined by

biotic interactions (Brown et al. 1996). In the latter case, therefore, species are expected to be constrained by the community. Owing to this supposition I clarify that results from this thesis are only in reference to northern range boundaries.

This was the first attempt to move beyond the use of the hydrodynamic modelling approach of larval connectivity in a static sense, to its use in the context of species responses to climate change. However, the findings within Chapter 6 must be considered in light of model limitations discussed below (see Quality of Evidence) and recognised as a first step towards combining long-term empirical data with hydrodynamic modelling to achieve greater understanding of marine connectivity.

Unfortunately, it was not possible to conduct this analysis for woodland species because the spatial extent of the data coverage did not include range boundaries. Terrestrial populations are thought to be relatively closed and marine populations to be relatively open. The sea was thought to provide an unrestricted medium, through which propagules could spread unhindered. In contrast, terrestrial species are thought to encounter many barriers to dispersal. However, analyses in Chapter 6 (Objective 4) add to the recent evidence that suggests marine environments are less open than previously assumed and local retention of propagules is common. Although I did not test the impact of dispersal barriers on terrestrial species, it is already recognised as an important factor in the ability of terrestrial species to adapt through dispersal and subsequent range changes (Sutherland et al. 2008) and therefore did not require further demonstration. Chapter 6 of this thesis therefore highlights the similarity of climate tracking limitations for terrestrial and marine species.

Will the individualistic limitations alter under scenarios of future environmental change?

According to the hydrodynamic model, sea level rise scenarios have the potential alter connectivity of rocky shore species (Chapter 6, Part II). However, further tests are required that use better validated models before this can be more definitively established. The indicated difference in

connectivity was small but the model only accounted for bathymetric changes and did not account for changes in coastal morphology. demonstrated that climate change have a direct effect on the medium of marine propagule dispersal through sea level rise. However, to the best of my knowledge, such a possibility has not been considered for terrestrial plants. I suggest that for those plants that disperse via seeds, this possibility would be interesting to explore. For example, climate change can affect dispersal of riparian species due to increased frequency of high-flow events (Truscott et al. 2006) and wind dispersed species, for which long distance dispersal is positively correlated with temperature (Kuparinen et al. 2009). For those species that depend on animal dispersers, particularly highly specialised co-evolved species such as the fig tree and fig wasp (Anstett et al. 1997), the ability of the animal vectors to track climate or escape changing environmental conditions may outpace that of long-lived plants, potentially resulting in the loss of a dispersal vector. An example of such a situation was observed through reduction in the recruitment for an endemic tree following the loss of bird dispersers from forest fragments in Tanzania (Cordeiro & Howe 2003). This analysis has been submitted to *Biology Letters*.

7.4. QUALITY OF EVIDENCE

7.4.1. Long-term data

Long-term data aided identification of biodiversity change that may not have been evident on shorter time scales. The multi-decadal time scales are very likely to have contributed to the detection of homogenization of the woodland plant communities because a similar analysis of Countryside Survey data over two decades demonstrated functional homogenization, a more coarse increase in similarity caused by homogenization of the presence of functional groups, (Smart et al. 2006) but did not find evidence for the more subtle taxonomic homogenization I observed with the 70 year time scale. This suggests that datasets that span longer time scales will be more likely to demonstrate an impact of environmental change. This may be particularly likely when long generation times are present within the community and when the underlying drivers of change are gradual. The

comparison of inter-annual and inter-decadal assemblage change (Chapter 4) showed that intertidal assemblage change was not evident on a short time scale. I have gained new insights into metacommunity structure through the availability of long-term data, which led to establishment of methodology to compare two points in time (Chapter 5). Data on past and present range boundary locations also permitted an assessment of physical dispersal barriers on climate tracking (Chapter 6).

Despite the insights afforded by the long term data within this thesis, fully parallel comparisons of these marine and terrestrial ecosystems were prevented because of differences in data that were available for each. Long-term data is often imperfect and has missing values and the data I used in this thesis was no exception. The plant data did not contain missing values, however, the intertidal data contained many. This necessitated a reduction of the species and sites that were usable because not enough data were available for a robust analysis. Even with the reduced number it was necessary to perform multiple imputation to fill in missing values. Imputation was the best available option and statistically valid but nevertheless was no substitute for complete data. This highlights a trade-off between insights potentially gained from long-term data and its quality. Barnard & Thuiller (2008) stated “As we pursue greater methodological refinement, greater rigour, more comprehensive datasets and additional robustness, we are also at risk of a tragic complacency” with regard to global change and biodiversity research, suggesting we must take advantage of rare long-term data as best as possible. Therefore, the problems of the data were outweighed by the insights gained.

A further caveat regards the use of snapshot data representing only points in time. Therefore, I explored differences between two points in time rather than changes over time, which would have required time series data. Snapshot data contains no information of presence or abundance in between these two points in time and this is problematic. For example, time series data would have allowed greater understanding of the process of change because it would have been possible to determine whether differentiation occurred prior to homogenization, which would suggest the common species immigrated prior to the loss of the rare species, indicating a

potentially strong role for competition. However, even seven decades may not be long enough to capture the true extent of woodland change because generation times of some woodland tree species exceeds this. For the analyses within this thesis the vast majority of species recorded were herbs, reducing the potential effect of tree species generation time issue within this thesis.

Time series data would also have permitted greater certainty in the attribution of sea surface temperature (SST) as the likely cause for assemblage convergence because SST has fluctuated over the last 50 years with the warming trend only apparent in the last two decades. The 1950s were a warm period so the snapshot data provided a conservative estimate of change, which would very likely have demonstrated greater difference if the historical comparison data were from the colder decades of the 1960s or 1970s. Furthermore, it may have shown the impact of disturbance as a result of an oil spill (Hawkins & Southward 1992; Smith 1968) and TBT pollution (Matthiessen et al. 1995; Smith et al. 2008; Spence et al. 1990). Although TBT pollution did not directly affect the species within our assemblage, it may have had an indirect effect through species interactions or resource (most often space on rocky shores) availability.

7.4.2. Metacommunity approach

Despite its shortcomings, the Elements of Metacommunity Structure analysis is extremely useful because it provides a single test for multiple structures (Presley et al. 2009). Unfortunately, such a test is not yet available for determining the dynamics that operate within a metacommunity according to the four paradigms of neutral, mass effects, species sorting and patch dynamics (Leibold et al. 2004; see Chapter 1). Although analyses of these dynamics are available within the literature, the paradigms are tested separately (e.g. Noda 2009). Even when multiple paradigms are tested within a single paper, this involves multiple analyses (Ellis et al. 2006).

Furthermore, paradigm conformity is often complex because the paradigms are not mutually exclusive. The lack of mutual exclusivity explains why metacommunity paradigms were not assessed alongside

structure within this thesis – I was not able to generate testable hypotheses that would identify metacommunity dynamics. Ellis et al. (2006) concluded that tree hole mosquito dynamics did not fit into any single paradigm but spanned expectations of all four. Invertebrate rock pool communities were assessed for paradigm importance using a comparison of community pair matrices based on similarity, actual distance, connected neighbours and environmental distance (Vanschoenwinkel et al. 2007). The rock pool metacommunity was best explained by the species sorting paradigm, however, results also alluded to a mixture of paradigms observed at different amounts of dispersal (Vanschoenwinkel et al. 2007).

The question of which paradigm is most important becomes further complicated in comparisons of regions. Analogous amphibian metacommunities in two regions were structured by different paradigms, despite their apparent similarity in species composition (Richter-Boix et al. 2007). The paradigms were species sorting and mass effects so both were ultimately controlled by local environmental factors but the difference was in the dispersal amount (Richter-Boix et al. 2007). In light of this and other similar analyses, there have been calls to integrate the species sorting and mass effects because they are often both identified as important dynamics in such analyses (Parris 2006; Urban 2004).

The overlap of paradigms highlights a wider problem with the approach, which is that some taxa or assemblages may form community modules that act in relative isolation from the rest of the community, with each module subject to a different paradigm. The conclusion of this idea is that it may be impossible to test the structure of metacommunities for all but the simplest because data are not obtainable for all species within the community. To exemplify this point, I refer to Chapter 5 of this thesis where I analysed a woodland plant metacommunity. Limitation of the analysis to a plant metacommunity disregards the impact of other species, for example, herbivores, soil microbes and fungi, which are strongly linked to plant survival and fecundity. Other metacommunity analyses have also followed this compartmentalised approach out of necessity (e.g. Brooks et al. 2008; Cottenie et al. 2003; MacNeil et al. 2009; Presley & Willig 2010) and none, other than highly controlled species-poor microcosm experiments (e.g. Hunt

& Bonsall 2009), have tackled the entire metacommunity. This is a fatal flaw within metacommunity analyses and suggests that the concept may be more appropriately termed the ‘meta-assemblage’ concept.

However, I do not advocate that the concept be dismissed but instead that it be discussed in light of the relevant caveats. Cautious use of results from metacommunity studies has the potential to inform conservation. For example it would be useful for conservation managers to account for metacommunity dynamics, even if these are multiple, when devising strategies to increase species richness or resist invasive species (Fukami 2005). Mouillot (2007) applied the metacommunity concept to biodiversity management of brackish lagoons. The application discussed the process, ecological attributes and management strategies of three of the paradigms (neutral theory was rejected outright because of the high functional variability of species in the habitat) and demonstrates that, although the metacommunity concept is still in its early stages, it can be utilised to inform conservation management (Table 1). It is also important to note that the dynamics of metacommunities are open to alterations under climate change. *Daphnia* species were found to have altered colonisation rates following hotter, drier summers, therefore potentially affecting metacommunity dynamics (Altermatt et al. 2008). Knowledge of such patterns could aid predictability of colonisation and extinction (Baldi 2003).

7.4.3. Hydrodynamic modelling and graph-theoretic approach

Modelling approaches often include high uncertainty as a result of, *inter alia*, resolution, estimated parameter values and stochasticity (e.g. Pearson et al. 2006). Despite the limitations, models are an extremely useful way to explore theory and hypotheses in a situation where variables can be controlled. This is particularly useful for ecological research on the impacts of environmental change, which would be difficult or unethical to explore through experimental manipulation of the environment (Witman & Roy 2009). Furthermore, models can provide predictions or forecasts of future biodiversity impacts that can be vital for conservation planning (Gilman 2009).

The modelling approach used in Chapter 6 allowed assessment of larval dispersal but, as with all models, was also subject to limitations. The background on larval dispersal modelling is included within Chapter 6 and suggests that larval dispersal modelling is increasingly including individual based components that can incorporate larval behaviour. This advance is of great importance for fish and decapod larvae, which are capable of strong horizontal swimming behaviour (North et al. 2009). Smaller invertebrate larvae carry out vertical positioning within the water column to align with different currents and inclusion of this within the model would have improved the accuracy of the output.

In developing the model I considered whether to include specific numbers of larvae, however, to determine the correct input for the model would require adult density, fecundity, area for each release site, and larval mortality. Mortality is largely unknown for these species because it is extremely difficult to track a cohort of larvae throughout its pelagic phase and record mortality. These data were not available for the majority of sites and would have led to over-parameterization. Another improvement to the model would have been achieved by running the hydrodynamic simulation over multiple years. Although I do not know of any particular anomalies in 2009, water movement is subject to stochasticity and therefore will vary between years. Furthermore, an issue with my model was that the spring tide occurred approximately two weeks into the simulation so did not affect the seven day and fourteen day larval durations. However, it could be argued that this necessarily reflects reddening within the marine environment i.e. greater variation with greater time period.

The hydrodynamic component of the model was sufficiently validated by ABPmer, however, the particle tracking component was validated for only the 28 day larval duration. This was due to a lack of suitable data to achieve validation from the other larval durations and limited my approach. The best approach to model validation would be to compare the genetic similarity to the connectedness of populations. This type of validation has been used by other larval modelling approaches with high success (Gilg & Hilbish 2003; Hedgecock et al. 2007). However, this does not invalidate the whole model because one would expect that an

accurate 28 day larval duration in the model would mean the time leading up to that point would also have to be accurate.

The use of graph theory and network analysis to explore the differences in connectivity was unsatisfactory for my analysis because it did not provide a function to compare two graphs in their entirety within the software I used (Pajek and igraph in R). Although the analysis was useful for individual metrics, the lack of an overall comparison suggests that use of this method would not be appropriate for rapid comparison, as might be desired by conservation. Furthermore, although the method allows capture of some emergent properties (e.g. graph diameter), the lack of overall graph comparison suggests that any emergent property that encapsulate a combination of multiple graph characteristics may be missed. The method therefore requires further modification before it can be readily and rapidly applied to ecological problems.

7.4.4. Climate tracking

The use of only one variable to create an envelope for the climate tracking analysis was potentially problematic. Although SST is thought to be the primary influence on range boundary for these species in the study area, it is certain other factors are involved to some extent. Another potential problem is that the approach assumes species distributions were in equilibrium with SST prior to 1990. This represents a more general problem of BEM techniques because many communities and populations are in disequilibrium due to recent disturbance, evolutionary factors or historical events. However, these limitations did not invalidate the results because the critique for BEM still holds regarding the need to include meso-scale physical barriers.

7.5. CONCLUSION AND FUTURE RESEARCH

I achieved my aim to undertake a programme of research on the impact of environmental change on communities and have contributed to knowledge in this area of ecology. The novel time scales provided the opportunity to test and find evidence for emerging concepts and the meso-scale provided an appropriate spatial scale for this. Although useful comparisons could be

drawn amongst marine and terrestrial environments, the difference in data from the two environments prevented fully parallel analyses, perhaps providing explanation for the lack of such analyses in the literature. Therefore, in addition to multi-disciplinary analyses, baseline data collection and monitoring must also become multi-disciplinary to enable cross-ecosystem comparisons in the future. However, despite limitations, I have presented a first attempt at the combination of ecosystems from terrestrial and marine environments within the same geographical area to investigate the impacts of environmental change.

This thesis has highlighted numerous avenues for future research. In the area of NACs, it would be very interesting to consider inter-specific interactions within their formation because this may explain the mechanism of formation and/or explain the lack of evidence for them within the woodland communities. The area of biotic homogenization would benefit from an investigation of whether indicator assemblages could provide a method for rapid assessment of beta-diversity loss because indicators are a current topic of great interest (UNEP-WCMC 2009).

Unfortunately, this thesis was not able to conduct analyses of limitations to plant dispersal owing to a lack of range boundary data. In particular it would be interesting to determine whether a similar pattern exists for plants whereby species that have short dispersal distances are more able to consolidate populations and therefore extend range boundaries. This would be a very useful result to inform bioclimatic envelope models. Further ideas for research are listed below but will not be expanded here:

- Determine whether biotic homogenization has occurred in marine environments through use of full community data, even if evidence must come from space for time substitutes
- Greater understanding of the mechanisms of biotic homogenization (using time series data)
- Identify dataset suitable for analysis of metacommunity structure in marine environment
- Genetic validation of the hydrodynamic model

- Establish parallel monitoring and surveying efforts for marine and terrestrial environments
- Synergistic effect of sea surface temperature rise and sea level rise on connectivity of rocky shore invertebrate species

In conclusion, this thesis adds to the growing call for consideration of impacts at the community level, inclusive of inter-specific interactions and individualistic responses in analyses of environmental change impacts.

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Appendix I

Evidence for Environmental Change and its

Impacts on Biodiversity

The literature on environmental change is vast and a fully comprehensive review would be much larger than a thesis will allow. Therefore, below I provide an overview of the most salient evidence for environmental change. All issues are revisited in more detail throughout thesis chapters.

I.1. EVIDENCE FOR ENVIRONMENTAL CHANGE

I.1.1. Climate Change

There is strong evidence that the Earth's climate is undergoing rapid change, exemplified by a mean rise in air surface and sea surface temperatures, greater cloud cover and increased frequency and ferocity of stochastic weather events (Solomon et al. 2007). 'Climate change' is a commonly used phrase with a wide range of definitions. For the purpose of this study I use the definition provided by the Intergovernmental Panel on Climate Change (IPCC) as follows: "Climate change refers to a change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer." (Solomon et al. 2007). Historically, the Earth has experienced many major climate change events, some associated with mass extinctions or mass radiation events, thus illustrating the power of climate over biological systems. Substantial changes in climate have been experienced at various scales from global (e.g. K-T, 65 mya) to regional (e.g. Little Ice Age, Europe, N. America and N. Asia ~A.D.1550-1850), and at various durations from decades to millennia. Typically, past events have occurred slowly enough for genetic adaptation or movement of individual species to prevent mass extinctions, however, some events have occurred too rapidly for widespread adaptation. For example, the Paleocene-Eocene thermal maximum saw temperature

increases of 4-5 °C, possibly comparable to those expected in the 21st century (Zachos et al. 2003) and coincided with a worldwide decline in palms (Morley 2000).

An increase in global average surface air temperature of 0.6 °C (\pm 0.2 °C) is believed to have occurred over the last 100 years (Harley, 2005; IPCC, 2001). The last 50 years have shown an even more dramatic warming, with global air surface temperature increasing by 0.13 °C (\pm 0.3 °C) decade⁻¹ over this period (Solomon et al. 2007). Temperature changes are accompanied by alterations in patterns of precipitation, with the northern hemisphere generally experiencing 10-15 % higher amounts now as compared to the 1961-1990 average whilst some areas, particularly Africa and Asia, are experiencing prolonged drought conditions and greater unpredictability of annual precipitation cycles (Houghton et al. 2001). CO₂ concentrations have undergone a dramatic increase, rising from a level of 280ppm in pre-industrial times to 370 ppm currently (Harley 2005) and are now the major political focus for mitigation of climate change effects (e.g. Kyoto Protocol).

In addition to global changes, there have also been observable changes at the national scale. UK land and sea temperatures have both increased following a similar trend as compared to the 1961-1990 average. The UK now experiences higher winter precipitation with increased intensity. In addition, average sea level around the UK has increased by 10 cm in the last decade. This figure incorporates adjustments for natural land movements (Hulme et al. 2002). Although the evidence for climate change appears conclusive, climatologists are first to acknowledge the limitations of available climate data. Measurements rely on a globally standardised system and as a result of the demands for representative measurements, systems are expected to operate in extreme conditions (Le Treut et al. 2007). Gaps and errors in data can be caused by processes such as snowfall gauges damaged by ice; lost oceanographic floats; and satellite changes altering carefully calibrated trends (Schiermeier 2007). Therefore, uncertainty and potential error is an inherent part of climatic data.

The cause of the observed climate changes are the subject of debate. According to the IPCC Fourth Assessment Report (AR4) (Parry et al. 2007),

temperature variability about seven centuries prior to 1950 is very likely to be attributable to natural external forcing because models of climate change over this period that include only natural forcing match the observed changes. A combination of solar activity indicators show that a peak of solar activity was reached in 1985 (Lockwood & Frohlich 2007; Stott et al. 2000b). Prior to this there is likely to have been a solar impact on global temperatures. However, since this date, solar activity is unlikely to be associated with warming of average global temperatures (Lockwood & Frohlich 2007). Overwhelming consensus of opinion is that although solar radiation has influenced climate change, anthropogenic activity has also played a key role (Solomon et al. 2007). The comparison of observed global mean surface temperature over the last 100 years with modelled simulations for the same period for natural external forcing only and for natural external forcing combined with anthropogenic forcing, indicates anthropogenic forcing as a likely explanation (Solomon et al. 2007). It is specifically noted that this explanation is particularly for the last 50 years, concurrent with the points above. The IPCC alludes to a $> 90\%$ probability that observed climate change in the last 50 years has been caused by the production of high concentrations of greenhouse gases, particularly CO₂, CH₄ and NO₂ (Solomon et al. 2007; Stott et al. 2000a; Stott et al. 2001; Zamostny et al. 1999).

Conversely, IPCC assessment reports are open to criticism. Oppenheimer et al. (2007) suggest AR4 includes some vague points that are not explored in depth because of the risk of losing consensus and therefore advocate that scientific debate becomes stifled. However, the AR4 is not a substitute for original data and debate but rather seeks to synthesise the scientific literature to identify consensus. The data deadline for AR4 was in 2005 so data obtained since then are not included or considered (Schiermeier 2007). Furthermore, comparison of observed warming with potential forcings are problematic because of a statistical phenomena called degeneracy (Ingram 2006). Degeneracy is where different physical processes (e.g. solar radiation, volcanic activity) are too similar in shape to be accurately distinguished. Therefore, although caution should be taken, on balance the evidence suggests that climate change during the last 50 years is

attributable to a combination of anthropogenic forcing and natural external forcing.

Climate change impacts have been recorded across the globe but most strongly in the Northern Hemisphere. This can be exemplified by the rapid depletion of sea ice coverage in the Arctic, both in thickness and in extent, in comparison with the possible slight cooling of surface temperature over the Antarctic and thickening in its ice sheet (Alley et al. 2005; Johannessen et al. 2004). However, the Antarctic air is now beginning to become warmer above the surface (in the troposphere), recent weather balloons have recorded a 0.5 - 0.7 °C increase every 10 years for the past 30 years (Turner et al. 2006). The Greenland ice sheet is also retreating dramatically, and in some areas is slipping into the sea at a rate of up to 14 km yr⁻¹ (Chen et al. 2006; Henson 2006).

Permafrost is below the active layer (that which contains ice/snow that regularly thaws and re-deposits) within which ice crystals bond with soil particles to form a permanently frozen layer. Increasing global temperatures have already resulted in observable decreases in the active layer depth and melting of the permafrost layer (Frauenfeld et al. 2004; Solomon et al. 2007). The melting of permafrost layers is problematic because it disrupts the structural stability of the ground, removes a potential water source for local vegetation, and can release greenhouse gases and other pollutants thus amplifying warming (Callaghan et al. 2004; Eugster et al. 2000).

The oceans, in addition to increases in sea surface temperature, have demonstrated a surface pH decrease of 0.1 indicating increased acidity and increased salinity, accompanied by a rise in sea level from 1961 – 2003 of 1.8 mm (± 0.5 mm) yr⁻¹ (Solomon et al. 2007). The rise in sea level is attributed to thermal expansion and ice sheet melt (Solomon et al. 2007). Regionally, the English Channel has increased in both sea surface and sea bottom temperatures since the 1920s, although there was a slight cooling period in the 1950s and the 1970s (Southward & Butler 1972; Southward 1960; Southward & Roberts 1987).

An increased frequency of category four and category five Atlantic hurricanes has been observed between 1970 and 2004, correlating strongly

with rising sea-surface temperatures (Hoyos et al. 2006). Additional environmental impacts, *inter alia*, are increased duration of heat-waves (Solomon et al. 2007), desertification (Foden et al. 2007) and increased precipitation variability with increases in rainfall reported primarily in the northern hemisphere paralleled by rainfall decreases primarily reported in the southern hemisphere (Dore 2005; Solomon et al. 2007)

I.1.2. Forecasts for future climate change

Scenarios for future climate change generally infer a further increase in global temperatures (AR4 – 99 % probability that hot days will become more intense and frequent; Solomon et al. 2007), particularly in the northern hemisphere. The worst case scenario shows an average global surface air temperature increase of up to 4 °C above the current global average within the next century. In addition, precipitation will continue to alter and extreme weather events are likely to be more frequent and of greater intensity (Solomon et al. 2007).

Climate change scenarios should always be viewed with the caveat that climate prediction is not an exact science. Incidences have been shown whereby a seemingly insignificant change to a variable or parameter fed into a climate model can result in large global changes of the model outcome. An example of such an incidence is in the consideration of cloud cover. Comparisons between model outcomes showed a strong dependency on the model used (Cess et al. 1989). Senior & Mitchell (1993) demonstrated a temperature outcome range of 1.9-5.4 °C simply by altering cloud radiative properties in a model. This exemplifies the fact that climatology remains a science of tentative forecasts rather than of certainties.

A variety of climate models have been developed by climatologists and six different models were employed to create the SRES scenarios. A few models incorporate biotic feedbacks, such as the effect of deforestation on atmospheric carbon dioxide concentrations. However, this is still a relatively new development and is extremely difficult to model owing to its inherently dynamic nature (Schiermeier 2007). Climate forecasts are improving because instead of simply running a single model based on a single baseline of variables, models are run many times. Each

iteration is based on a slightly different baseline of variable values, eventually creating a 'forecast ensemble'. The ensemble allows the relative uncertainty to be assessed for each outcome dependent on how many times that outcome is presented as a solution in the model (Murphy et al. 2009).

Projected environmental changes become increasingly severe in line with increases in temperature, with changes in water availability and increased storm and flood damage are the major environmental changes projected by Parry et al. (2007). Climatologists expect a rise in sea level, consistent with a rise in global average surface temperature (Cabanès et al., 2001). The specific amount of sea level rise is contentious, with AR4 stating 18-59 cm by 2100 (Solomon et al. 2007), despite the fact that this does not account for the potential rapid and dynamic process of the melting of the Greenland ice sheet and West Antarctic Ice Sheet (WAIS). The WAIS potential has been witnessed through the rapid degradation of the Larsen B ice shelf that disintegrated within three months during 2002. This allowed glaciers behind the ice sheet to subsequently accelerate into the ocean, demonstrating powerful processes that are as yet not captured by ice-sheet models (Oppenheimer et al. 2007; Schiermeier 2007).

Oceanic processes also require further elucidation. In particular, the effect of CO₂ absorption by the ocean is unknown, specifically with respect to feedback mechanisms. Such mechanisms are expected to be heavily influenced by marine organisms that employ calcification in shell and skeletal formation (Schiermeier 2007). It is expected that oceans can act as a sink for carbon but consideration of the effect on marine ecosystems is negligible. Recent evidence of ocean acidification suggests the impact of carbon sequestration on the oceans will be considerable (Feely et al. 2004).

The carbon absorption potential of established forests is high, and can result in increased soil carbon even after trees reach maturity. For example, a forest reserve in Guangdong, China, containing an established forest has increased its soil carbon by 68 % in 25 years (Zhou et al. 2006). Conversely, models suggest that increased atmospheric CO₂ reduces the amount of water lost from plants via transpiration. Therefore, although trees may be effective carbon sinks, this sinking effect has the potential to reduce water availability (Gedney et al. 2006). This places in doubt the long-term

sustainability of trees as a carbon sink because reduced water availability may negatively feedback into the system. In addition, calculations of expected carbon emissions discussed by Mahli & Phillips (2004) suggest that even with a 25 % increase in all vegetative Amazonian biomass, anthropogenic warming would only be delayed by 4-5 years. ‘Extreme events’, for example flooding, heat-waves, storms, and ice sheet collapse are predicted to increase in frequency in the next century (Mitchell et al. 2006).

I.1.3. Non-climatic environmental change

A simplified model of species dispersal and colonisation ability under habitat destruction and climate change suggested the creation of a “deadly anthropogenic cocktail” and forecasts a significantly reduced ability of species to deal with multiple disturbances (Travis 2003). The combination of these threats is culminating in rapid global biodiversity loss (Ehrlich & Pringle 2008; Mace et al. 2005). Therefore, in addition to the impacts of climate change, we must also consider other drivers of environmental change. These drivers are many and varied so here I provide only a brief overview of the most salient for biodiversity loss, concentrating on the “evil quartet” of habitat loss, over-exploitation, extinction cascades and introduced species (Brook et al. 2008).

Habitat change, often equated with habitat loss, and fragmentation were the subjects most analysed in the three largest conservation biology journals from 2001-2005 (Fazey et al. 2005) and are recognised as significant drivers of environmental change and biodiversity loss (Haila 2002; Sala et al. 2000). However, analyses of fragmentation are hindered by the continuing debate over its definition. Fragmentation can describe loss of habitat and change in configuration (Haila 2002), or alternatively is used only to describe the latter (Fahrig 2003). Regardless of precise definition, habitat fragmentation and loss are usually explored from either a species-oriented or a pattern-oriented approach (Fischer & Lindenmayer 2007). The first approach is from the perspective of individual species and is useful for providing insight into impacts on native species. In contrast, the pattern approach uses a human perspective to assess habitat loss and fragmentation across an entire landscape, providing applicability to multiple species but

losing the finer detail of the species oriented approach (Fischer & Lindenmayer 2007). The best results would inevitably be achieved by synergistic approaches that combine the perspectives.

Most habitat loss occurs through human exploitation of natural resources and urban development (Brook et al. 2008). Globally, in 2008 mapping studies demonstrated that 50 % of all temperate grasslands, tropical dry forests, and temperate broad-leaved forests have been converted to human dominated uses (Hoekstra et al. 2005). During 2000-2005, South-east Asia experienced annual percentage deforestation of 1.5 %, closely followed by Sub-Saharan Africa with 1.4 % (Sodhi et al. 2010). Projections have estimated that South-east Asia will experience further loss of 72-90 % habitat area by 2100 (Brook et al. 2003). Many fragmentation or habitat loss scenarios are associated with thresholds at which biodiversity is disrupted (Betts et al. 2007; With & Crist 1995). For example, Bascompte & Rodriguez (2001) observed a significant drop in species richness when matrix cover increased to 65 %.

In marine environments, habitat degradation is more common than complete loss, and is often related to reduced structural complexity, such as a shift from canopy forming algae to turf forming algae (Airoidi et al. 2008). This is particularly a problem in coral reef habitats, some of which have become flattened since the 1980s owing to a mass bleaching event, and the decline of sea urchin and the structurally complex *Acropora* hard corals throughout the Caribbean (Alvarez-Filip et al. 2009). Destructive fishing is also a cause of severe habitat degradation, ranging from dynamite fishing to trawling (Mace et al. 2005).

In Europe, habitat loss primarily occurs through the conversion of natural or semi-natural habitats into agricultural or urban land. Urban development does not always equate with low biodiversity. Angold et al. (2006) found urban habitat patches to be rich in biodiversity but note the importance of connectivity and green corridors for dispersal of urban species. Agricultural land is more problematic and often takes the form of intensive monocultures. However, it is not only the direct conversion process that elicits environmental change. Agricultural practice can have a strong impact on the surrounding environment. Fertiliser run-off and

intensive livestock farming has led to nitrogen enrichment of soil (Keith et al. 2009), and toxic eutrophication of rivers, lakes (Khan & Ansari 2005) and coastal seas (Howarth 2008). In addition, this surrounding land is often subject to management. Very little of the UK landscape is natural owing to a long history of management, reflected in the fact that most woodlands are referred to as semi-natural. Changes in management regimes, which constitute an integral part of some ecosystems, can therefore create environmental change. Management strategies have begun to deal with human introduced non-native species (Waage & Reaser 2001), many of which were introduced to fuel trades in ornamental plants and fish (Chang et al. 2009), and fish stocking for angling (Stokstad 2010). Some of these species have become established in the wild and can drive environmental change, particularly habitat forming plants such as the rhododendron (Thomson et al. 1993).

Over-exploitation is thought to be the most important driver of environmental change in marine ecosystems, having a direct impact on biodiversity (Nelson 2005). To prevent confusion, I discuss over-exploitation as a driver separate from habitat loss, for example, the extraction of non-timber forest products (Ticktin 2004), the bushmeat trade (Barrett & Ratsimbazafy 2009) and over-fishing (Pauly et al. 2005; Worm et al. 2006). In the marine environment, over-exploitation is a critical issue and has led to a rapid worldwide decline of predatory fish (Pauly et al. 2005; Worm et al. 2006), in turn creating a trophic cascade (Heithaus et al. 2008) that has generated large-scale environmental change (Casini et al. 2008; Frank et al. 2005).

I.2. IMPACTS OF ENVIRONMENTAL CHANGE ON BIODIVERSITY

Owing to the character of environmental change whereby controlled experiments are generally not a possibility for large scale phenomena, many analyses of such impacts are based on correlational evidence (Parmesan & Yohe 2003; Thuiller 2007). Correlations cannot establish cause and effect (i.e. attribution). However, it is the volume of such correlations, the issue of parsimony and the use of long-term datasets that begin to add weight to the

suggestion that environmental change is a powerful driver of biodiversity change (McCarty 2001; Parmesan et al. 2005; Thuiller 2007).

Climate change has already had an impact on biodiversity at the global scale. Two syntheses, one of 143 studies, and one of 1,700 species, demonstrated that a ‘fingerprint’ of global warming already exists in the sense of a long-term, unidirectional and large-scale shift in densities, phenology, morphology and genetic frequencies (Parmesan & Yohe 2003; Root et al. 2003). Community, temporal and spatial shifts were validated using the diagnostic pattern of ‘sign-switching’. This involves comparing shifts occurring under warmer temperatures to shifts under previous cool periods. The synthesis of 1,700 species provided validation of climate change as the cause of range shifts because 84 % of species showed ‘sign-switching’ in the direction predicted by climate change (Parmesan & Yohe 2003). Globally, some butterfly and marine species have shown range shifts in the direction anticipated by climate change validated by sign-switching (Mieszkowska et al. 2006; Parmesan et al. 1999). A review by McCarty (2001) further supports large-scale, unidirectional changes. It is useful to note that range shifts do not necessarily indicate a movement from a lethal environment but there can be movement from an environment in which the species shows a reduced ability to reproduce or grow (Southward 1958; Thompson et al. 2002).

Climate scenarios can be used in conjunction with associated models of biome and species range shifts to explore the potential impacts of climate change on biodiversity. These models can be used to forecast rates of range shifts and extinctions. The specific methodologies surrounding model production vary but all come with caveats and limitations (Araujo & New 2007; Araujo et al. 2005a; Araujo et al. 2006; Araujo et al. 2005b; Botkin et al. 2007; Hansen et al. 2001; Pearson & Dawson 2003; Pearson et al. 2006). Risk assessment estimates from the most all-encompassing study so far provide estimates of the percentage of endemic and ‘near endemic’ species “committed to extinction” by 2050 at ~18-35 % (Thomas et al. 2004). Further to this, climate change was identified as a greater risk than habitat destruction in many regions when working from the IUCN Red List criteria (Thomas et al. 2004). However, this study was based on the range change

depicted by climate-envelope models and largely failed to include biotic factors. The assessment only covers terrestrial species, excluding both marine and freshwater, and so cannot be seen as a comprehensive 'global' assessment.

In European forests, it is thought that nemoral herbs will lose a median of 31-33 % of their range and, perhaps more importantly, that the range lost will be concentrated in the most genetically diverse southerly area, thus affecting phylogenetic diversity (Svenning & Skov 2006). A study of threats to plant diversity in Europe concluded that, although there is the potential for over half the studied species to become vulnerable or extinct by 2080 under the most extreme scenario tested, the figures of Thomas et al., (2004) are an overestimation of extinction risk (Thuiller et al. 2005). In addition, Thuiller et al. (2005) produced results indicating that areas with the lowest predicted species diversity loss, namely the Boreal region, were also the areas with the highest predicted species turnover. This therefore suggests that species diversity loss within a region can only be averted via a high turnover level of species, presumably from the invasion of non-native species. The severity of impacts of climatic change on rocky intertidal species is expected to increase by 2020, resulting in shifts in competitive ability at temperature boundaries between northern and southern species (Thompson et al. 2002). Range shifts, extensions and contractions are expected to continue in the same direction as observed since the 1980s (Mieszkowska et al. 2005), contributing to shifts in community composition (Thompson et al. 2002).

Land use change can result in habitat alteration and loss, consequently creating a degraded and/or fragmented landscape (Fahrig 2003). The effect of this threat to biodiversity can be complex and is often associated with thresholds of habitat cover at which impacts occur on species richness (With & Crist 1995). This was demonstrated empirically by the decline in woody vegetation cover observed at a Kansas prairie that only occurred above a threshold of 65 % matrix cover (Bascompte & Rodriguez 2001). This type of environmental change is also strongly associated with extinction debt, whereby a time lag is experienced from the disturbance

event to the final resultant species extinction (Jackson & Sax 2010; Kuussaari et al. 2009).

A key impact of land use change on biodiversity is through its effect on connectivity and subsequent dispersal, a property that is increasingly recognised as essential to maintenance of biodiversity (Sutherland et al. 2006). Most work on land use change is focused on the terrestrial and freshwater environments. However, the marine environment is also subject to modification for anthropogenic use. Offshore wind farms, aquaculture and shipping are some of the most obvious examples of marine use that impact biodiversity by altering the physical environment. The building of large offshore structures further impacts the hydrodynamics of the surrounding ocean, on which marine species are often highly dependent for dispersal of pelagic larvae (Cowen et al. 2007). Recent evidence has suggested that instead of the marine species experiencing unrestricted dispersal as was previously thought, there is in fact a continuum from fully open to fully closed communities, determined by a large extent by hydrodynamics (Cowen et al. 2007; Cowen et al. 2000; Hill 1990; James et al. 2002; Jessopp & McAllen 2008; Largier 2003; Lefebvre et al. 2003; Mitarai et al. 2008). This issue is discussed in greater depth within Chapter 6 of this thesis.

The concentration of organic nitrogen in the soil can have a strong impact on biodiversity, particularly for primary producers such as terrestrial plants and aquatic algae. Plant species vary in their tolerance of nitrogen, with species that thrive in a high nitrogen environment referred to as nitrophiles (Hill et al. 2004). Nitrogen deposition over time has been associated with decreased biodiversity of plants within Europe (Dupre et al. 2010) and coastal ecosystems globally (Howarth 2008; Sala & Knowlton 2006). The influx of nitrogen from rivers to coastal environments is predicted to increase by 13 % globally over the next 30 years following increased food production requirements (Bouwman et al. 2005). Such a large increase will lead to problematic eutrophication in coastal areas and can create dead zones through hypoxia and stratification as plankton blooms are decomposed (Bouwman et al. 2005). I discuss the role of nitrogen deposition further in Chapter 3 of this thesis.

The issue of biotic exchange refers to the influx of non-native species. These species arrive via many different routes including purposeful anthropogenic introduction (Gozlan et al. 2010), accidental introduction via ballast water (Crisp 1958) and range shifts in response to climate change (Parmesan & Yohe 2003). Non-native species can affect an area positively, negatively or have no observable effect. Only those exchanges that result in a negative effect are threats to biodiversity. Within the UK, the proportion of non-native species that are threats to native biodiversity is low and these species illicit such threats through, *inter alia*, competition, predation, herbivory and disease (Manchester & Bullock 2000). Impacts of non-native species on β -diversity are discussed Chapter 3 of this thesis in the context of biotic homogenization (Keith et al. 2009; McKinney & Lockwood 1999).

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Appendix II

Additional Analyses in Support of Chapter 3

II.1. INTRODUCTION

Greater depth of analysis was conducted on the woodland resurvey data than was presented in Chapter three. This additional analysis was exploratory and provided further detail on: (1) individual species responses and, (2) the contribution of individual species and associated traits to the observed patterns. Within this appendix I provide some additional information on the Good data, and methods, results and a brief conclusion for these analyses.

II.2. METHODOLOGY

II.2.1. Additional information on the Good Archive

The Good Archive resides with the Dorset Environmental Records Centre (DERC) and consists of approximately 7575 stands surveyed for presence of vascular plant species from 1931-1939. The species lists for each stand have now been digitised by DERC. The dataset consists of 285,864 records in a variety of habitats (Table A1). The maximum number of species recorded in any one stand was 130, whilst the average number of species per stand was forty (Horsfall 1979). All loci were revisited during the 1980s by Horsfall and assigned a status of change revealing 53 % were unchanged, 14 % were partly changed and 33 % were totally changed (Horsfall 1979; Horsfall 1980; Horsfall 1981; Horsfall 1984a; Horsfall 1984b; Horsfall 1986). No species lists were recorded during these surveys.

Some resurvey work recording species presence has been carried out on heathland (Byfield & Pearman 1996) and hedgerow loci (Button 2003). In addition to these specific resurveys, some of Good's loci overlap with Sites of Special Scientific Interest (SSSI) and National Nature Reserves (NNR) and therefore may have been 'resurveyed' unintentionally as part of regular monitoring. In addition, approximately 1250 loci overlap with Sites of Nature Conservation Importance (SNCI). However, these data are

mismatched in size and extent, often with a single SNCI, SSSI or NNR covering multiple Good loci.

Table. A1. The Prof. R. Good Archive Dataset – Habitats included in stands and number of stands surveyed per habitat
(<http://www.derc.org.uk/projects/goodHabitat.htm>)

Habitats	Stands surveyed
Aquatic vegetation: Rivers, Riversides, Streams, Lakes, Ponds, Pools	350
Marshes, Marshy meadows, Swamps	315
Maritime stands: Cliffs, Undercliffs, Rocky shores, Shingle Mud flats, Salt marsh. Sand Dunes	240
Heathland stands: Grass heath, Boggy heath, Bracken heath, Heath tracks	505
Grassland stands: Meadows, Pastures and hayfields, Embankments, roadsides	1504
Hedgebanks, Boundaries, Drove roads and Trackways	1700
Thickets: (Scrub) mixed with grassland	431
Woodland: Deciduous and Coniferous woodland, Parkland and copses etc	1535
Arable fields	365
Walls	111
Other stands: Quarries, Rabbit warrens, Fallow fields	572

II.2.2. Data Analysis

Responses of individual species were assessed by plotting bar charts to illustrate changes in number of sites occupied over time. A SIMPER analysis was then performed on the data matrix to identify which species contributed most to the discrimination between survey times. SIMPER analysis uses high-dimensional resemblance measures between species and between groups to complete two stages. We used a cut-off point of 25 % of variable (species) contributions to ensure a manageable variable list length. The two stages of SIMPER are:

- 1) Calculation of the average similarity value for each survey time and production of a list of species that provide the largest relative contribution to similarity within survey times.

- 2) Calculation of the average dissimilarity across survey times and identification of species that provide the highest contribution to discrimination between the two survey times.

Only the second stage is fully detailed within the results section here because the first stage duplicates information already provided in Chapter 3. We classified species as ‘winners’ (species that have increased in the number of sites occupied) or ‘losers’ (species that have decreased in the number of stands occupied) in line with previous publications regarding the effect of environmental change on species (e.g. Berry 2003). Standard linear regression was performed to look for a relationship between vascular plant species outcome and predictor variables. Only those species that showed a significant change in the number of sites occupied over time through McNemar’s test were included in the model, providing a total of 129 species (78 losers, 51 winners). The Empirical Log Odds Ratio (eLOR) (McCullagh & Nelder 1989) for species change in sites occupied over time allowed conversion to a continuous variable with normally distributed residuals, therefore making a suitable dependent variable (DV) for linear regression. The ratio is calculated as below:

$$\text{Empirical LOR} = \log \frac{(r_2+0.5)(n_1-r_1+0.5)}{(r_1+0.5)(n_2-r_2+0.5)}$$

Where n_1 is the total number of sites at time 1, r_1 is the number of sites occupied at time 1, n_2 is the total number of sites at time 2, and r_2 is the number of sites occupied at time 2. ELOR has a different precision for species dependent on the number of sites occupied at both times. To check the severity of the precision differences we calculated the $\text{Var}(\text{ELOR})$.

$$\text{Var}(\text{ELOR}) = \frac{1}{(n_{01}+0.5)} + \frac{1}{(n_{11}+0.5)} + \frac{1}{(n_{02}+0.5)} + \frac{1}{(n_{12}+0.5)}$$

A min/max ratio of more than two would render the ELOR unsuitable, however, less than two means the ELOR is suitable. For our analysis the Var(ELOR) min/max ratio was 0.09 / 2.69 and therefore was acceptable. The ELOR residuals for each model were tested for normality using the Shapiro-Wilk test (Life History Traits model: $W = 0.985$; $p = 0.201$; Distribution model: $W = 0.988$; $p = 0.348$). Normality of the ELOR residuals indicated the ratio was suitable for use in linear regression. It was not possible to use ELOR for a Patch model because we were testing a different dependent variable. Linear regression was also not appropriate because the dependent variable (change in species number within a patch) was not normally distributed ($W = 0.954$; $p = 0.004$).

Independent variables (IVs) were split into two subsets (Table 2). This also allowed avoidance of a large ratio of predictor variables to cases in the model, preventing inflated error values and failure of convergence (Tabachnick & Fidell 2001). Categorical IVs were made suitable for linear regression by the creation of dummy variables. IVs were tested for correlation using Spearman's Rho and a correlation matrix was created using SPSS syntax. An IV was removed if a pair of variables were correlated with a value of $r \geq 0.7$ (Pallant 2007). IVs were checked for multicollinearity by whether they had a tolerance value of < 0.10 and/or VIF of > 10 required removal of an IV (Pallant, 2007). In the event of correlation or multicollinearity, the IV with the highest correlation with all other IVs was removed. Mahalanobis distance critical value for $p < 0.001$ was used to detect outliers (Pallant 2007; Tabachnick & Fidell 2001). The β coefficient was deemed reliable if the 95% confidence intervals did not encompass the value zero because a zero value would indicate that the direction of the coefficient in indicating a decrease or increase in DV with change in IV was unreliable.

The usefulness of individual variables in model fit was tested using the change in r^2 . When using dummy variables this test is more appropriate than the default t-test (Tabachnick & Fidell 2001). Variables provide a unique significant contribution to the model if the change in unique r^2 value is significant at an α value of 5 %, and if the 95 % confidence intervals for the β coefficient did not encompass a value of zero (Pallant 2007). Standard

deviations of the DV were provided to aid interpretation of the β coefficients, because with one standard deviation increase in the IV, the DV will change in value the amount of the β coefficient (Pallant 2007). Percent of variance in the DV explained by each uniquely contributing variable was determined from the change in unique r^2 value.

The IVs included in the Life History Traits model were obtained from PLANTATT (Hill et al. 2004) and Grime (1988) and represent life history traits associated with each species (Table A2). Ellenberg indicator values are associations with habitat characteristics and are therefore representative of life history traits rather than traits in their own right (Diekmann 2003; Hill et al. 1999). Some categories in PLANTATT were amalgamated for the purpose of this regression to increase effective sample sizes and reduce problems of small samples (Tabachnick & Fidell 2001).

Table A2. Independent variables used in linear regression models. All variables apart from 'Competitive', 'Ruderal' and 'Stress-tolerant' are sourced from PLANTATT (Hill et al. 2004).

Independent variable	Description	Categories
DISPERSAL	Mode of dispersal	Abiotic Biotic Unspecialised Unknown
COMPETITIVE	Plant strategy (Grime et al. 1988)	Yes/No
RUDERAL	Plant strategy (Grime et al. 1988)	Yes/No
STRESS-TOLERANT	Plant strategy (Grime et al. 1988)	Yes/No
PERRENATION	Perrenation	Annual Biennial Perennial
LIFE FORM	Modified from the original Raunkiaer system	Chamaephyte Geophyte Hemicryptophyte Hydrophyte Phanerophyte Therophyte
WOODINESS	(woody and semi-woody categories were amalgamated)	Woody/semi-woody Herbaceous
CLONALITY	Vegetative reproduction combined with lateral spread (clonal categories were amalgamated)	Clonal Not clonal
LIGHT	Ellenberg indicator value for light	Scale of 1 to 10
MOISTURE	Ellenberg indicator value for moisture	Scale of 1 to 10
pH	Ellenberg indicator value for pH (reaction)	Scale of 1 to 10
NITROGEN	Ellenberg indicator value for nitrogen	Scale of 1 to 10
BIOME	Biogeographic element. Broad occurrence (Wide-temperate and temperate categories were amalgamated)	Boreo-temperate Wide-temperate/Temperate Southern-temperate
EASTERN LIMIT	Biogeographic element. Eastern limit of occurrence	Suboceanic European Eurosiberian Eurasian Circumpolar
WOOD	Broad habitat association with 'Broadleaved, mixed and yew woodland' and 'Coniferous woodland'	Associated Not associated
GRASS	Broad habitat association with 'Neutral grassland', 'Calcareous grassland' and 'Acid grassland'	Associated Not associated
MARSH	Broad habitat association with 'Fen, marsh and swamp (not wooded)'	Associated Not associated
URBAN	Broad habitat association with 'Built-up areas and gardens'	Associated Not associated

II.3. RESULTS

By 2008, 47.7 % of the sites had increased in species number by a mean of 45.78 %, and 50 % had decreased in number by a mean of 27.3 % (Table A3). The mean magnitude of increases was therefore larger than that of decreases.

Table A3. Summary statistics for terrestrial survey of vascular plants

	1930s	2008
Total number of species across all sites	391	324
Mean number species per site	57	53
Standard Deviation	25.63	15.16
Coefficient of Variation	44.79 %	28.71 %
Range	116 (17-133)	77 (19-96)
% stands increased in species number	-	48.84
Mean % increase	-	45
% stands decreased in species number	-	48.84
Mean % decrease	-	-28
% stands no change in species number	-	2.33

A greater number of species decreased in the number of patches occupied since the 1930s than increased (Fig. A1). For those species that were present for both surveys, 68.8 % showed either no change or changed occupation by ≤ 10 sites indicating that the majority of species did not experience dramatic changes. Out of those species that demonstrated a change of > 10 sites, the species with the largest increase was holly (*Ilex aquifolium*), which increased from 23 sites occupied in the 1930s to 71 sites occupied in 2008, an increase of 209 %. The species with the largest decrease was wild strawberry (*Fragaria vesca*), which decreased from 57 sites occupied in the 1930s to 21 sites occupied in 2008, a decrease of 63 %. 25 species did not change in the number of sites occupied over time. More species showed a decrease than an increase, illustrated by the concentration of bars to the left of the graph (Fig. A1). The mean change in number of sites occupied was -0.86 with a variance of 91.44.

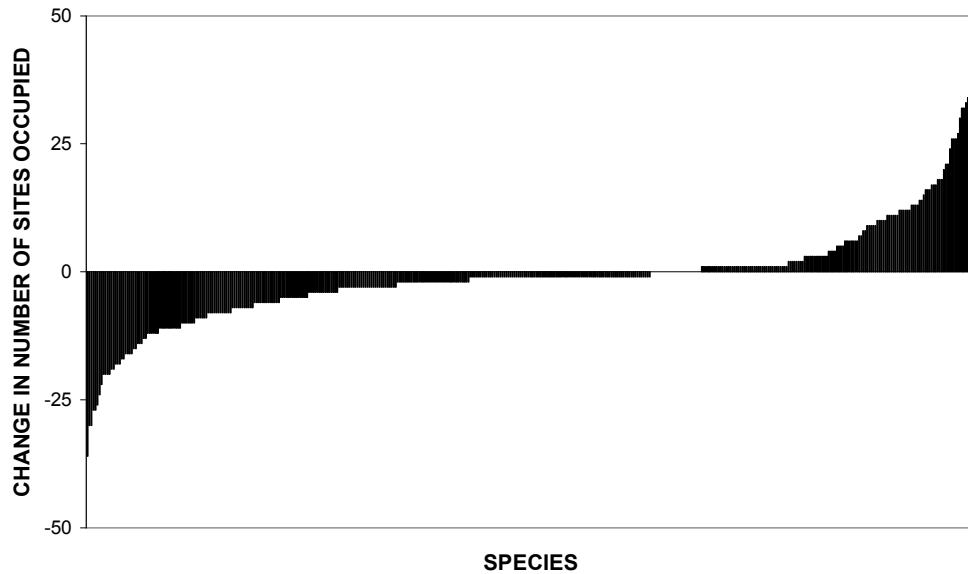


Fig. A1. Change in the number of patches occupied since the 1930s for all species that were present for both surveys. Each bar represents one species.

In light of the fact that species show individual responses, a SIMPER analysis was used on the data matrix to aid interpretation of the differences between the survey dates. The similarity value for all samples within the 1930s survey is 32.58 and for all samples within the 2008 survey is 46.36. Average dissimilarity between the two surveys is 64.93. *Ilex aquifolium* is the highest contributor to discrimination, contributing 0.99 % of the total (Fig. A2). Although this sounds like a small percentage, there are 441 species in total and therefore *I. aquifolium* contributed a four-fold higher proportion than expected if all species contributed equally.

Of the nine species contributing > 80 % to discrimination between the 1930s and 2008, eight have increased the number of sites occupied over time (Fig. A3). *Fragaria vesca* is the only one of the top nine discriminatory species to have decreased. Therefore, the largest discriminatory changes are increases. All the top nine species show a large change in number of sites occupied over time, with the top discriminator also being the species that has experienced the most change. Many of these species are also common. *Carex sylvatica* has experienced the least change but is common overall.

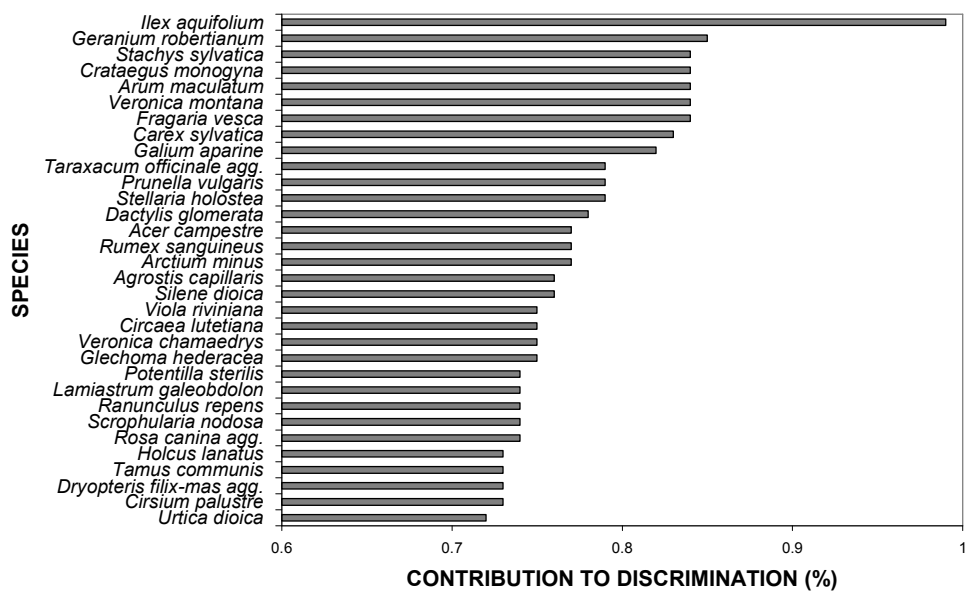


Fig. A2. Contribution of species to discrimination between the 1930s and 2008 surveys. Cumulative contribution of above species is 25.02 %.

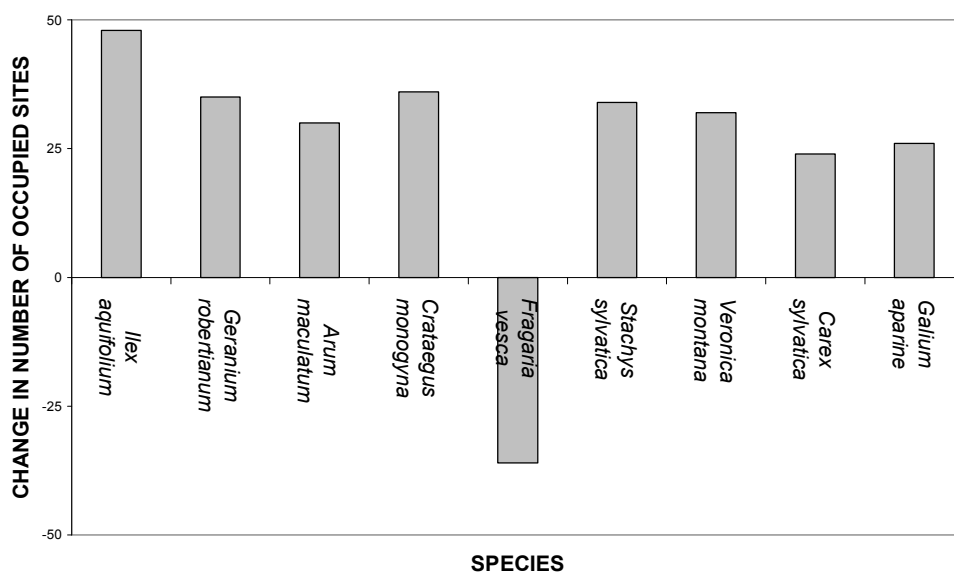


Fig. A3. Change in the number of sites occupied by species contributing > 0.80 % to discrimination between the 1930s and 2008 surveys.

Site occupation in the 1930s of lost and decreased species in comparison with gained and increased species was significantly different ($U = 16364$, $p = 0.020$). Mean rank was higher for the loser species (218.06) than winner species (188.82) indicating that loser species generally occupied a higher number of sites in the 1930s than winner species. Only those species that significantly increased (51 species) or decreased (78 species) according to McNemar's test ($p < 0.05$) were included in analysis of winner and loser characteristics (Table A4).

Table A4. Species that have significantly changed in number of sites occupied between survey times according to McNemar's test ($p < 0.05$). n_1 = number of sites occupied at time 1 (1930s); n_2 = number of sites occupied at time 2 (2008); n_{1-2} = change in number of sites occupied from 1930s to 2008. Empirical log odds ratio (LOR) used in linear regression is listed.

SPECIES	n_1	n_2	n_{1-2}	McNemar's (p)	Empirical LOR
WINNERS					
<i>Ilex aquifolium</i>	23	71	48	0.000	1.10
<i>Crataegus monogyna</i>	39	75	36	0.000	0.90
<i>Geranium robertianum</i>	35	70	35	0.000	0.79
<i>Stachys sylvatica</i>	19	53	34	0.000	0.74
<i>Taraxacum</i>	15	48	33	0.000	0.76
<i>Urtica dioica</i>	46	78	32	0.000	0.91
<i>Veronica montana</i>	24	56	32	0.000	0.67
<i>Arum maculatum</i>	28	58	30	0.000	0.62
<i>Rumex sanguineus</i>	46	73	27	0.000	0.68
<i>Galium aparine</i>	37	63	26	0.000	0.55
<i>Hedera helix</i>	51	77	26	0.000	0.75
<i>Stellaria holostea</i>	22	48	26	0.000	0.56
<i>Dactylis glomerata</i>	29	50	21	0.000	0.43
<i>Digitalis purpurea</i>	14	35	21	0.000	0.54
<i>Ribes rubrum</i>	17	37	20	0.000	0.48
<i>Phyllitis scolopendrium</i>	15	33	18	0.009	0.46
<i>Potentilla sterilis</i>	26	44	18	0.003	0.38
<i>Rosa arvensis</i>	22	40	18	0.000	0.40
<i>Alliaria petiolata</i>	2	19	17	0.000	0.99
<i>Carex remota</i>	12	29	17	0.000	0.49
<i>Geum urbanum</i>	56	73	17	0.003	0.47
<i>Fagus sylvatica</i>	16	32	16	0.001	0.41
<i>Glechoma hederacea</i>	46	62	16	0.002	0.35
<i>Poa nemoralis</i>	0	16	16	0.000	1.61
<i>Circaea lutetiana</i>	48	63	15	0.007	0.33
<i>Allium ursinum</i>	10	24	14	0.003	0.46
<i>Stellaria media</i> agg.	7	21	14	0.015	0.54

WINNERS						
<i>Fraxinus excelsior</i>	61	74	13	0.011	0.39	
<i>Juncus effusus</i>	21	34	13	0.026	0.30	
<i>Pteridium aquilinum</i>	53	66	13	0.001	0.31	
<i>Ranunculus repens</i>	50	63	13	0.030	0.29	
<i>Anemone nemorosa</i>	22	34	12	0.031	0.28	
<i>Carex pendula</i>	20	32	12	0.002	0.29	
<i>Hyacinthoides non-scripta</i>	60	72	12	0.012	0.34	
<i>Lonicera periclymenum</i>	57	69	12	0.011	0.31	
<i>Rubus fruticosus</i> agg.	69	81	12	0.004	0.57	
<i>Acer pseudoplatanus</i>	20	31	11	0.019	0.27	
<i>Cardamine flexuosa</i>	4	15	11	0.013	0.60	
<i>Lamium galeobdolon</i>	32	43	11	0.013	0.22	
<i>Rhododendron ponticum</i>	1	12	11	0.001	0.98	
<i>Rumex obtusifolius</i>	8	19	11	0.013	0.43	
<i>Aegopodium podagraria</i>	0	10	10	0.002	1.38	
<i>Equisetum sylvaticum</i>	0	10	10	0.002	1.38	
<i>Spiraea salicifolia</i> agg.	0	10	10	0.002	1.38	
<i>Anthriscus sylvestris</i>	6	15	9	0.035	0.43	
<i>Corylus avellana</i>	69	78	9	0.004	0.37	
<i>Prunus avium</i>	0	9	9	0.021	1.33	
<i>Malus sylvestris</i> sens.lat.	4	12	8	0.039	0.49	
<i>Prunus cerasifera</i>	0	6	6	0.031	1.15	
<i>Poa trivialis</i>	0	3	3	0.016	0.86	
<i>Hypericum maculatum</i>	0	1	1	0.000	0.48	
LOSERS						
<i>Fragaria vesca</i>	57	21	-36	0.000	-0.77	
<i>Centaureum erythraea</i>	31	1	-30	0.000	-1.51	
<i>Prunella vulgaris</i>	51	21	-30	0.000	-0.65	
<i>Brachypodium sylvaticum</i>	38	11	-27	0.000	-0.72	
<i>Myosotis arvensis</i>	38	11	-27	0.000	-0.72	
<i>Bellis perennis</i>	37	11	-26	0.000	-0.70	
<i>Agrimonia eupatoria</i>	25	1	-24	0.000	-1.37	
<i>Salix cinerea</i>	35	13	-22	0.000	-0.57	
<i>Poa pratensis</i> sens.lat.	22	2	-20	0.000	-1.07	
<i>Potentilla reptans</i>	26	6	-20	0.000	-0.73	
<i>Sagina procumbens</i>	20	0	-20	0.000	-1.73	
<i>Succisa pratensis</i>	20	0	-20	0.000	-1.73	
<i>Arctium minus</i>	50	31	-19	0.005	-0.39	
<i>Veronica serpyllifolia</i>	24	5	-19	0.000	-0.76	
<i>Viburnum lantana</i>	23	5	-18	0.000	-0.74	
<i>Viburnum opulus</i>	23	5	-18	0.000	-0.74	
<i>Clinopodium vulgare</i>	18	1	-17	0.000	-1.19	
<i>Stachys officinalis</i>	21	4	-17	0.000	-0.78	
<i>Angelica sylvestris</i>	23	7	-16	0.000	-0.59	
<i>Athyrium filix-femina</i>	19	3	-16	0.000	-0.84	
<i>Euonymus europaeus</i>	21	5	-16	0.000	-0.69	
<i>Scrophularia nodosa</i>	47	31	-16	0.026	-0.33	
<i>Bromopsis ramosa</i>	29	14	-15	0.003	-0.41	

LOSERS

<i>Hypericum pulchrum</i>	22	7	-15	0.001	-0.57
<i>Listera ovata</i>	26	12	-14	0.005	-0.42
<i>Persicaria hydropiper</i>	15	1	-14	0.000	-1.09
<i>Viola riviniana</i>	61	47	-14	0.027	-0.30
<i>Polystichum aculeatum</i>	15	2	-13	0.000	-0.86
<i>Viola hirta</i>	19	6	-13	0.001	-0.55
<i>Cerastium fontanum</i>	29	17	-12	0.045	-0.31
<i>Ligustrum vulgare</i>	36	24	-12	0.017	-0.27
<i>Potentilla erecta</i>	32	20	-12	0.026	-0.29
<i>Rubus caesius</i>	12	0	-12	0.003	-1.46
<i>Torilis japonica</i>	13	1	-12	0.000	-1.02
<i>Anagallis arvensis</i>	13	2	-11	0.007	-0.79
<i>Anthoxanthum odoratum</i>	24	13	-11	0.035	-0.33
<i>Cerastium glomeratum</i>	11	0	-11	0.001	-1.42
<i>Hypericum tetrapterum</i>	15	4	-11	0.003	-0.60
<i>Lotus pedunculatus</i>	19	8	-11	0.013	-0.43
<i>Mentha arvensis</i>	17	6	-11	0.013	-0.49
<i>Milium effusum</i>	11	0	-11	0.013	-1.42
<i>Scrophularia auriculata</i>	15	4	-11	0.004	-0.60
<i>Crepis capillaris</i>	11	1	-10	0.002	-0.94
<i>Galium palustre</i>	25	15	-10	0.031	-0.28
<i>Odontites vernus</i>	10	0	-10	0.002	-1.38
<i>Poa annua</i>	17	7	-10	0.006	-0.43
<i>Pulicaria dysenterica</i>	11	1	-10	0.000	-0.94
<i>Ranunculus acris</i>	12	2	-10	0.002	-0.75
<i>Chamerion angustifolium</i>	12	3	-9	0.012	-0.60
<i>Dipsacus fullonum</i>	10	1	-9	0.004	-0.89
<i>Euphrasia</i>	9	0	-9	0.004	-1.33
<i>Juncus acutiflorus</i>	11	2	-9	0.039	-0.71
<i>Teucrium scorodonia</i>	19	10	-9	0.022	-0.32
<i>Veronica arvensis</i>	11	2	-9	0.004	-0.71
<i>Achillea millefolium</i>	8	0	-8	0.008	-1.27
<i>Aphanes arvensis</i>	10	2	-8	0.008	-0.67
<i>Gnaphalium uliginosum</i>	9	1	-8	0.021	-0.84
<i>Helianthemum nummularium</i>	8	0	-8	0.008	-1.27
<i>Hypochaeris radicata</i>	10	2	-8	0.039	-0.67
<i>Lathyrus pratensis</i>	12	4	-8	0.008	-0.49
<i>Leontodon saxatilis</i>	8	0	-8	0.021	-1.27
<i>Ranunculus flammula</i>	9	1	-8	0.021	-0.84
<i>Rumex crispus</i>	11	3	-8	0.021	-0.56
<i>Trifolium dubium</i>	11	3	-8	0.039	-0.56
<i>Moehringia trinervia</i>	17	10	-7	0.049	-0.26
<i>Veronica beccabunga</i>	7	0	-7	0.001	-1.21
<i>Adoxa moschatellina</i>	6	0	-6	0.031	-1.15
<i>Callitriche</i>	6	0	-6	0.031	-1.15
<i>Chaerophyllum temulum</i>	7	1	-6	0.031	-0.73
<i>Galium saxatile</i>	9	3	-6	0.031	-0.47
<i>Juncus bufonius</i>	10	4	-6	0.021	-0.40
<i>Juncus bulbosus</i>	7	1	-6	0.039	-0.73

LOSERS						
<i>Molinia caerulea</i>	6	0	-6	0.016	-1.15	
<i>Sonchus oleraceus</i>	10	4	-6	0.039	-0.40	
<i>Ulmus</i>	7	1	-6	0.016	-0.73	
<i>Potentilla anglica</i>	8	4	-4	0.031	-0.30	
<i>Hypericum montanum</i>	2	0	-2	0.003	-0.71	
<i>Carex viridula subsp.oedocarpa</i>	2	1	-1	0.000	-0.23	

Standard linear regression assessed the ability of plant and patch attributes to predict species outcome i.e. empirical log odds ratio (LOR). Three models were created, one with independent variables representing life history traits (Table A5) and one with independent variables representing distributional information (Table A6) to determine which suite of information was a better predictor.

The total variance explained by the model ‘Life History Traits’ overall was 50 % (44 % adjusted), predicting species outcome significantly better than the intercept only model ($F = 9.041$; $df\ 12, 110$; $p < 0.001$). The model had two outliers but these were not largely above the maximum Mahalanobis distance and therefore were accepted in the model. No independent variables required removal due to multicollinearity. Four independent variables made a significant unique contribution to the model, whereby coefficient 95% confidence intervals did not include the value zero and therefore the direction of the coefficient is reliable. These variables in order of importance were Nitrogen ($p < 0.001$; $\beta = 0.56$; 12.4% of DV variance), pH ($p < 0.001$; $\beta = -0.37$; 7.7 % of DV variance), Light ($p = 0.056$; $\beta = -0.30$; 5.6 % of DV variance), and Perrenation ($p = 0.046$; $\beta = 0.28$; 1.9 % of DV variance). The β coefficient represents the amount and direction of change in the IV with one standard deviation change in the DV. Therefore, with increasing LOR, nitrogen and perrenation will increase whilst light and pH will decrease.

The total variance explained by the model ‘Distribution’ overall was 30 % (27 % adjusted), predicting species outcome significantly better than the intercept only model ($F = 8.31$; $df\ 6, 114$; $p < 0.001$). The model had no outliers. No independent variables required removal due to

multicollinearity. Three independent variables made a significant unique contribution to the model, whereby coefficient 95 % confidence intervals did not include the value zero. These variables in order of importance were Wood ($p = 0.001$; $\beta = 0.34$; 7.4 % of DV variance), Grass ($p = 0.015$; $\beta = -0.23$; 3.7 % of DV variance) and Urban ($p = 0.036$; $\beta = 0.18$; 2.7 % of DV variance). Therefore, with increasing LOR, wood and urban will increase whilst grass will decrease.

Table A5. Linear regression model information for 'Life History Traits' model and for each independent variable included. Variables that made a unique significant contribution to the model are in bold.

Independent Variable	Unique r^2		Coefficient			Tolerance
	Change	(p)	B	CI Lower	CI Upper	
Dispersal	0.000	0.820	0.02	-0.11	0.14	0.76
Competitive	0.000	0.806	0.02	-0.25	0.32	0.52
Ruderal	0.000	0.925	0.01	-0.26	0.29	0.54
Stress-tolerant	0.003	0.460	-0.06	-0.33	0.15	0.73
Perrenation	0.019	0.046	0.28	0.01	0.60	0.24
Life form	0.005	0.281	0.14	-0.59	0.29	0.26
Woodiness	0.002	0.494	-0.08	-0.17	0.33	0.35
Clonality	0.002	0.529	0.05	-0.15	0.04	0.66
Light	0.056	0.001	-0.30	0.18	0.39	0.61
Moisture	0.006	0.274	-0.08	-0.06	0.22	0.76
pH	0.077	0.000	-0.37	-0.38	-0.13	0.55
Nitrogen	0.124	0.000	0.56	-0.29	-0.08	0.40

1 S.D. of Empirical LOR (DV)	0.76
dfs for Mahalanobis	12
critical value for Mahalanobis (at $p < 0.001$)	32.91
Maximum Mahalanobis value in model	40.14

Table A6. Linear regression model information for 'Distribution' model and for each independent variable included. Variables that made a unique significant contribution to the model are in bold.

Independent Variable	Unique r^2		Coefficient			Tolerance
	Change	(<i>p</i>)	B	CI Lower	CI Upper	
Biome	0.000	0.777	0.03	-0.17	0.23	0.77
Eastern limit	0.009	0.225	-0.11	-0.18	0.04	0.80
Wood	0.074	0.001	0.34	0.22	0.80	0.65
Grass	0.037	0.015	-0.23	-0.68	-0.07	0.69
Marsh	0.013	0.151	-0.13	-0.64	0.10	0.80
Urban	0.027	0.036	0.18	0.03	0.97	0.89

1 S.D. of Empirical LOR	0.75
dfs for Mahalanobis	6
critical value for Mahalanobis (at $p < 0.001$)	22.46
Maximum Mahalanobis. value in model	18.19

The models both predict significantly better than the intercept only model, however, the 'Life History Traits' model accurately predicted more variance and therefore was the superior model. The models allow characteristics of attributes to be associated with increasing and decreasing species (Table A7).

Table. A7. Summary of characteristics of attributes associated with winner and loser species determined from linear regression models 'Life History Traits' and 'Distribution', and Patch characteristic correlations.

Model	Attribute	Increased species Characteristic	Decreased species Characteristic
Life History Traits	Light	Semi-shade conditions	Well lit conditions
	Nitrogen	Richly fertile soils	Intermediately fertile soils
	pH	Moderately acidic	Weakly acidic
	Perrenation	Perrenial	Annual
Distribution	Wood	Associated with woodland broad habitat	
	Grass		Associated with calcareous/ neutral/acid grassland broad habitat
	Urban	Associated with built-up areas and gardens broad habitat	

CONCLUSION

The analyses presented within this appendix demonstrate the individualistic responses of woodland plant species. Species that provided the greatest contribution to discrimination of the two survey times were overwhelmingly species that had increased in site occupation, suggesting that increases were more important to overall community composition than decreases. Those species that have increased in site occupation are more characteristic of cooler, semi-shaded woodland or urban areas with richly fertile, weakly acidic soils. In contrast, decreased species are more characteristic of warmer, well-lit grassland with intermediately fertile, moderately acidic soils.

II.5. REFERENCES

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Appendix III

Additional Literature Review in Support of

Chapter 6

III.1. LARVAL TRANSPORT AND CONNECTIVITY

III.1.1. Intertidal invertebrate dispersal

There are three larval types pertaining to different reproductive strategies: direct developers (or non-pelagic larvae), lecithotrophic larvae, and planktotrophic larvae (Vance 1973). Direct developers progress through all larval stages within an egg that remains in the intertidal environment and emerge onto the shore as juveniles. The strategy has low risk of predation and a reliable food supply, however, fewer young can be produced because it is more energetically costly and dispersal is severely curtailed (Nybakken & Bertness 2005). Lecithotrophic species produce larvae that have a self-contained yolk supply and develop within the pelagic environment. Such larvae are liberated from dependence on plankton for food whilst being able to disperse efficiently, however, few larvae can be produced because of the associated energetic cost (Nybakken & Bertness 2005). Planktotrophic larvae are dependent on plankton in the pelagic environment for food. Many larvae can be produced because food supplies are not required, however, the risk of predation and unreliability of food is increased (Nybakken & Bertness 2005). The length of the pelagic phase varies from days to weeks, and can be up to one year (Dibacco et al. 2006; Nybakken & Bertness 2005).

Therefore, the majority of marine species have a pelagic larval phase early in their life history that is the dispersing propagule (Dibacco et al. 2006; Nybakken & Bertness 2005). The term ‘larval dispersal’ is inclusive of brooding and release of larvae, pelagic transport, settlement and recruitment (Pineda et al. 2007). The evolutionary purpose behind larval dispersal is uncertain but may include competition reduction, increased food

supply, increasing resilience to stochastic catastrophes, and avoidance of parental predators (Gaines et al. 2007). An alternative possibility is that the pelagic phase evolved to take advantage of the rich nutritional resources available offshore, and transport is simply a by-product (Gaines et al. 2007).

Larval transport, although just one aspect of dispersal, is arguably one of the most important areas for current research because it is key to effective planning of marine reserve networks (Jones et al. 2007; Warner & Cowen 2002). In the current era of rapid environmental change, unhindered dispersal is essential for the persistence of species. Traditionally larval transport was viewed as a diffusive process, with equal distance of larval movement in all directions from a source point. However, the influence of advection (along-shore directional transport) and hydrodynamic features such as currents and eddies is critical (Alexander & Roughgarden 1996) and are an integral consideration in larval transport. Some larvae can actively swim vertically through the water column to position themselves within particular currents, and/or horizontally in search of food or suitable settlement sites (Pineda et al. 2007). Larval choice is thought to be stimulated by a variety of environmental and biochemical stimuli, including phototaxis and pheromone release from adult populations (Jenkins 2005; Keough & Downes 1982; Kingsford et al. 2002; Nybakken & Bertness 2005; Sponaugle et al. 2002). However, when currents exceed the swimming speed of larvae, advection and diffusion become the prominent factors controlling larval transport.

Larval development is highly variable among marine species and can include multiple developmental stages, such as the nauplii and cyprid stages of barnacle larvae, each of which has different life history characteristics (Tapia & Pineda 2007). Stages are often referred to as 'pre-competent' when first released and later as 'competent' once they have reached a stage capable of settlement (Jackson & Strathmann 1981; Rilov et al. 2008). The duration of competent stage(s) generally exceed or are equal to pre-competent stages (Jackson & Strathmann 1981). Furthermore, the duration of pelagic larval development can be influenced by environmental factors and has been explicitly linked to temperature as a constant quantifiable

effect across many species, revealing a predictable effect of ocean temperature on larval development (O'Connor et al. 2007).

Pelagic larval duration varies greatly between marine species. The duration of the pelagic larval phase affects larval retention by keeping larvae closer to its natal population (Sponaugle et al. 2002) and mortality rates because the longer a larva is in the plankton, the more likely it is to be predated upon (Dibacco et al. 2006; Jackson & Strathmann 1981). The concepts of the “growth-mortality hypotheses” have been offered as an explanation of larval survival whereby those larvae that are large, fast growing and rapidly move through stages of development are the most likely to survive (Hawn et al. 2005; Pineda et al. 2007).

III.1.2. Connectivity

Connectivity is important to consider when seeking understanding of changes in community composition because colonisation is not possible unless connectivity exists between a reproductive population and the currently unoccupied patch. Furthermore, the concept is essential in determining spatially explicit management strategies for marine systems (Cowen et al. 2007; Jones et al. 2007).

The connectivity of intertidal invertebrate communities is largely dependent upon the dispersal of pelagic larvae during the early stages of the life-cycle (Cowen et al. 2007). This is particularly true when the adult form of the species is sessile because it is often the only dispersive part of the life cycle. Occasionally adults raft to new locations; however, this is thought to be a chance event and not the primary mode of dispersal. Connectivity for terrestrial species can be defined for a wealth of spatial and temporal scales (Crooks & Sanjayan 2006), however, there is no single clear definition for connectivity of marine systems owing to the plethora of different spatial and temporal scales (Gaines et al. 2007; Pineda et al. 2007).

In a recent overview, Cowen et al. (2007) suggest there are four prongs to developing our grasp of the currently understudied field of marine connectivity: “Observation, explanation, consequences, and application”. Furthermore, in order to make useful predictions, we must gain a process-

based understanding of larval dispersal (Cowen et al. 2007). Marine systems were originally assumed to be open because pelagic larval phases were not subject to barriers (Cowen et al. 2000). However, it is becoming increasingly obvious that this is not the case and that local retention of larvae is common (Cowen et al. 2007; Cowen et al. 2000; Hill 1990; James et al. 2002; Jessopp & McAllen 2008; Largier 2003; Lefebvre et al. 2003; Mitarai et al. 2008). Complete and semi-permeable barriers to larval transport affect the connectivity and subsequently the recruitment of rocky shore invertebrates (Gaines et al. 2007; Gaylord & Gaines 2000; Rilov et al. 2008), therefore, an area may remain uncolonised despite suitable climatic conditions because of its inaccessibility to propagules (Crisp & Southward 1953).

Headlands separating bays are often associated with hydrodynamic features such as eddies (Largier 2003) that create turbulence, causing high larval mortality, thus amplifying the barrier effect of the landmass (Jessopp 2007). For example, Start Point on the south-west coast of England was shown to pose a significant barrier to the westward movement of *Mytilus edulis* larvae (Gilg & Hilbish 2003). Upwelling is another hydrographic feature that can affect larval transport (Alexander & Roughgarden 1996). It is often followed by a relaxation event and it is the timing and duration of each of these events that can carry larvae either away from or onto the shore (Alexander & Roughgarden 1996; Schiel 2004).

Larvae must overcome additional barriers as they are transported onshore. The surf zone is one example of a semi-permeable barrier that was suggested as the reason for a decoupling of near-shore larval abundance and onshore recruitment of mussel larvae (Rilov et al. 2008). The final approach of larvae to shore is much understudied but is likely to be affected by the presence of reefs, kelp forests and the rocky shore (Gawarkiewicz et al. 2007).

Connectivity between protected areas is especially important in ensuring an ecologically coherent reserve network. In the English Channel, there are eight Special Areas of Conservation (SACs) and nine Special Protected Areas (SPAs) with marine components (Marine Natura Project Group 2007). The two designations often overlap on the same site,

exemplified by a focal point of protected areas around Southampton and the Solent. A focus on this area is particularly interesting because it is central along the southern England coastline, and therefore is likely to be an important connective area between west and east. However, it is also an area of low recruitment in some intertidal invertebrates leading it to be suggested as a bottleneck to larval transport (Herbert et al. 2007). An ‘ecologically coherent’ national network of such marine protected areas, with any shortfall in network design addressed through newly designated marine conservation zones (MCZs) is under development in accordance with the UK Marine Bill, with site designations expected to be completed by 2012 (JNCC 2009; Parliamentary Office of Science and Technology 2008).

III.1.3. Methods in Larval Transport Research

The major data required to study larval transport is data on source populations and larval destinations (Cowen et al. 2007). The availability of such data at present is limited and requires much effort to enhance. However, studies of larval movement in the open ocean are difficult. The need for empirical data to inform models is essential (Pineda et al. 2007) and much of what we currently have should be treated as steps on the way to a full understanding and capability to predict larval transport.

Larval transport is currently studied using a variety of approaches: visual tracking, isolated or point source larval release sites, inference of dispersal profiles, modelling, geographic surveys of genetic variation, and tagging of larvae using artificial or natural tags (Dibacco et al. 2006). Visual tracking is only suitable for large, easily visible larvae and therefore is not possible for most species. Isolated or point source larval release is site-specific and therefore is not applicable to most species/regions. Grantham et al (2003) inferred dispersal profiles for 91 species based on their life history characteristics and grouped by habitat. Although this may provide a useful base-line estimate there are many assumptions to this approach. In light of these limitations, the other three methods are the most common.

Numerical models that have been described to date are often ‘advection-diffusion models’, however, such models have neglected to incorporate biological parameters (e.g. Marinone et al. 2008). Colby (1988)

advocated that passive advection and diffusion should be the null hypothesis for larval transport studies, with larval behaviour acting as the experimental ‘treatment’. Gaylord & Gaines (2000) also note that some models are limited because they do not incorporate the lag between pre-competent and competent larvae, and non-reproducing juveniles and reproducing adults. More dynamic ‘advection-diffusion-mortality’ models provide a more accurate picture of larval transport (Hill 1990). For example, Norway lobster larvae retention and mortality was found to be best explained by advection and could not be explained by simple diffusion (Hill 1990). In a study of regional scale dynamics of reef fish metapopulations, larvae were simulated with a passive larval stage before moving onto an actively motile larval phase allowing accurate estimates of larval retention (James et al. 2002). Rule-based models may be able to incorporate larval behaviour, however, prior to establishing these models further empirical information is required on those behaviours (Pineda et al. 2007). Gilg & Hilbish (2003) combined the use of oceanographic modelling with genetic analysis to assess connectivity of two mussel species around a hybrid zone and found good agreement between the two methods. Genetic analysis is a useful method in assessing connectivity, however, it may not be appropriate for small spatial and temporal scale studies (Hedgecock et al. 2007). One of the most recent advances in modelling larval transport used a graph-theoretic approach to model larval transport in an area of coral reef (Treml et al. 2008). The method allows connectivity metrics to be readily gained for models with various assumptions, however, the methodology surrounding such modelling is still in its infancy and is not yet user-friendly.

Tagging allows mark-recapture studies and can be achieved using artificial or natural tags. Artificial tags are very difficult to use with the often microscopic larvae of intertidal invertebrates. However, artificial marks applied through immersion of larvae in marker chemicals (e.g. fluorescent compounds) or from environmental perturbations (e.g. thermal signals on otoliths) can be efficient, cost effective and highly robust (Thorrold et al. 2002). Alternatively, natural markers can be harnessed. Genetic markers can be artificially bred into selected individuals prior to release or transgenic individuals can be created, although the effort required

for such a method is large (Thorrold et al. 2002). ‘Elemental fingerprinting’ has much potential in enhancing larval transport studies and involves identifying chemical signatures indicative of source areas that are incorporated into the tissues of the focal species, primarily into their hard body parts (Becker et al. 2007; Thorrold et al. 2002). The method has been used to demonstrate the difference in connectivity of two mussel species (Becker et al. 2007).

III.1.4. Graph-theoretic approach

Connectivity of intertidal rocky shore patches could be modelled using a graph-theoretic approach (Treml et al. 2008; Urban & Keitt 2001; Urban et al. 2009; Urban et al. 2008). The approach has been used with increasing frequency in the terrestrial environment (Urban et al. 2009) but only once in the marine environment (Treml et al. 2008). Connectivity models are created based upon distance, probability and/or adjacency matrices. For the intertidal environment, a null connectivity model can be based on geographic distances, therefore assuming only the influence of distance with no influence of barriers (Treml et al. 2008). Experimental connectivity models can be based on distance (days) between patches determined through the hydrodynamic model described in the following section, which incorporates potential barriers to dispersal (Treml et al. 2008). The hydrodynamic model simulates the number of days required for larvae to be transported from each patch (i) to every other patch (j) (Treml et al. 2008). This information will create a distance matrix \mathbf{D}_{ij} and/or a probability matrix \mathbf{P}_{ij} . Distances will need to account for settlement competency so larvae must reach the patch within their competency window for those patches to be considered connected.

A graph based upon these matrices is then created whereby patches of intertidal shore are termed ‘nodes’ and connections between patches are termed ‘edges’ (Fig. A4). Edges can vary in their strength of connectedness, for our purpose representing probability of dispersal between nodes. Graphs can be unidirectional or directional, the latter is called a ‘digraph’ (Urban & Keitt 2001). Each node can be assigned specific attributes e.g. spatial coordinates, area, size, productivity. Once the graph is created it can be used

to explore various graph properties that equate to connectivity metrics and scenarios, for example, least-cost pathways and the effects of removing particular edges and/or nodes (Treml et al. 2008; Urban & Keitt 2001).

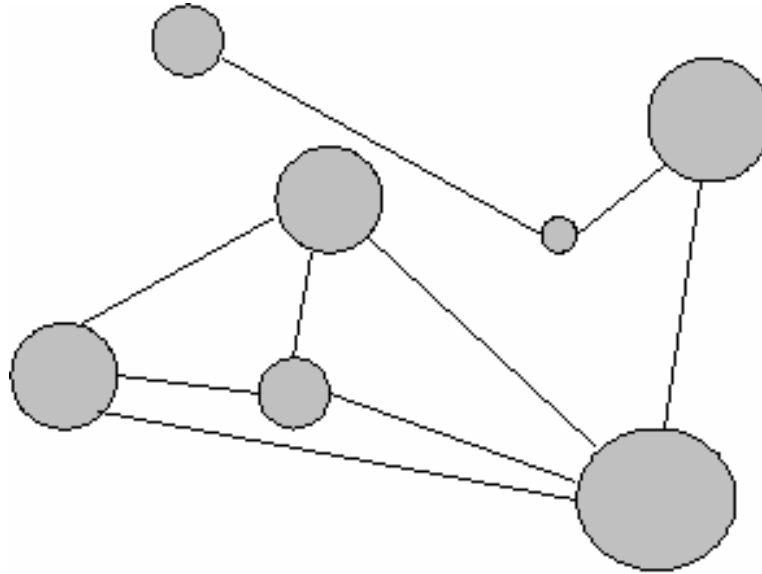


Fig. A4. Example of a graph of connectivity used for in the graph theoretic approach. Grey circles represent ‘nodes’ (patches), lines between nodes are ‘edges’ (connections between patches). In application to meso-scale ecology, it depicts potential dispersal pathways.

Using this approach it is possible to generate connectivity model for various scenarios and for species with different dispersal modes (direct, short planktonic, long planktonic) and use the models to identify which scenario best explains observed range shifts or to predict future range shifts.

III.2. BIOCLIMATIC ENVELOPE MODELLING

Models of species bioclimatic envelopes (i.e. required environmental parameters for survival of a species) are an oft used method to examine potential range shifts as an impact of environmental change, for example, ‘Modelling natural resource responses to climate change’ (MONARCH 1, 2, 3) (Hossell et al. 2003; Walmsley et al. 2007) and ‘Assessing Climate Change Effects on Land use and Ecosystems; from Regional Analysis to The European Scale’ (ACCELRAATES) (Rounsevell et al. 2006). However, these models are based on many assumptions that have not been tested with

empirical data. It is vital that we are aware of and understand the potential flaws within these models to enable improvements to be made to their predictive capability. I outline the main criticisms of bioclimatic envelope models (BEMs) here.

BEMs generally do not include biotic interactions such as competition and predator-prey relationships that are major factors influencing a species' range. Although this may provide an acceptable projection of future range at a large scale, this technique is inappropriate at the local scale (Pearson & Dawson 2003). Model outputs of projected red squirrel (*Sciurus vulgaris*) range exemplifies the limitations. Red squirrels have been projected by BEMs to disperse across the entire UK under climate change. However, we know that this is not possible because of competition and viral transmission from the grey squirrel (*Sciurus carolinensis*) (Tompkins et al. 2003). The extension to ACCELERATES incorporates dispersal into the model at a categorical level, improving the realism. However, with so many interactions unaccounted for, these models cannot provide robust community composition predictions. Conversely, it would be an impossible task to account for every community interaction within a community and, although improvement is possible, the limits of our understanding should be recognised.

BEMs can only use observed realised niche as a basis to create a species envelope, creating an immediate paradox with Hutchinson's definition of the niche: "The niche is a set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes." (Hutchinson 1957). The fundamental niche is determined by abiotic conditions, whereas the realised niche is further constrained by biotic conditions. Therefore, the paradox lies in the use of the realised (i.e. observable) niche to provide model outputs for a fundamental niche. BEM can only use observed realised niche as a basis to create a species envelope and therefore must assume equilibrium with the climate (Pearson & Dawson 2003). Although this may be the case for some species, we know that at least for herptiles this is unlikely (Araujo & Pearson 2005; Araujo et al. 2006). As further illustration, amphibian and reptile distribution is suggested to be more a function of past ice-age refugia than a function of current

climate (Araujo & Pearson 2005; Webb 1986; Williams et al. 2001). Therefore, BEM outputs may fail to include potential future range areas.

Niche conservatism is a principle of BEMs. This conservatism assumes the species will have no evolutionary potential in the projected amount of time. This may well be the case for species with a long generation time and species restricted by land use barriers (Opdam & Wascher 2004). However, short generation species may be capable of adapting to altered climate in the time-frame used in these projections. Adaptations to climate have already been observed in bush crickets, butterflies and navelwort (Pearson & Dawson 2003). Furthermore, if niches are conserved, by what process can speciation occur? Conversely, niche conservatism can be used to argue against individualistic species responses because it states that species cannot move geographically because they are limited by their niche and exist in 'niche-assembled communities' (Alonso et al. 2006). Therefore, it may be more pertinent to induce neutral theory to explain individualistic response whereby species community is 'dispersal-assembled' (Hubbell 2001). However, if this is done, this fundamentally contrasts with the use of BEMs based on niche theory. Although neutral theory has received criticism (Alonso et al. 2006), it was originally created as a null theory. It also highlights the plethora of conceptual theory surrounding range determination of species, which through only considering niche-assembled communities, BEMs have disregarded.

The scale at which such models are used is important and the most appropriate scale has a dependence on characteristics of the target species (Guisan & Thuiller 2007). For example, a highly mobile species would be best examined at a larger scale than a relatively sessile species. Opdam and Wascher (2004) suggest such modelling should be at the landscape scale. Midgley et al. (2002) expand on this issue by noting the discrepancies of using a single species model versus a biome scale model. The study concluded that the biome level significantly underestimated species loss although it was much faster and more pragmatic to run.

Finally, most BEMs clearly delineate different habitat types while in practice, habitats often show a gradual transition. The quality of surrounding habitat is suggested to be high importance to the survivability of the core

habitat for species (Moilanen & Wintle 2007). This was manifested as the ‘boundary-quality penalty’ (BQP) and could be incorporated into future BEMs.

In conclusion, the usefulness of current modelling studies for analysis of community composition must be treated cautiously. However, BEMs do provide a good coarse estimate of individual species occurrence in the future on large scales (Araujo & New 2007; Araujo & Pearson 2005; Araujo et al. 2005; Pearson & Dawson 2003; Pearson et al. 2006; Thuiller et al. 2003; Thuiller et al. 2004), and although ecological traits have a significant effect on accuracy of the models, this effect is suggested to be small (McPherson & Jetz 2007). Therefore, whilst not providing evidence for or against individualistic species responses, these models could give a coarse estimate of species assemblages in particular areas in the future.

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Appendix IV

Sensitivity Analyses for Particle Tracking Module

The particle tracking module used within the hydrodynamic modelling approach to larval transport required parameter values (Table A8). The decay parameter was not used because estimates of larval mortality were subject to very large errors. Particle mass within ‘Class’ and horizontal dispersion were subjected to sensitivity analysis. This involved variation of the parameter values across five orders of magnitude to determine whether there was a substantial effect on the model output. Model output was represented by the number of particles that settled on each rocky shore.

Table A8. Larval input parameters available in particle tracking module

Parameter	Description	Option Chosen	Input Value
Class	Class of particles i.e. larvae	EUM	Specify unit of measurement of particle e.g. Kg, milligram...
		Particle mass	Specify particle mass
Source	The source location of the particles i.e. rocky shore centroids	Maximum particle age	If particle became older than this it will be excluded from the simulation.
		Fixed location	Grid coordinates. Specify projection, in this case British National Grid, and ensured it's the same projection as that used for HD model. Also required depth of larval release.
		Varying in time	dfs0 file with time series data. Input flux value for each time step. For this application this represents brooding season.
Decay	Decay rate of particle i.e. larval mortality rate	None	
Dispersion	Horizontal	Dispersion coefficient formulation	Value estimate measured by m s^{-1}
Drift profile	Movement of particles		Selected ‘from HD’

Particle mass was not substantially altered when the values were varied from 0.06825 μg to 682.5 μg (Fig. A5). Therefore it can be concluded that error in this parameter would not greatly effect the result. This also suggested that the model was suitable for the entire larval duration inclusive of numerous larval stages of increasing mass, and was applicable to a wide variety of species because larvae of different mass would experience the same transport. In contrast, horizontal dispersion coefficient did substantially impact the model output (Fig. A6). This parameter is notoriously difficult to estimate. To address this issue I sought expert advice from a contact at HR Wallingford. Sensitivity analyses were conducted for 10 rocky shore sites that corresponded to those used for recruitment validation (see Chapter six). Here I present the sensitivity analysis results from one site only because all sites demonstrated a similar pattern.

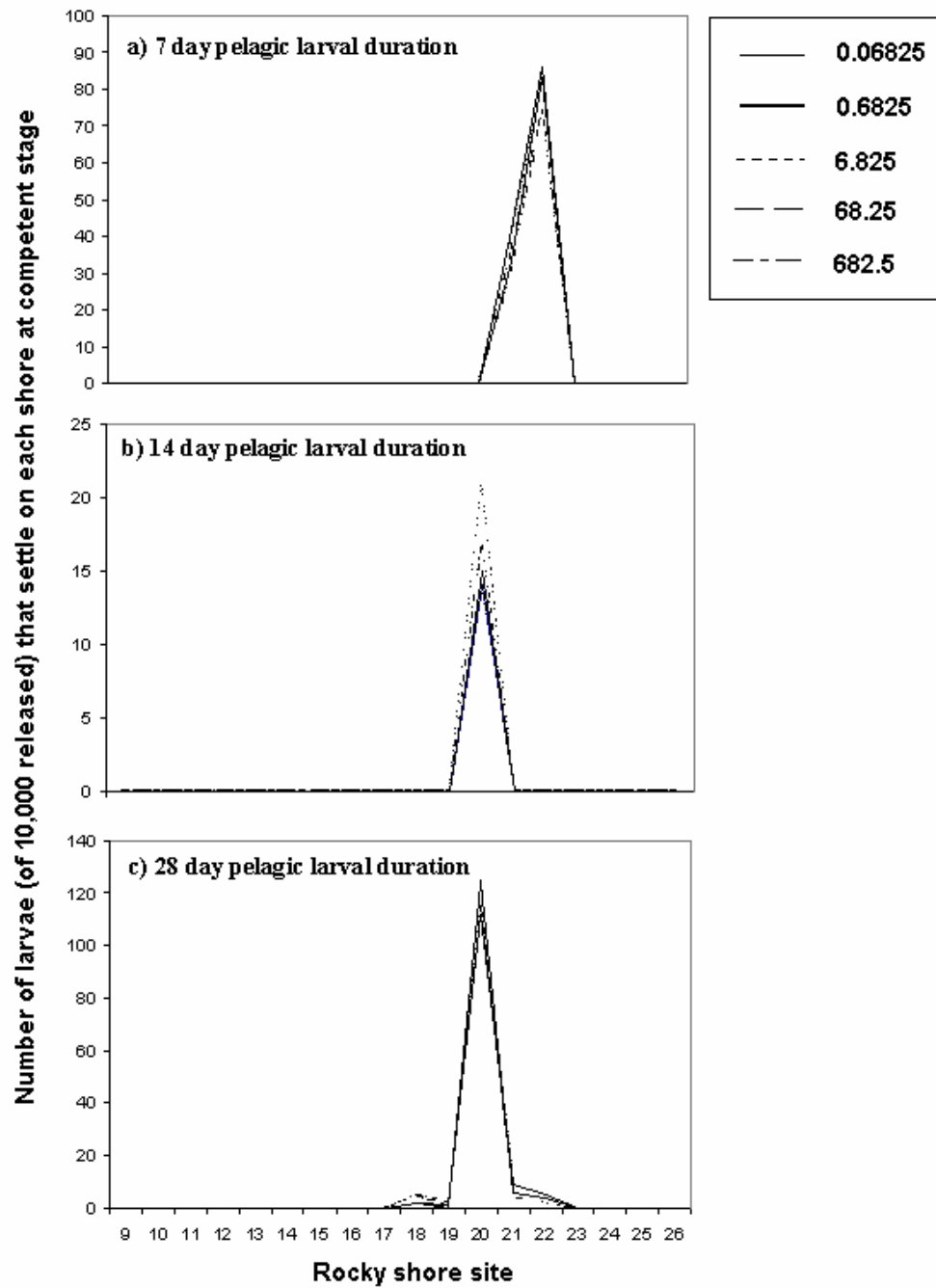


Fig. A5. Particle mass sensitivity analysis for larval release from rocky shore site 21 at each pelagic larval duration. Values tested are measured in μg .

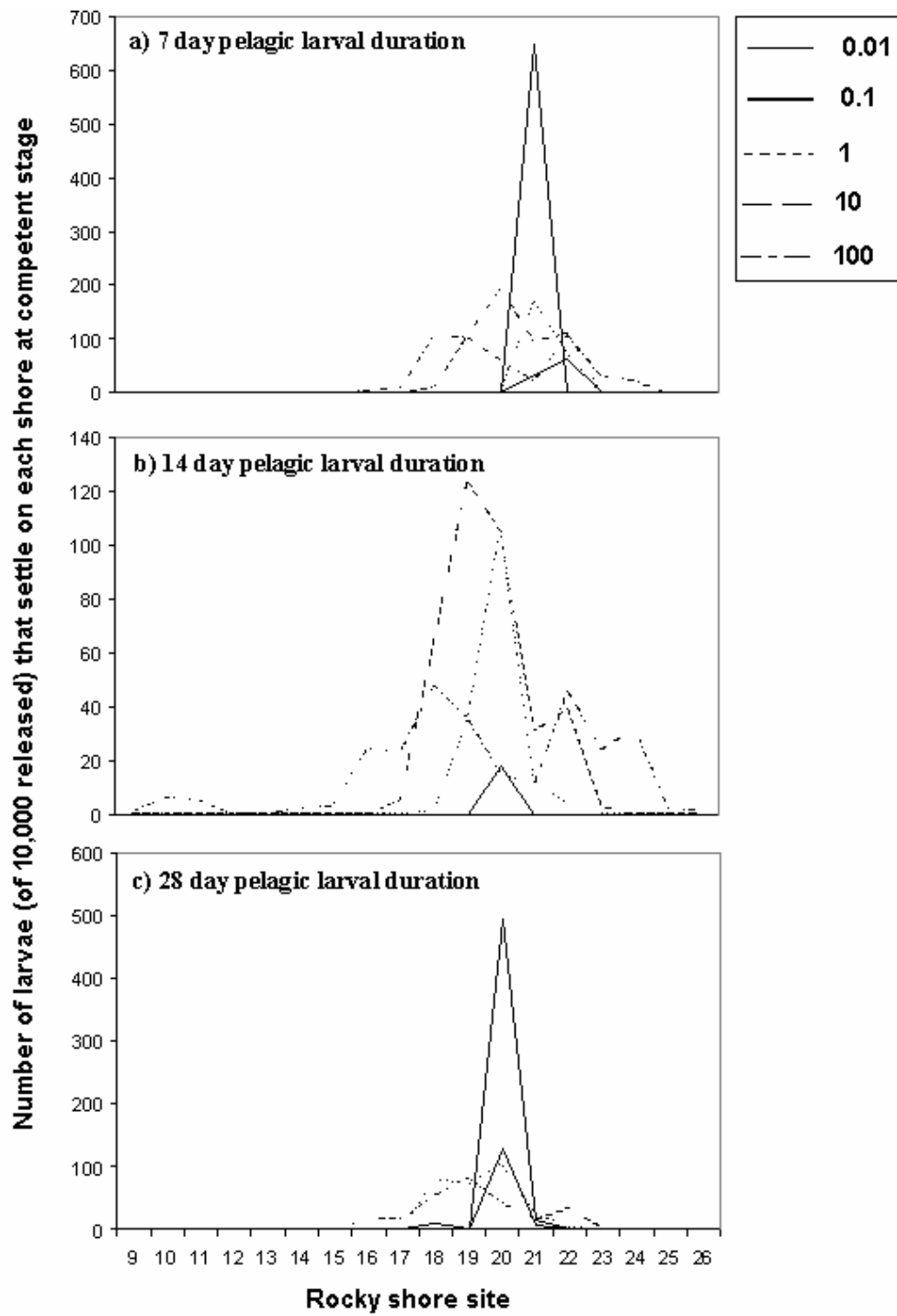


Fig. A6. Horizontal dispersion coefficient sensitivity analysis for larval release from rocky shore site 21 at each pelagic larval duration. Values tested are measured in m s^{-1}