Pattern and Process in Macroecology

KEVIN J. GASTON
Royal Society University Research Fellow
Department of Animal and Plant Sciences,
University of Sheffield,
Sheffield

TIM M. BLACKBURN
Leverhulme Special Research Fellow
Imperial College (London University),
Silwood Park,
Ascot

Blackwell Publishing

Pattern and Process in Macroecology

Pattern and Process in Macroecology

KEVIN J. GASTON
Royal Society University Research Fellow
Department of Animal and Plant Sciences,
University of Sheffield,
Sheffield

TIM M. BLACKBURN
Leverhulme Special Research Fellow
Imperial College (London University),
Silwood Park,
Ascot

Blackwell
Publishing

BLACKWELL PUBLISHING
350 Main Street, Malden, MA 02148-5020, USA
9600 Garsington Road, Oxford OX4 2DQ, UK
550 Swanston Street, Carlton, Victoria 3053, Australia

First published 2000

2 2006

Library of Congress Cataloging-in-Publication Data

Gaston, Kevin J.
Pattern and process in macroecology / Kevin J. Gaston, Tim M. Blackburn.
p.cm.
Includes bibliographical references (p.).
ISBN 0-632-05653-3
1. Ecology. I. Blackburn, Tim M. II. Title.

QH541.G38 2000
577—dc21 00-029739

ISBN-13: 978-0-632-05653-8

A catalogue record for this title is available from the British Library.

Set by Graphicraft Ltd, Hong Kong
Printed and bound in the United Kingdom
by TJ International, Padstow, Cornwall

The publisher's policy is to use permanent paper from mills that operate a sustainable forestry policy, and which has been manufactured from pulp processed using acid-free and elementary chlorine-free practices. Furthermore, the publisher ensures that the text paper and cover board used have met acceptable environmental accreditation standards.

For further information on
Blackwell Publishing, visit our website:
www.blackwellpublishing.com

Contents

Preface

The first photographs of the Earth to be taken from outer space are said to have had a profound influence on how humanity perceives its place in the Universe. They provided a true visual representation of the broad sweep of the planet we inhabit and how little of it each of us has explored, and, perhaps more importantly, set against the vastness of the cosmos they gave a sense of the vulnerability of this tiny spherical piece of rock. The significance of these images results above all else from the difficulty which humans have in comprehending phenomena at large spatial scales. It is now possible to traverse thousands of kilometres in a few hours, but most people live out their day-to-day existence in thousands of metres. In this sense our lives are perhaps little changed from those of our prehistoric ancestors. Almost inevitably, in consequence we are best adapted to detecting and responding to patterns and processes at such limited scales. After all, it is these which determine who we meet, where we gain food and shelter, and what threatens our existence from moment to moment.

It would be surprising indeed if the scales on which humans typically operate were not strongly to influence the way we conduct many of our affairs. This applies just as much to the way in which science is carried out as it does to other aspects of wider society, despite the attempts of scientists to strive for absolute objectivity. Thus, in ecology, the majority of studies are conducted over small areas—experimental plots seldom span the size of the average back yard—and explanations for observed findings are usually couched in terms of processes which act at the scale of the locality of interest. Just as most natural historians have a 'local patch', whose denizens they come to know, so many ecologists have a 'study plot', the activities of whose denizens both stimulate research questions and supply the answers.

Although humans detect and respond best to patterns and processes at local scales, it is obvious that wider forces have always been at work on their lives. Arguably, attempts to explain, influence and ameliorate the unpredictable vicissitudes of a world beyond the comprehension of people occupying only a small part of it have influenced the establishment of a number of religions. The most obvious manifestation of such wider forces (especially to two Englishmen) is in the effect of large-scale changes and differences in the climate on the fortunes of human societies around the world. For example, the so-called Little Ice Age in the middle of the second millennium AD is thought to have been responsible for the extinction of the small Viking colony established on Greenland around four hundred years earlier. The climatic change meant that the crops on which these people subsisted could no longer be maintained, while essential imports from Europe dried up as the voyage to Greenland became impossibly harsh.

More dramatically, Diamond (1998) argues convincingly that large-scale differences in the climate, geography and biogeography of the various continents have had significant effects on the development of human societies over the last 13 000 years. He suggests that Eurasia was the cradle of agriculture mainly because, for reasons of biogeography, most suitable crop plants and domesticable animals were found in this region. Then, the east–west orientation of this land mass would be particularly amenable to the widespread adoption of this suite of agricultural species, because latitudinal gradients in climate make it easier for organisms to spread within latitudes than across them. Agriculture led to more populous societies, but removed the need for all members to produce or collect food. This in turn opened the way for governing and soldier classes to develop. Large populations were also a natural source of innovations and inventions, including the development of writing, that would have given the societies that possessed them a technological advantage over those that did not. The sum of these and other processes over many millennia was to lead to the current global dominance in wealth and power of peoples of Eurasian origin (Diamond 1998).

The influence of regional patterns and processes on the course of human history is enhanced by the interconnectedness of societies. While developments occurring thousands of kilometres from a local community may seem irrelevant to the day-to-day activities of its members, this interconnectedness effectively embeds all individuals in a broad-scale web of interactions, and makes the Earth a smaller place than in some senses it might otherwise seem. Just how small is shown by the mathematics of so-called 'small-world networks' (e.g. Collins & Chow 1998; Watts & Strogatz 1998). This deals with the number of connections required to link together nodes in a network. For example, if every person in a society knew about 100 individuals, and each of those people also knew about 100 individuals, and so on, then in theory every person in a population of one billion would be connected to every other person through a chain of no more than six mutual acquaintances, or six 'degrees of separation' (Collins & Chow 1998). Degrees of separation will only be this low in a population if connections amongst individuals are random. This is clearly unlikely in human societies, where people tend to know friends of friends. However, it only takes a few well-connected individuals for the degree of separation in a real network to approach the low level found in one that is randomly connected (Watts & Strogatz 1998). The potential this creates for the spread of ideas, innovations, religions, political movements and diseases is readily apparent.

Scarce well-connected individuals typify populations of other animal species as much as they do humans. Thus, while in most bird species the majority of individuals will die within a short distance of where they were born, and will interact with relatively few others, a few individuals will move large distances in their lifetimes effectively connecting disparate populations. Such interconnectedness will enhance any regional-scale forces acting on these species. Thus, adverse climatic conditions in one region will influence populations in another, through differences in the numbers, condition and behaviour of individuals which move between the two. Just as for humans, regional forces are likely to have major impacts on patterns and processes at the local scales on which other species also typically operate. Indeed, the community of plants and animals at a local site will depend on such things as the composition of the regional pool of species potentially available to occupy that site, their abundance, distributions and other characteristics, and on the location and history of the region which have moulded the composition of this pool.

To date, there have been few expositions of the role of regional forces in structuring local species communities and assemblages. In major part, this is an inevitable by-product of the emphasis that has been placed on ecological studies at small spatial scales, and covering relatively brief periods. This book is our attempt to show how an understanding of ecological patterns improves with a broader vision, and some of the implications of the broader view. In short, it is an attempt to forge a link between the micro- and mesoecology which humans find easy to perceive, because this is the scale at which we typically operate, and the macroecology which is more difficult to comprehend, but which is just as important to the structure and function of the natural environment we inhabit.

Just as human affairs in general are influenced by regional forces, the writing of a book is seldom isolated from the influences of a wide range of friends and colleagues. The creation of this one has been no exception. First, and foremost, we express our deepest gratitude to John Lawton and Mark Williamson. John has been a constant source of encouragement and support for our research on macroecology from its earliest days, despite the weight of other demands on his time and attention.

Mark found space in a busy schedule to read and comment on the entire manuscript. His comments were by turn perceptive, challenging and cautionary; they were uniformly helpful. Steven Chown, Richard Duncan, Jeremy Greenwood, Richard Gregory, David Griffiths, John Harte, John Lawton and Phil Warren all read one or more individual chapters, and we thank them for the comments and insights they shared. In addition to all these, other individuals have helped shape our thinking about the topics addressed in this book, or have provided practical help with data or analyses. In particular, we would thank Andy Brewer, Brian Enquist, Sian Gaston, Andy Gonzalez, Paul Harvey, Bob Holt, Peter Kabat, Dawn Kaufman, Ron Kettle, Bill Kunin, Natasha Loder, Brian Maurer, Brian McArdle, Stuart Pimm, Andy Purvis, Rachel Quinn, John Spicer and Diane Srivastava. Linda Birch at the Edward Grey Institute library, and the staff of the libraries at the University of Sheffield and at Silwood Park have helped us trace many an obscure reference. Financial support was provided by the Royal Society, the Leverhulme Trust, the National Environment Research Council and the Centre for Population Biology. Part of the book was written while T.M.B. was visiting the Ecology and Entomology Group, Lincoln University, New Zealand, and he is especially grateful to Richard and Sue Duncan, David and Joy Coombes, Claire Newell, Steve Wratten and other staff and students of the university for their kind hospitality during his stay. It was a pleasure to work with Ian Sherman and Karen Moore at Blackwell Science on the book's production. K.J.G. thanks Sian and Megan for their constant encouragement, especially as he obtains first-hand experience of the scale of the world in which we live. T.M.B. thanks his parents and sister for their support over the years, and Clare for her patience and understanding during the preparation of this book.

K.J. Gaston & T.M. Blackburn
September 1999

1 The Macroecological Perspective

One's ideas must be as broad as Nature if they are to interpret Nature. [Arthur Conan Doyle 1887]

1.1 Introduction

We first visited Eastern Wood, Bookham Common, in the spring of 1998, on an unseasonally cold April morning. Snow had fallen across much of south-east England the previous day, and an overnight frost meant that some snowy patches were left in the grass around the car park. We emerged from our cars through the clouds of our own breath.

The birdwatching at this small (16-hectare) oak woodland in the southern English county of Surrey (Fig. 1.1) was distinctly, though predictably, disappointing, and made even thoughts of a return to our computer keyboards (and mugs of hot tea) an attractive proposition. Between 07.30 and the first drops of rain two and a half hours later, we tallied a mere 25 species (Fig. 1.2), none of which we had not seen on hundreds of previous occasions. The initial flurry of sightings, as we located those species determined enough to sing despite the cold, soon gave way to a slow but steady accumulation of fresh records (about one every 10 minutes) that continued until the weather forced us to cut short our observations. Although Fig. 1.2 suggests that we would have seen more species had we persisted through the rain, the additions would inevitably have slowed even further, and unlike the weather, would soon have dried up completely. Given that this is true, the morning in Eastern Wood offered scant inducement to pay the site a return visit: almost any woodland in southern England would have provided as much ornithological excitement, and we know several sites that would have yielded much more. It is not credible (to us at least) that the poor species list we generated could be a consequence of poor ornithological skills, and so it must in some measure reflect the composition of the avian community of Eastern Wood.

Like so many places, however, the merits or otherwise of Eastern Wood should not be judged on the basis of a single visit. The site is well known to many ecologists as the result of a study by the London Natural History Society (LNHS) of the composition of its breeding avifauna. This work began in 1946

Fig. 1.1 The location of Eastern Wood within Surrey, of Surrey within Britain, and the geographical position of Britain in the world. Lines on the bottom map represent roads; the M3 and M25 are motorways.

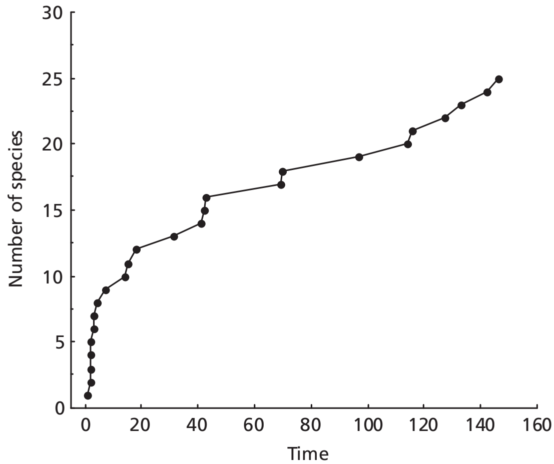

Fig. 1.2 The cumulative number of bird species recorded with time (minutes) in 2.5 hours in Eastern Wood on the morning of 16 April 1998; 0 minutes is 07.30 hours.

with population censuses of the robin (scientific names of bird species cited in the text throughout the book are listed in Appendix I), blackbird and chaffinch (Beven 1976). In 1949, the survey was extended to all species bar the blue tit and dunnock, and from 1950 to 1979 complete censuses of the breeding birds were carried out in every year (except 1957, when there was no census). The data amassed permit a range of features of the assemblage to be quantified, allowing our own observations to be set in perspective. This context reveals a number of interesting patterns.

Perhaps the most notable feature of our morning in Eastern Wood was that while it was not an especially suitable day for censusing birds (the cold discouraging most individuals from raising their voices above the drone of London's air traffic), the tally of 25 species meant that in three hours we recorded more than half (in fact, 56%) of the bird species recorded breeding in the wood over the period from 1949 to 1979 (Fig. 1.3; data for this period used here and elsewhere in the book are referenced and listed in Appendix II). Moreover, our sightings constituted 69% of the maximum number of species recorded breeding at the site in any one of those years (36 in 1972 and 1975). While we could not prove in a single visit that any of the species we observed were actually breeding on the site (although a great spotted woodpecker was watched excavating a nest hole), most of them do breed there annually, and only one that we saw (jackdaw) was not recorded breeding in the wood between 1949 and 1979 (Beven 1976; Williamson 1987). Several of the regular breeders we did not observe are summer migrants that on the date of our visit had probably not yet returned to the site from their wintering grounds. In sum, the short list of species we recorded is a fair reflection of the richness of the breeding avifauna.

A second striking feature of the bird assemblage we encountered in

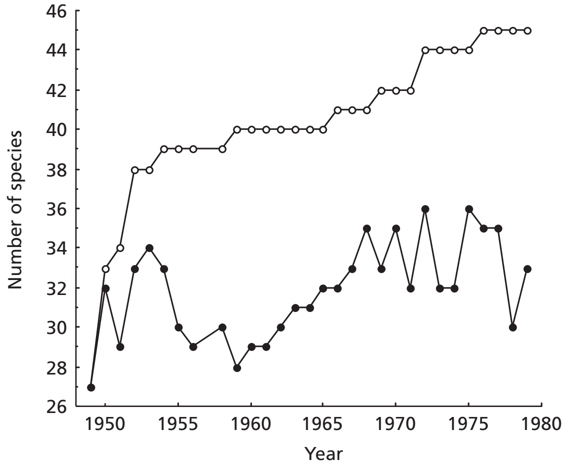

Fig. 1.3 The cumulative number of bird species recorded breeding in Eastern Wood in the period 1949–79 (open circles), and the number of species recorded breeding in each separate year (filled circles).

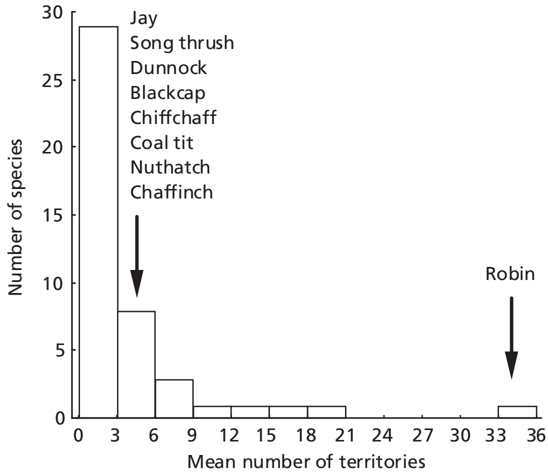

Fig. 1.4 The frequency distribution of the mean number of territories (when present) held in Eastern Wood by breeding bird species in the period 1949–79.

Eastern Wood was that the majority of species were rather scarce at the site. Thus, while the songs of robins and the calls of blue tits provided a near continuous background to our walk, we encountered only singletons of pheasant, green woodpecker, sparrowhawk, willow warbler, nuthatch, bullfinch and chaffinch, and only two coal and two marsh tits. Thus, more than one-third of the species tallied were represented by only one or two individuals. Such a pattern of abundance is demonstrated even more strikingly by the observations of the LNHS survey team (Fig. 1.4). Commonness, as exemplified by the robin, is the exception. Rarity, as exemplified by the nuthatch, is the rule.

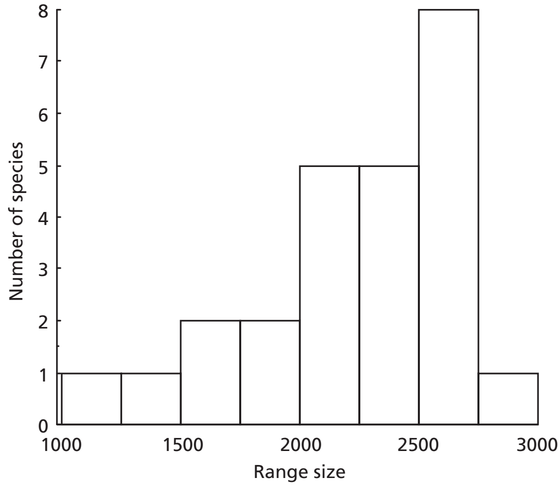

Fig. 1.5 The frequency distribution of range sizes in Britain (number of occupied squares on the 10 × 10-km British National Grid; Gibbons *et al*. 1993) of bird species recorded in Eastern Wood on the morning of 16 April 1998. The maximum range site possible is 2830 squares.

A third feature of the Eastern Wood bird assemblage, albeit one that is much less immediately striking, was that most of the species encountered are relatively widely distributed across Britain. The geographical distributions, or range sizes, of all bird species breeding in Britain have twice been mapped by teams of volunteer recorders in schemes organized by staff of the British Trust for Ornithology (BTO). These projects resulted in two distribution atlases, mapping bird occurrences in the 10 × 10-km squares of the British National Grid over the periods 1968–72 (Sharrock 1976) and 1988–91 (Gibbons *et al*. 1993). If we examine the species we recorded at Eastern Wood using data from the more recent of the two atlases (Gibbons *et al*. 1993), most are found to occupy a high proportion of all possible 10 × 10-km squares (Fig. 1.5). Indeed, only the marsh tit and nuthatch are found in less than 50% of squares, and only six species occupy fewer than 70%. Similar patterns pertain to the entire breeding avifauna of the wood in the period 1949–79 (Fig. 1.6). We did not have to go to Eastern Wood to see the species we did.

One final characteristic of the bird species we observed in Eastern Wood was that most were rather small bodied (Fig. 1.7). Almost two-thirds had average masses of less than 100 g, while the median mass was just over 20 g. This pattern also is not a quirk of the set of species we happened upon on a single visit. The distribution of body masses of all birds recorded by the LNHS as breeding in Eastern Wood is also highly skewed towards small species (Fig. 1.8), with a median mass of 23.4 g.

All these observations attest that, while the weather on the day we first visited Eastern Wood may have been unusual for the site at that time of year, the set of species encountered there certainly was not. We discovered an avifauna composed of a reasonably small number of generally small-bodied species,

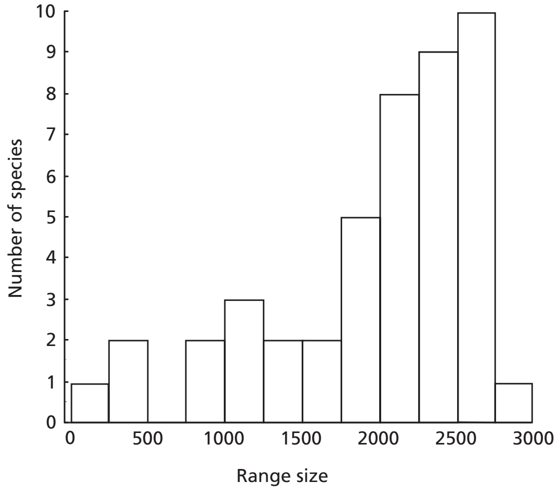

Fig. 1.6 The frequency distribution of range sizes in Britain (number of occupied squares on the 10 × 10-km British National Grid; Gibbons *et al*. 1993) of bird species observed breeding in Eastern Wood in the period 1949–79.

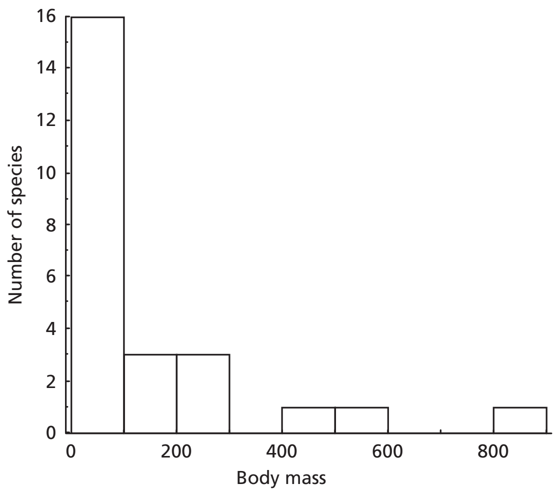

Fig. 1.7 The frequency distribution of body masses (g) of bird species recorded in Eastern Wood on the morning of 16 April 1998.

mostly present in low numbers at the site but widely distributed across Britain. These are all features confirmed by the more detailed and prolonged LNHS survey. With the possible exception of the wide distribution of species, similar observations could also be made about the avifauna of almost any locality in Britain.

In fact, similar observations could be made about the avifaunas of sites the world over (although, subjectively, there are many sites that are far more exciting to visit than Eastern Wood). For example, Holmes *et al*. (1986) censused the

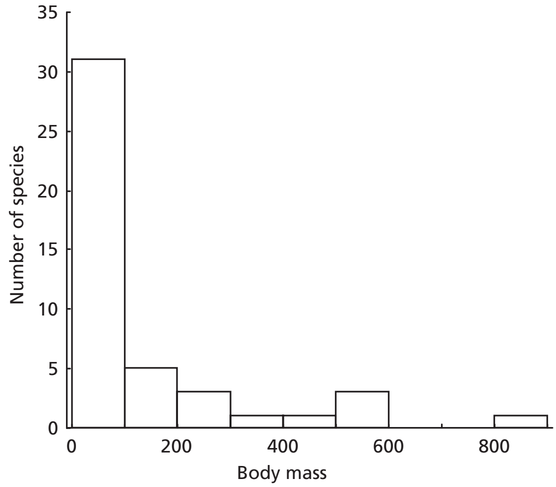

Fig. 1.8 The frequency distribution of body masses (g) of bird species recorded breeding in Eastern Wood in the period 1949–79.

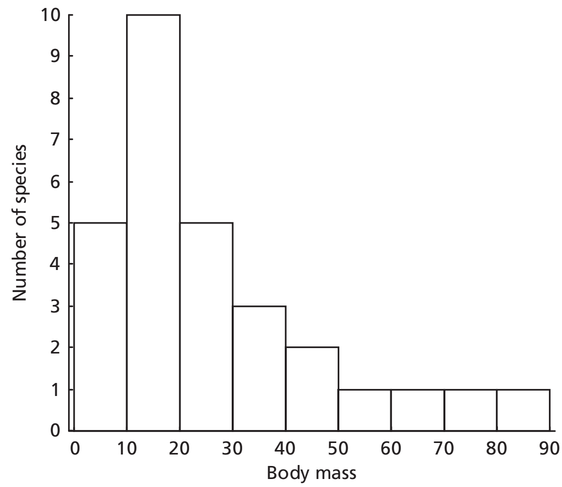

Fig. 1.9 The frequency distribution of body masses (g) of bird species recorded breeding in a 10-hectare plot of deciduous forest at Hubbard Brook, New Hampshire, in the 16-year period 1969–84 (Holmes *et al.* 1986); $n = 29$. Body mass data were kindly supplied by B. Maurer.

avifauna of a 10-hectare patch of deciduous forest at Hubbard Brook, New Hampshire, USA. As in Eastern Wood, most species recorded breeding in the American wood were small bodied (Fig. 1.9), and most were scarce at the site even when present (Fig. 1.10).

Although on opposite sides of the Atlantic, Hubbard Brook and Eastern Wood are not dissimilar in terms of physiognomy. Both are temperate zone deciduous forests. Most of the trees at Hubbard Brook would be clearly akin to

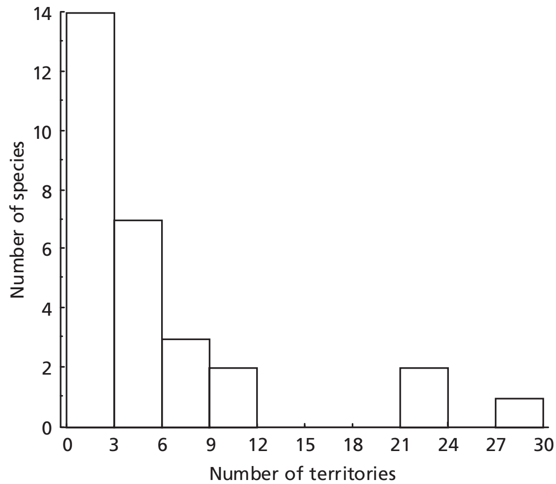

Fig. 1.10 The frequency distribution of average number of territories (when present) for bird species recorded breeding in a 10-hectare plot of deciduous forest at Hubbard Brook, New Hampshire, for the 16-year period 1969–84; $n = 29$. From data in Holmes *et al.* (1986).

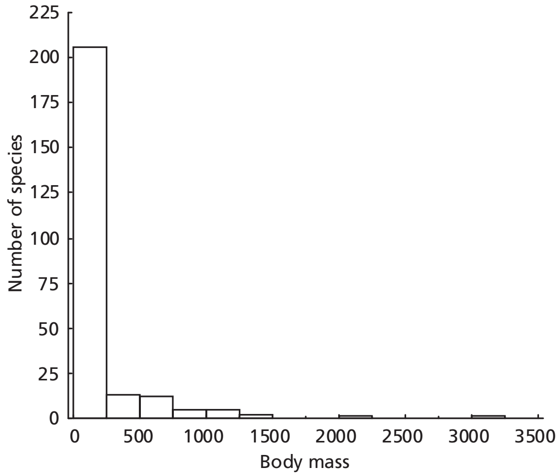

Fig. 1.11 The frequency distribution of body masses (g) of bird species recorded holding territory in a 97-hectare plot of floodplain forest in Manu National Park, Amazonian Peru, in a 3-month census period in 1982; $n = 245$. From data in Terborgh *et al.* (1990).

species familiar in Britiain and the two sites even share a bird species in common (the wren). However, the broad similarity in the structure of the avifaunas of the two sites is not a consequence of this alone. Terborgh *et al.* (1990) censused the avifauna of a 97-hectare patch of floodplain forest in Manu National Park, Amazonian Peru. The species richness of this tropical site was hugely greater than that of Eastern Wood (245 territorial species recorded in

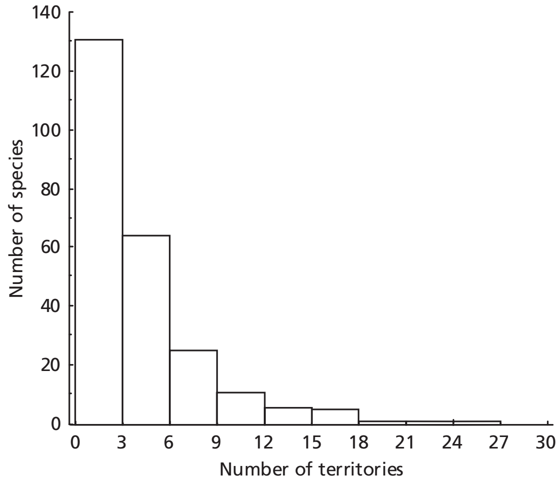

Fig. 1.12 The frequency distribution of number of territories (per 100 hectare) of bird species recorded holding territory in a 97-hectare plot of floodplain forest in Manu National Park, Amazonian Peru, in a 3-month census period in 1982; $n = 245$. From data in Terborgh *et al.* (1990).

3 months versus 45 in 30 years; see Chapter 2), although the most abundant species maintains fewer territories, on average, than the most abundant in the much smaller patch that is Eastern Wood. However, the qualitative patterns are the same. Most species present were small bodied (Fig. 1.11) and in low numbers (Fig. 1.12). Thus, the structure of the avifauna of Eastern Wood is not particularly unusual, excepting that it has been especially well studied.

1.2 Scale and avian ecology

Ecologists have spent several decades attempting to understand what structures animal assemblages at local sites such as Eastern Wood. That is, they have been trying to determine why most species are scarce and a few are abundant, why most are small and a few large, and so on.

With some significant exceptions, answers have predominantly been sought at the spatial scales of these localities, or sometimes at even finer scales. Broader contexts have, by and large, been ignored. We distinguish between cartographic and colloquial definitions of scale, because unfortunately what is small scale according to the former is large scale according to the latter (Curran *et al*. 1997). Here, following convention in this field, scale is used in the latter sense, as a synonym of words such as size and area; small scale refers to a small area, and large scale to a large area.

Reference to *Ibis*, one of the most highly rated journals publishing studies of avian ecology, reveals the extent of the preoccupation with small scales in this field. Local-scale studies never comprised less than 55% of all published

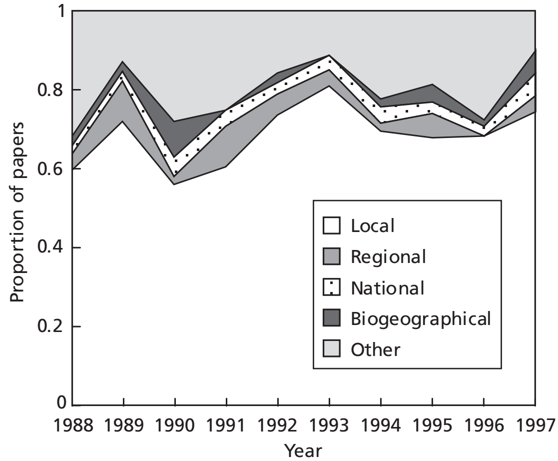

Fig. 1.13 The proportion of papers in the journal *Ibis* in the 10-year period 1988–97 concerning different spatial scales. This classification does not include short communications (comments) or papers in supplements. Studies were classified as 'local' if they were performed over restricted areas (e.g. at well-defined sites), or if they were performed at a few reasonably well-separated sites but this separation was irrelevant to the aim of the study. Thus, the paper by Yamagishi and Eguchi (1996) on the comparative foraging ecology of Madagascan vangids was classified as local, even though it involved work at several well-separated sites. The separation was irrelevant to the study, which could equally well have been carried out at one site had all the vangid species been present. By contrast, Matthysen's (1997) study of geographical variation in nuthatch song types, which was carried out at nine sites in northern Belgium, was classified as regional, because here the site separation was relevant. 'Regional' studies were those concerning scales roughly equivalent to an English or American county, or a restricted part of a country. The 'national' scale refers to studies across regions roughly equivalent to whole countries, whereas 'biogeographical' studies consider multinational, continental or global scales. Studies that could not readily be assigned to any class in this scheme, or for which scale was not relevant, were lumped into the 'other' category. These principally comprised taxonomic, experimental and review papers.

papers in the 10-year period 1988–97 (Fig. 1.13). The second largest category is usually 'other', which includes all those studies that cannot be categorized by spatial scale. Large-scale studies (lumping regional, national and biogeographical categories) generally contributed only between 10 and 15% of the papers published in *Ibis* in any one year, and just over 10% of the papers in total. There is no hint that this proportion has been increasing over the last decade.

This emphasis on small spatial scales is typical of ecology in general (Kareiva & Andersen 1988; May 1994a; Baskin 1997; Lawton 1999). In a similar vein, most ecological studies are of very short duration, usually two or three years at the most (Weatherhead 1986; Tilman 1989; Elliott 1994; Malmer 1994; Baskin 1997). Most focus on just a few species, and there is some evidence that both the proportion of community studies and the number of species per community study have recently been in decline (Pimm 1986; Shorrocks 1993; Kareiva 1994).

The preoccupation with small spatial scales implicitly assumes that it is forces operating within sites which determine their faunal structures. Nonetheless, the success of this approach has been mixed. On the one hand, it has revealed a wealth of important details, including data on the determinants of the reproductive success of individuals and species, patterns of foraging, the temporal dynamics of populations and the influences upon them, and the effects of competition and predation. On the other hand, these studies have largely failed to answer the bigger questions as to why avian assemblages are broadly structured in the ways in which they are. Indeed, arguably this failure was sufficiently acute that, until recently, attempts to resolve these issues had to some marked degree been abandoned. There appears, for example, to have been a significant hiatus in such studies between the late 1960s and the mid to late 1980s.

1.3 A wider perspective

The species richness and the abundance and body size structures of local avian assemblages are among their most apparent features. This is so whether or not the observer is overtly interested in birds and, if interested, whether the context be amateur or professional. Understanding the determinants of these patterns would therefore seem to be a priority. However, it has become readily apparent that the answers lie in a much broader perspective. Local species assemblages are influenced not only by local forces, but also by those at larger scales.

This point has been recognized by a number of ecologists, whether specialists on birds or otherwise (e.g. MacArthur 1972; Maurer 1985, 1999; Brown & Maurer 1987, 1989; Ricklefs 1987; Wiens 1991; Cornell & Lawton 1992; Holt 1993; Ricklefs & Schluter 1993; Brown 1995; Lawton 1999). Thus, in his 1991 Witherby Lecture, Goss-Custard (1993, p. 82) argued that: ‘if the populations of such mobile animals [as birds] are to be properly understood, we must address more directly the factors and processes that determine numbers over very large areas and throughout the year, and not just in one locality at a particular time of year. Indeed, because numbers in one study locality are likely to be affected by the size of the greater population of which the local group forms a part, studies on larger geographical scales may be needed even to understand numbers in a particular place.’ Similarly, Haila (1988, p. 89) noted that a: ‘population decrease on the regional scale is likely to lead to local “extinctions” in small plots, but these cannot be interpreted in terms of a local “equilibrium” ’. Much earlier, in their *The Theory of Island Biogeography*, MacArthur and Wilson (1967, p. 182) concluded that: ‘(g)lobal patterns of distribution also need to be reconsidered. We know that species diversity, relative abundance

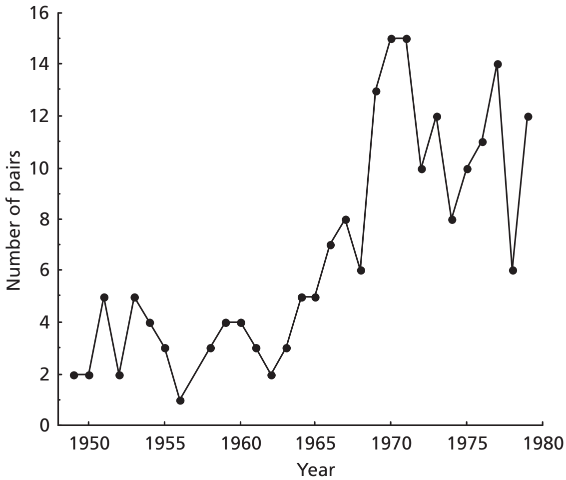

Fig. 1.14 The number of pairs of woodpigeon recorded breeding in Eastern Wood in each year from 1949 to 1979.

and population geometry change with climate. Such variation affects the structure, stability, and energy flow of the plant and animal communities.' Their message is clearly that an understanding of community structure requires consideration of the region within which the community sits. The point was recognized by Holt (1993), who wrote that: 'an important item on the agenda for community ecology will be to grapple with the messy reality that local communities contain species that experience the world at vastly different scales. The structure of a community will surely reflect the interplay of disparate regional processes.'

The avifauna of Eastern Wood well illustrates the significance of events at broader scales. The wood is embedded in a landscape of other woods, agricultural lands and suburban areas. Changes in this landscape and its management change the regional abundances of species, which must in turn impact abundances within the wood. For example, the numbers of breeding woodpigeons in Eastern Wood have shown a marked increase from the early to mid 1960s (Fig. 1.14). Beven (1976) noted this in his summary of changes in the avifauna, but offered no explanation. However, it coincides with the widespread adoption of oilseed rape as an agricultural crop, which provides the woodpigeon with an important source of winter food. Significant preference for this crop in winter seems to decrease winter mortality (Inglis *et al*. 1990), and so may have contributed to the higher breeding numbers seen in Eastern Wood. Other agricultural changes have had similarly marked effects on the structure of British bird communities, albeit mainly for open habitat species such as the grey partridge, skylark and corn bunting, which have not been recorded by the Eastern Wood survey. The recent rise in woodpigeon numbers

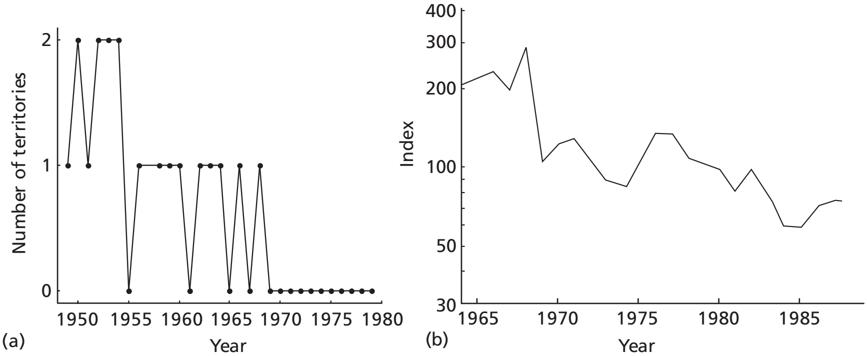

Fig. 1.15 (a) The number of territories of whitethroat recorded in Eastern Wood in each year from 1949 to 1979. (b) Variation in an index of the number of whitethroat breeding on woodland census sites across Britain in the period 1962–88. From Marchant *et al*. (1990) and data in Appendix II.

must be set against sharp declines in the abundances of most other bird species typical of farmland (Gibbons *et al*. 1993; Fuller *et al*. 1995).

A number of the species breeding and wintering in Eastern Wood are migratory. Their presence and the numbers in which they occur are therefore influenced by events many hundreds of kilometres away. For example, while never common, the whitethroat and the garden warbler have both shown steady declines in numbers on the site, to the extent that they became extinct as breeding species in the late 1960s and early 1970s. The whitethroat last bred there in 1968 (Fig. 1.15a). In fact, 1969 was a disastrous year in general for this species, as only one-quarter of the British breeding population returned from the drought-stricken wintering grounds in Sahelian Africa (Winstanley *et al*. 1974). The population has not subsequently recovered to the precrash level (Fig. 1.15b). The population of the garden warbler was also affected, although as this species mainly winters south of the Sahel, the consequences have been less severe and less persistent (Fig. 1.16b). Indeed, the garden warbler managed to re-establish, albeit tenuously, as a member of the Eastern Wood breeding bird community following its initial extinction (Fig. 1.16a). Nevertheless, the decline of the garden warbler and extinction of the whitethroat as breeding species in Eastern Wood seem likely to be direct consequences of events occurring several thousand kilometres from the site (for more examples, see Järvinen & Ulfstrand 1980; Terborgh 1989; Baillie & Peach 1992; Newton 1995, 1998). In a local context, these population changes might at best have been attributable to stochastic effects. In a regional context, they are clearly explicable in terms of specific identifiable causes.

Subsequent chapters will reveal the extent to which features of the Eastern Wood bird assemblage, such as species richness, abundance patterns and body size structure, are influenced by processes operating at large spatial and

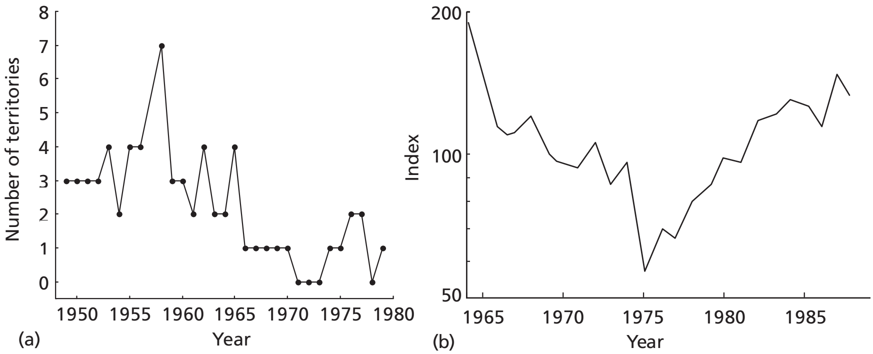

Fig. 1.16 (a) The number of territories of garden warbler recorded in Eastern Wood in each year from 1949 to 1979. (b) Variation in an index of the number of garden warbler breeding on woodland census sites across Britain in the period 1964–88. From Marchant *et al*. (1990) and data in Appendix II.

temporal scales. Some of these effects, such as the role of conditions on the wintering grounds in determining breeding abundances, will probably not be particularly surprising. Others are much more subtle, and there are all shades in between. Of course, many of these regional phenomena are also of interest in their own right, irrespective of their effect on the structure of local assemblages. There is a need to understand why there are general regularities in the distribution and abundance of bird species that transcend specific and regional idiosyncrasies, at least as much as to understand the interactions between individual birds at local sites. Nevertheless, it is the influences of large-scale patterns and processes at the small scale most readily perceived by humans that are most persuasive of their more general importance.

Although large-scale processes clearly influence the community structure of local sites, we do not wish to imply that local processes are not also important. A number of the temporal changes in the avifauna of Eastern Wood may be ascribed to these. For example, a decrease in the willow warbler population (Fig. 1.17) is not mirrored more widely across Britain (Gibbons *et al*. 1993), and seems to be a consequence of changes in management of the wood (Beven 1976). Until the early 1950s, trees had periodically been felled to be sold for timber, and the wood had also been thinned by shrub clearance. The cessation of these practices (in response to requests by the team censusing the bird populations) led to a greater proportion of mature trees, and encroachment of scrub onto open areas and grassy rides. The grassy areas provided nesting sites for the willow warbler, and the simultaneous reduction of both in Eastern Wood is suggestive of a connection. The increase in populations of tits and starlings (Fig. 1.18) seems likely to be a consequence of the greater availability of nest holes in mature and dead trees, which previously would have been felled (Beven 1976). Interestingly, the encroachment of scrub at Eastern Wood should have

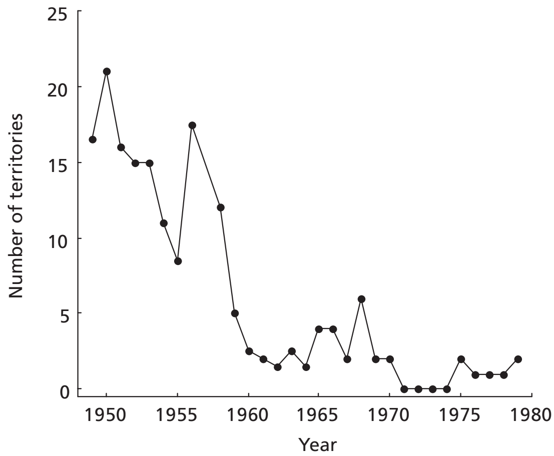

Fig. 1.17 The number of territories of willow warbler recorded in Eastern Wood in each year from 1949 to 1979. From data in Appendix II.

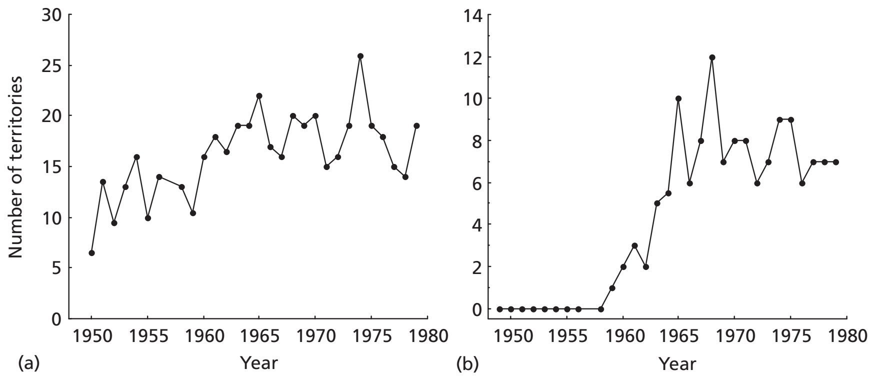

Fig. 1.18 The number of territories of (a) blue tit recorded in Eastern Wood in each year from 1950 to 1979 and (b) starling recorded in Eastern Wood in each year from 1949 to 1979.

benefited the garden warbler, which prefers woods containing such habitat (e.g. Fuller 1982). Indeed, the population of this species did increase there in the late 1950s (Fig. 1.16a). However, its subsequent decline in the late 1960s mirrors its general decline in British woodland (Fig. 1.16b). Variation in the Eastern Wood garden warbler population serves to emphasize that a range of perspectives are required to understand such dynamics.

1.4 The macroecological approach

Recognition of the importance of a regional perspective for understanding the structure and dynamics of local assemblages, and of regional-scale issues in their own right, has in major part stimulated emergence of the field of macroecology (Gaston & Blackburn 1999). Macroecology is concerned with understanding the abundance and distribution of species at large spatial and temporal scales (Brown & Maurer 1989; Brown 1995; Blackburn & Gaston 1998; Gaston & Blackburn 1999; Maurer 1999). It covers the point of intersection of several other fields of biology, including ecology, biogeography and macroevolution.

The philosophy underlying the macroecological approach has been discussed by Brown (1995), Gaston and Blackburn (1999) and Maurer (1999), although the basic ideas have a long and distinguished pedigree. The starting point of this philosophy was typically well described by MacArthur (1972) when he wrote that: '(m)ost scientists believe that the properties of the whole are a consequence of the behaviour and interactions of the components. This is not to say that the way to understand the whole is always to begin with the parts. We may reveal patterns in the whole that are not evident at all in its separate parts.' Macroecology seeks to develop an understanding of ecological systems through the study of the properties of the whole (a 'top-down' approach). This can be contrasted with a more traditional approach, which seeks to develop such an understanding through study of the component parts ('bottom-up'). However, the two are clearly complementary. For example, an examination of the properties of an ecological community might suggest the features of its component species that are of particular importance in its structure, while the behaviours of the species might suggest features of the community that could benefit from more detailed attention. By following both 'bottom-up' and 'top-down' paths, a better understanding is reached than would have been derived from either approach alone. This philosophy is not peculiar to macroecology. A complete understanding of most, if not all, scientific disciplines is likely to arise only by incorporating observations made from a range of viewpoints, or at a variety of scales (Gaston & Blackburn 1999). The focus often changes as a field develops, and important gaps in knowledge are identified. Of course, large- and small-scale approaches are both simply tools for examining and trying to understand the complexity of ecological systems. The systems themselves are continuous over all scales, and the differentiation between large- and small-scale processes is simply arbitrary, manufactured for convenience (for example, see Wilber 1979). Macroecologists recognize that their interests are informed by ecological studies at smaller spatial and temporal scales, but the reverse is also true.

The large-scale approach has advantages and disadvantages. Arguably, one of the principal advantages is that it takes a sufficiently distant view of ecological systems that the idiosyncratic details disappear, and only the important generalities remain (Brown 1995). A fitting analogy is that it attempts to see the wood for the trees. Adopting a distant viewpoint reveals patterns that in some cases would at best otherwise have been difficult to predict, and at worst would have been overlooked. Active research programmes have developed around many such patterns, as will become apparent throughout this book.