
Chapter 3: Patterns in space

Aims of the chapter

This chapter reviews the various approaches that have been used to characterise the spatial patterns of plants and animals on the terrestrial land surface.

Learning objectives

By the end of this chapter you should be able to:

- explain how life in the biosphere is organised on different spatial scales
- explain the nature of biomes and how they differ from plant and animal kingdoms or realms
- explain the distribution and extent of floristic and faunal kingdoms or realms
- explain and exemplify what are meant by cosmopolitan, disjunct and endemic biota
- discuss what is meant by the term 'species diversity' and the relation between species diversity and latitude, altitude and area
- discuss the hypotheses that are used to explain patterns of species diversity.

Essential reading

Begon, M., C.R. Townsend and J.L. Harper *Ecology: Individuals, populations and communities*. (Oxford: Blackwell Publishing, 2005) fourth edition [ISBN 1405111178]. Chapters 1, 4, 5 and 8.

Brown, J.H., B. Riddle and M.K. Lomolino *Biogeography*. (Sunderland, Mass.: Sinauer Associates, 2005) third revised edition [ISBN 0878930620]. Chapters 4 and 7.

Millennium Ecosystem Assessment *Ecosystems and human well-Being: Current state and trends: Findings of the Condition and Trends Working Group Series* (Washington, D.C.: Island Press, 2005) [ISBN 1559632283]. The Foreword, Chapters 1, 4 and 10 are essential reading, and are listed below under lead author. Pdfs of all chapters from www.maweb.org/en/Condition.aspx¹

¹ Pdf of this paper from www.maweb.org/en/Condition.aspx

Recommended reading

Archibold, O.W. *Ecology of world vegetation*. (London: Chapman and Hall, 2003) [ISBN 0412443007].

Arita, H. T., P. Rodriguez, and E. Vasquez-Dominguez 'Continental and regional ranges of North American mammals: Rapoport's rule in real and null worlds', *Journal of Biogeography* 32 2005, pp. 961–971.

Balvanera et al. 'Quantifying the evidence for biodiversity effects on ecosystem functioning and services', *Ecology Letters* 9(10) 2006, pp. 1146–1156.

Chapin, F. S., E.S. Zavaleta, V.T. Eviners, R.L. Naylor, P.M. Vitousek, H.L. Reynolds, D.U. Hooper and S. Lavorel 'Consequences of changing diversity', *Nature* 405, 2000, pp. 234–242.

Drakare, S., J.L. Lennon and H. Hillebrand 'The imprint of the geographical, evolutionary and ecological context on species-area relationships', *Ecology Letters*, 9 2006, pp. 215–227.

- Flessa, K.W., D.B. Barnett, M.A. Cornue, N. Lomaga, M.A. Lombardi, J.M. Miyazaki and A.S. Murer 'Geologic implications of the relationship between mammalian faunal similarity and geographic distance', *Geology* 7 1979, pp. 15–18.
- Gaston, K.J. 'Global patterns in diversity', *Nature* 405 2000, pp. 220–227.
- Hillebrand, H. (2004) 'On the generality of the latitudinal diversity gradient', *American Naturalist* 163, pp. 194–211. A excellent recent review of the LDG.
- Lamoreux, J.F., J.C. Morrison, T.H. Ricketts, D.M. Olson, E. Dinerstein, M.W. McKnight and H.H. Shugart 'Global tests of biodiversity concordance and the importance of endemism', *Nature* 440 2006, pp. 212–214.
- Mace, G., Masundire, H., and J. Baillie et al. 'Biodiversity', in *Millennium Ecosystem Assessment Ecosystems and human well-being: Current state and trends: Findings of the Condition and Trends Working Group Series* (Washington, D.C.: Island Press, 2005) [ISBN 1559632283]. Chapter 4, pp.77–122. Pdf www.maweb.org/en/Condition.aspx
- Margules, C.R. and R.L. Pressey 'Systematic conservation planning', *Nature* 405 2000, pp. 243–253.
- McCann, K.S. 'The diversity-stability debate', *Nature* 405 2000, pp. 228–233.
- Meyers, N. 'Biodiversity hotspots revisited', *BioScience* 53(10) 2003, pp. 916–917.
- Meyers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. daFonseca and J. Kent 'Biodiversity hotspots for conservation priorities', *Nature* 403(6772) 2000, pp. 853–858.
- Olson, D.M. et al. 'Terrestrial eco-regions of the world: A new map of life on Earth', *BioScience* 51(11) 2001, pp. 933–938. www.worldwildlife.org/science/ecoregions/terrestrial.cfm
- Purvis, A. and A. Hector. 'Getting the measure of biodiversity', *Nature* 405 2000, pp. 212–219.
- Reich, P.B., M.B. Walters and D.S. Ellsworth 'From tropics to tundra: Global convergence in plant functioning', *Proceedings of the National Academy of Sciences, USA* 94 1997, pp. 13730–13734. Pdf from www.pnas.org/cgi/reprint/94/25/13730.pdf
- Sala, O.E. Biodiversity across scenarios, in *Millennium Ecosystem Assessment Ecosystems and human well-being: Current state and trends: Findings of the Condition and Trends Working Group Series* (Washington, D.C.: Island Press, 2005) [ISBN 1559632283]. Chapter 10, pp. 375–408. Pdf from www.maweb.org/en/Condition.aspx
- Scheiner, S.M. 'Six types of species-area curves', *Global Ecology and Biogeography* 12 2003, pp. 441–447.
- Scholes, R., R. Hassan and N.J. Ash 'Summary: Ecosystems and their services around the year 2000, in millennium ecosystem assessment', *Ecosystems and human well-being: Current state and trends: Findings of the Condition and Trends Working Group Series* (Washington, D.C.: Island Press, 2005) [ISBN 1559632283]. Preface, pp.1–13. Pdf www.maweb.org/en/Condition.aspx
- Tilman, D. 'Causes, consequences and ethics of biodiversity', *Nature* 405 2000, pp. 208–211.
- Thompson, R.S., K.H. Anderson and P.J. Bartlein Atlas of relations between climatic parameters and distributions of important trees and shrubs in *North America. US Geological Survey Professional 1990 Paper 1650 A,B.* (Reston: US Geological Survey, 1990). Online at (<http://pubs.usgs.gov/pp/p1650-a>).
- Woodward, F. I., M.R. Lomas and C.K. Kelly 'Global climate and the distribution of plant biomes', *Philosophical Transactions of the Royal Society of London B*, 359 2004, pp. 1465–1476. Online at www.journals.royalsoc.ac.uk/content/102022

Further reading

An extensive and detailed list of further reading is provided on the University of London External Programme web site in the EMFSS student area, following the link for 'Further unit subject guides'.

Internet resources

Species diversity

African Mammals Database

www.gisbau.uniroma1.it/amd and

www.fao.org/gtos/tems/mod_div.jsp?div_PAGE=divdata.htm

The FAO TEMS link is very fast. The fauna relevant to this chapter can be found at this web site, from where you can download relevant species distribution maps. You should note that the last letter in 'uniroma1' is a numeral '1', not a letter 'l'. Each map is accompanied by a detailed description of the species range and an extensive bibliography.

Animal Diversity Web, University of Michigan Museum of Zoology

<http://animaldiversity.ummz.umich.edu>

Covers all the animal groups, with lots of information and illustrative material.

Biodiversity and Conservation: A hypertext book

<http://darwin.bio.uci.edu/~sustain/bio65/Titlepage.htm>

This is an excellent introductory text with lots of useful material and links.

BIOMAPS Project, Bonn

www.botanik.uni-bonn.de/system/biomaps.htm

An excellent site co-ordinated by Professor Barthlott, with lots of material, maps and explanations. The map of global biodiversity of vascular plants is widely used and downloadable. Especially useful is the discussion of methods of biodiversity mapping.

Centres of Plant Diversity: The Americas

www.nmnh.si.edu/botany/projects/cpd/na/na-cpde.htm

Site run by the Smithsonian Institute, Washington, DC. Provides fairly detailed ecological information on major centres of plant diversity, animals and pictures and bibliography. Excellent. For examples, see SA44: Chile Mediterranean Region and La Campana National Park and SA43: Atacama Desert.

Conservation International Biodiversity Hotspots

The definitive site on biological hotspots, resources and hotspots by region.

www.biodiversityhotspots.org/xp/Hotspots

Flora Europaeae Atlas Database

www.fmnh.helsinki.fi/english/botany/afe/publishing/database.htm

An interactive sample downloadable program. With this program you can plot (but not print) species maps of the European flora.

Natural History Museum London Biogeography and Conservation Laboratory

www.nhm.ac.uk/science/projects/worldmap

An excellent set of pages on biodiversity; good review of methods of biodiversity mapping.

TEMS Terrestrial Ecosystem Monitoring Sites

www.fao.org/gtos/tems/mod_div.jsp?div_PAGE=divdata.htm FAO

Site that provides links to biodiversity databases, including African Mammals Databank.

World Conservation Monitoring Centre (WCMC)

www.unep-wcmc.org

WCMC has a superb paper – Biodiversity: An Overview.

World Resources Institute

<http://biodiv.wri.org>

The WRI has a very useful site entitled Biodiversity, as well as the Millennium Ecosystem Assessment portal.

World Wildlife Fund (WWF) Terrestrial Ecoregions

www.worldwildlife.org/science/ecoregions/terrestrial.cfm

This site is part of the WWF Wild World Terrestrial Ecoregions, which aims to provide a definitive list of terrestrial ecosystems in terms of their biological distinctiveness and conservation status. Sites listed are subdivided into floristic regions, which are in turn subdivided into biome and ecosystem types. Detailed ecological information about the flora and fauna is then given. An excellent site.

Introduction

Spatial patterns can be described in several major ways:

- at the biome level
- in the floristic and faunal kingdoms, or regions, which were identified and described in the eighteenth and nineteenth centuries. They are regions of the earth that are distinctive in terms of either their flora or fauna
- taxonomically, by plotting, describing and analysing the distributions of individual families, genera and species
- by spatial variation in global species richness and diversity (an approach that is becoming increasingly important)
- at the ecosystem level, or at the community level of organisation, which involves describing and analysing the distributions of ecologically distinctive associations and species populations of plants and animals. This may be accomplished by either qualitative descriptions of plant associations or by using quantitative statistical methods. We will discuss this aspect of community ecology in later chapters.
- through the use of the concept of the plant association, which was generally attributed to Humboldt (1805) and then developed by Schouw in 1832, when he first used the suffix 'tum' to describe communities dominated by one or more species. Thus Western European heathland and moorland, which are often dominated by heather – *Calluna vulgaris* – are referred to as '*Callunetum*'. This eventually developed into the widely used classification system of Braun-Blanquet² (1921). David Shimwell's (1971) *Description and classification of vegetation* also provides a useful review of the historical development of plant community description.

Obviously each one of these approaches poses different questions about the origin and nature of species and species associations. The remainder of this chapter will review the first geographical and ecological approach applied to the global scale, then patterns of species and finally global patterns of species diversity. We will then briefly review the various explanations that have been advanced to explain these present day patterns.

Scales of biological variation – biomes

On a global scale, regions with the same or similar environmental conditions usually have biota that have similar functional forms, life strategies and adaptations. The major control on these biological communities is global climate³, so that the biosphere is partitioned into distinctive, predominantly latitudinal biomes.⁴ Biomes are composed of the climax vegetation, associated successional communities, associated soil orders and soil processes, plant functional types in terms of characteristic plant anatomy and physiology and the associated faunal elements

² See www.wku.edu/~smithch/chronob/BRAU1884.htm for a brief resumé.

³ See the review by Woodward et al. (2004).

⁴ See www.eoearth.org/article/Ecoregion. The Nearctic ecology web site, which has lots of useful links, is worth exploring (www.nearctic.com/ecology/ecology.htm). The University of California Museum of Palaeontology has a useful overview at www.ucmp.berkeley.edu/exhibits/biomes/forests.php

(Archibold, 1995). It is synonymous with the term **formation-type**. We will review the major biome types in Section 4 of this subject guide.

The number of biomes recognised varies from nine (e.g. Archibold, 1995) – tropical forests, tropical savannas, arid regions (deserts), Mediterranean, temperate forests, temperate grasslands, coniferous forests, tundra (taiga) and terrestrial wetlands – to 17 in the most recent biome reconstructions.⁵

- Each biome is subdividable into regional subdivisions known as **formations**, which typically reflect local variations in soil, climatic and topographic within the biome.
- Each formation is floristically distinctive within its associated biome formation. Each formation can also be further subdivided into **plant associations** dominated by locally important species. For example, limestone areas in the European temperate deciduous woodland formation are usually dominated by beech (*Fagus sylvatica*), whereas the sessile oak *Quercus petraea* dominates on dry, acid, siliceous (sand-rich) soils. This emphasises the importance of edaphic (soil) factors at the association level.
- Finally, each association can be further subdivided into local-scale **communities**, with individual species responding to the gradients of local biotic and abiotic factors.

In this individualistic approach, each species has a distinctive ecological niche determined by its tolerance to abiotic and biotic stresses, such as:

- light
- temperature
- soil pH
- soil nutrient status
- competition
- predation.

Thus, spatial patterning at the local scale involves interactions with all abiotic and biotic factors, whereas at the global biome scale, vegetation patterning is largely determined by climate. Boundaries between these ecological units are called **ecotones**.

The WWF (formerly known as the World Wildlife Fund) have recently overseen the development of a ‘new map of life on earth’ – what they term **terrestrial ecoregions** (Olson et al., 2001). The basis of these terrestrial ecoregions is the subdivision of the earth into 14 biomes – which are further subdivided into 867 distinct ecological units (see Olson’s paper).⁶

Learning activity

Access the WWF Wild World site, locate your own geographical region and then click on the ecoregion number to obtain the ecological description. As an example, find ecoregion AA1204 (Jarrah-Karri forest and shrubland, Western Australia).

Having done this, select one of the biomes and list the floral and faunal differences between the formations. How do these differences relate to the abiotic controls of climate, soil and topography?

⁵ The Royal Society of London held a meeting in 2004, with 10 papers on biome origin, covering rainforest, savannas and temperate forests. Details are given at www.royalsoc.ac.uk/downloaddoc.asp?id=644

⁶ The sources for the ecoregions, technical descriptions, Olson’s paper and other data are available at www.worldwildlife.org/science/ecoregions/terrestrial.cfm, which you should consult. Underlying the map are very detailed ecological descriptions of the 867 units which are available online at www.worldwildlife.org/science/ecoregions/biomes.cfm

Attempts to predict the spatial distributions of biomes invariably involve climate. Most biogeographical texts reproduce diagrams that classify biomes in terms of temperature and precipitation (Whittaker, 1975) and evapotranspiration or both (Woodward et al., 2004). In order to reduce the huge floristic diversity of biomes to simpler descriptors, several researchers have put forward schemes that incorporate information on:

- architectural life form
- plant functional types.

Architectural life form

Raunkiaer⁷ (1934) used the arrangement of the perennating tissues of plants to identify five major life forms:

- phanerophytes (trees and tall shrubs)
- chamaephytes (Small shrubs and herbs)
- hemicytophytes (annual plants with buds protected by leaves and soil)
- cryptophytes (buds, bulbs and rhizomes completely buried)
- therophytes (annual regeneration from seeds)

and an additional form:

- epiphytes (growing on other woody vegetation above ground).

Thus, tropical forests are dominated by phanerophytes, whereas tundra are dominated by cryptophytes.⁸ This approach is descriptive and cannot be used to predict biome type.

Plant functional types

Typical attributes include:

- plant photosynthetic type (C3, C4, CAM)
- growth form (trees, shrubs, grasses, ferns and mosses)
- life form
- leaf properties
- biochemical properties
- phenology (seasonal development cycle).

Phenology is the study of the impact of seasonal climatic change on the development of processes such as leafing, flowering, breeding, etc. This approach has been successful in predicting the distribution of biomes under both present and past reconstructed climatic conditions. It is now widely used to model global vegetation.

Biogeographical realms or kingdoms⁹

The major biogeographic problems associated with the biome approach are that:

- It does not deal with individual properties/origins of families, genera and species.
- It does not represent the spatial distributions of families, genera and species of fauna and flora, which are not necessarily controlled by climatic factors. Thus the roles of evolution and plate tectonic change are ignored.

⁷ See Wikipedia at http://en.wikipedia.org/wiki/Raunki%C3%A6r_system_for_illustrations_of_life_forms.

⁸ See Begon et al. (2005), pp. 24–25, for illustrations. The paper by Batalha and Martins (2004) applies the system to Brazilian Cerrado vegetation and is available at www.scielo.br/scielo.php?script=sci_arttext&pid=S1519-69842004000200004

⁹ See Mace et al. (2005) Millennium Ecosystem Assessment, and WWF Ecoregions for maps at www.worldwildlife.org/science/ecoregions/terrestrial.cfm

- It deals with group properties, such as plant functional types.
- An individual biome will tend to have the same kinds of biological communities wherever it occurs; however, the species present will be different. Thus the dominant species present in tropical forests of the Amazon basin are different from those present in the dipterocarp evergreen rainforest of south-east Asia, which also differ from those of equatorial Africa.
- Life forms in different geographical regions within a biome tend to be ecological equivalents – that is, they ‘do’ the same kinds of things and occupy similar niches.

Over the past 250 years, collection and classification of the flora and fauna of the world have shown that the terrestrial biosphere could be subdivided into distinctive, taxonomic, flora regions – the **floristic kingdoms**:¹⁰

- boreal (North America, Europe, northern and central Asia, and North Africa)
- palaeotropical (Africa, Indo-Malaysian and Polynesian)
- neotropical (South and Central America, South Africa, Australia and Antarctic)
- Cape Province of South Africa.

and distinctive, taxonomic, faunal regions or **zoogeographic regions**¹¹ recognised by Alfred Russel Wallace in *The geographical distribution of animals*:¹²

- palaeartic (Europe, northern Africa, northern Asia)
- nearctic (North America and Greenland)
- Ethiopian (Africa south of the Sahara)
- oriental (India and south-east Asia)
- Australian
- neotropical (central and south America)
- Antarctica.

Comparison of these faunal and floristic kingdoms or regions shows that:

- The kingdoms are taxonomic entities, not vegetation units.
- The distributions of the global biomes and the floral and faunal regions do not coincide.
- The boundaries of the floral and faunal regions are not the same.
- There are marked differences in floral and faunal distributions in South Africa and Australasia.
- Terrestrial floras are generally older than their associated faunas and show the influence of earlier stages of crustal and climatic evolution.
- There are more families of living plants (300 with 12,500 genera) compared with families of living animals (only 100 with 1,000 genera).
- There are often sharp boundaries between biogeographic regions; two of the most distinctive marked by the range of many taxa are:
 - **Wallace’s line**¹³ between Borneo and Sulawesi, which separates the oriental and Australian regions
 - the **Isthmus of Panama**, which separates the biotas of North and South America
 - the **Sahara**, which separates the palaeotropical biotas from the palaeartic biotas.

¹⁰ Distribution maps are available from <http://bure.unep-wcmc.org/imaps/gb2002/book/viewer.htm>. Good (1974) discusses these kingdoms in considerable detail.

¹¹ E.g. at http://encarta.msn.com/media_461536032/Zoogeographic_Regions.html

¹² Alfred Russel Wallace was one of the first to draw attention to these biogeographic realms in his 1876 book *The geographical distribution of animals*. Many details of his life and work and copies of some of his papers can be found at the Alfred Russel Wallace page (www.wku.edu/~smithch/index1.htm). See also http://evolution.berkeley.edu/evolibrary/article/_0/history_16 for original illustrations.

¹³ See www.wku.edu/~smithch/index1.htm for a copy of Wallace’s original paper ‘On the zoological geography of the Malay Archipelago’ (553: 1859).

Learning activity

See what you can find out from the references and Internet resources given about the floristic and faunal kingdoms. Make a list of what factors might cause the discordance with biomes. In particular, you should think about the following:

- crustal change and plate tectonics
- evolution of floras and faunas
- climate change
- extinction events in the geological record
- effects of mountain barriers and oceans
- why the northern hemisphere patterns are so different from those of the southern hemisphere.

Particular questions that need answers are:

- Why is the flora of Cape Province of South Africa so distinctive, whereas the fauna is not?
- Why are the flora and fauna of Australia so distinctive from that of neighbouring south-east Asia?
- What has caused Central and South America to be distinctive from North America?

Present-day patterns of families, genera and species

In our earlier discussion of local distributions of genera and species, we discussed the concept of species range. When we investigate the global distribution families, genera and species, we find that plant and animal distributions fall into several distinctive groups, each with decreasing area:

- cosmopolitan and subcosmopolitan
- tropical
- temperate
- discontinuous or disjunct
- endemic.

Plant and animal distributions

Cosmopolitan and subcosmopolitan

The ranges of families, genera and species embrace both the tropical and temperate parts of the world. Plants that have cosmopolitan distributions at the family level include the grasses (Gramineae), which are a dominant component of most present-day ecosystems, closely followed by the Compositae and Cyperaceae. For animals, examples are the Colubridae snakes, the viper family (Viperidae) and the pit-vipers (Crotalidae), which typically have worldwide distributions. Other examples are the rat and bat families, hawks and cuckoos.

Tropical

Typical flora elements include the Palmae, Bauhinia, Eugenia, Hibiscus and Vitex. Animals include members of the cat families and primates.

Temperate

Plant examples include the Cruciferae, Juncaceae and Gentiana. Animal examples include the dogs, rabbits, bears and deers.

Discontinuous or disjunct

The best-known plant examples come from the south temperate zone and include Fagaceae (Nothofagus) and the Restionaceae. Other examples are the Magnoliaceae and Rhizophoraceae. Examples of animals are camelids, which occur in the Palearctic and Neotropical, and marsupials, which are split between the neotropical (Caenolestidae), neoarctic (Didelphidae) and Australia (all other marsupials). Ratite birds (emus, cassowaries, ostriches, rheas, tinamous and kiwis) are another well-known example.

Endemic

This literally means 'confined to one region'. Some are evolutionary relics, such as the Ginkgo. Two regions stand out for the richness of their endemic flora – the South African Cape region, where 500 of the 1,500 genera are endemic – and Australia, where there are also about 500 endemic genera. The Australian fauna is equally rich in endemics – eight out of nine mammal families are endemics – and marsupials. Monotremes are uniquely Australian.

The problem of disjunct and endemic patterns

The two distribution types that pose important biological questions are the disjunct and endemic floras and faunas. If, as Darwin hypothesised, evolution required descent from a common ancestor at a single location in the past (monophyletic origin of species), how can we explain the observed disjunct distributions? Similarly, how can we explain the endemic distributions discussed above?¹⁴

Two major sets of hypotheses have been invoked to explain disjunct patterns:¹⁵

- **Dispersal**, which is the migration of the taxon across a barrier (desert, mountain, ocean) from its source area A to a new area B. The colonisation of oceanic islands is evidence of this route, as is the migration of tree species into the British Isles in post-glacial times. Dispersal can take place along **corridors** (e.g. Bering Straits, Beringia, between Alaska and Siberia in the Cainozoic and the Isthmus of Panama), through **filters** (such as deserts or islands) and via **sweepstake routes** (e.g. ocean islands, where only a few, randomly selected species get through the barriers).
- **Vicariance**, which is the erection of a barrier (ocean, mountain, desert or sea-level rise) across the past distributional range of a taxon, breaking it into two or more separate areas was first advanced by L. Croizat.¹⁶ The most cited explanation for vicariance is plate tectonics.

In order to test these hypotheses, we need good evidence of past associations, such as fossil (palaeontological) data, phylogenetic trees, plate tectonic reconstructions and climatic reconstructions of distributions in the past. We will review this evidence in the next chapter.

Endemics can be classified in several ways, depending upon how their isolation was achieved:

- **Paleoendemics**: families, genera or species isolated by ancient environmental change, such as plate tectonic drift.
- **Neoendemics**: formed geologically recently by, for example, glacial retreat and isolation.
- **Taxonomic relics**: sole survivors of once more extensive taxa, such as the Ginkgoales, where the sole survivor, *Ginkgo biloba*, is only found in eastern China.

¹⁴ Chapter 10 of Lomolino et al. (2005) and Cox and Moore (2005), Chapter 9.

¹⁵ See Chapter 10 of Lomolino et al. (2005).

¹⁶ See www.sciencebuff.org/leon_croizat_biography.php

The present-day distribution of endemics is of vital importance to conservation.¹⁷ The leading **hotspots for endemics** are shown in Table 3.1. This table is only a partial listing of the 25 hotspots that Meyers et al. (2000) discuss.¹⁸ Other areas that equal or exceed the densities given above are the Cape Floristic Province, with a species/area ratio of 31.6 for plants and only 0.3 for vertebrates, New Caledonia (49.1 and 1.6, respectively) and the eastern arc and coastal forest of Tanzania and Kenya with (75 and 6.1, respectively). The congruence demonstrates that many areas are endemic hotspots for both plants and vertebrates. Most, but not all, of the hotspots are located within the tropics.

¹⁷ See the Nature special issue (Nature 2000, 405), Myers (2000) and Lamoreux et al. (2006).

¹⁸ Conservation International's web site Biodiversity Hotspots outlines the science and discusses the individual regions in detail. www.biodiversityhotspots.org/xp/Hotspots

Learning activity

At this stage it would be useful to find examples of local, regional and global distributions of plants and animals. Useful web site sources include:

- African Mammals Database
- Thompson (1999)
- Flora Europaeae Atlas
- National Botanical and Zoological Atlases.

Hotspot	Number of endemic plants (% global total of 300,000 plant species)	Species/area ratios per 100 km ² of endemic plants	Number of endemic vertebrates (% of global total of 27,298 of animal species)	Species/area ratios per 100 km ² of endemic vertebrates	Percentage congruence between plants and vertebrates
Tropical Andes	20,000 (6.7)	6.4	1,567 (5.7)	0.5	85
Sundaland (southeast Asia)	15,000 (5.0)	12.0	701 (2.6)	0.6	52
Madagascar	9,704 (3.2)	16.4	771 (2.8)	1.3	88
Brazil's Atlantic Forest	8,000 (2.7)	8.7	567 (2.1)	0.6	78
Caribbean	7,000 (2.3)	23.5	779 (2.9)	2.6	79
Subtotals (% rounded)	559,700 (19.9)		4,385 (16.1)		
Mesoamerica	5,000 (1.7)	2.2	1,159 (4.2)	0.5	41
Mediterranean Basin	13,000 (4.3)	11.8	235 (0.9)	0.2	21
Indo-Burma	7,000 (2.3)	7.0	528 (1.9)	0.5	83
Philippines	5,832 (1.9)	64.7	519 (1.9)	5.7	100
Grand totals	90,536 (30.1)		6,826 (25)		

Table 3.1 Leading endemic hotspots, with at least 2 per cent of the world's endemic species, based on Tables 3, 4 and 5 of Meyers et al. (2000)¹⁹

¹⁹ You can download the latest 2005 map of biodiversity hotspots from www.biodiversityhotspots.org/xp/Hotspots/resources/maps.xml

How similar are the global biotas?²⁰

It is possible to apply quantitative techniques to compare objectively the degree of similarity between the floras and faunas of different biogeographical regions. Thus, Flessa (1979) computed the similarity between mammalian faunas of various regions, using the Simpson Index²¹ of similarity ($C/N1$: where C is the number of taxa present in both regions and $N1$ is the total number of taxa in the first region). A high index is indicative of a close relation. Typical results at the genus level show that South America has the strongest links with North America ($SI=81$) and the weakest links with the rest of the world ($SI<7$). Similar results were found at the family level.²²

²⁰ See Millennium Ecosystem Assessment chapters by Mace et al. (2005), Sala (2005) and Scholes et al. (2005) for an overview.

²¹ You will find a useful discussion and illustration of diversity indices the World Agroforestry Centre: www.worldagroforestrycentre.org/sites/RSU/resources/biodiversity

²² Chapter 9 of Cox and Moore (2005) has an excellent discussion of this approach.

Biodiversity and species diversity²³

The World Conservation and Management Centre defined biodiversity as:

A contraction of biological diversity...and...describes the number, variety and variability of living organisms. (WCMC, 1995)

This is usually at the species (species diversity) and ecosystem levels. Usually it is viewed from three points of view:

- present-day global patterns of species richness
- biodiversity hotspots for conservation
- changes over time.

We will deal with this last topic in the next chapter.

Species diversity or richness is usually described by three measures:

- **Alpha (α) diversity:** a direct count of all the species in a local ecological community on a unit area basis, e.g. m^2 , hectare, km^2 .
- **Beta (β) diversity:** the change in the number of species within a selected area or along a transect line. It is a measure of turnover.
- **Gamma (γ) diversity:** the total number of species in an entire biome or, for example, the Amazon or Congo drainage basins.

²³ The collection of papers appearing in Nature (2000, 403 March 24) should be read for an up-to-date view of the importance of species diversity. Lomolino et al. (2005) contain especially good accounts.

²⁴ Conservation International's web site Biodiversity Hotspots outlines the science and discusses the individual regions in detail. www.biodiversityhotspots.org/xp/Hotspots

²⁵ See Chapters 14–16 of Lomolino et al. (2005).

Present-day global patterns of species richness²⁴

One global pattern of species diversity that has been widely reported²⁵ is the **latitudinal gradient** of species diversity, in which species richness is highest in the equatorial regions and decreases towards both poles.²⁶ Many different taxonomic groups show this pattern – land mammals in North and South America, bats, breeding land birds, snakes, termites, and trees, for example – indicating that most major biotic groups of organisms are involved. There are exceptions, such as pines, parasitic wasps and soil nematodes.

Various hypotheses have been advanced to explain this latitudinal gradient of species diversity and are fully reviewed by Hillebrand (2004):²⁷

- **Productivity:** ecosystems with higher rates of net primary production (NPP), which is related to incoming photosynthetically active radiation (PAR), support more species. Available energy increases towards the equator.
- **Climatic stability:** climatic fluctuations increase away from the equator. Reduced climatic fluctuations lead to greater stability, more niche specialisation and smaller niches.

²⁶ Hillebrand, H. (2004) 'On the generality of the latitudinal Diversity gradient', *American Naturalist* 163, pp. 194–211, reviewed 581 studies of the latitudinal distribution of both fauna and flora. He concluded that both terrestrial and marine gradients were the norm, with few exceptions. Moreover, both the area-energy hypothesis and the evolutionary time hypothesis are most widely supported by his meta-analysis.

²⁷ Chapter 23 of Krebs (1994), and Chapters 17 and 21 of Begon et al. (2006) give excellent discussions of these hypotheses.

- **Habitat heterogeneity** increases towards the equatorial regions, supporting greater niche specialisation.
- **Time:** more time allows for greater habitat saturation and less undersaturation. Here the effects of the quaternary glaciations are important in temperate latitudes.
- **Interspecific interactions** via competition: these may either reduce niche breadth or eliminate species due to competitive exclusion or predation, which retards competitive exclusion.

The other commonly observed gradient of species diversity is the **altitudinal gradient**, which is seen in most major mountain ranges.

Associated with both these gradient changes are three other associated patterns:

- **Rapport's rule:**²⁸ in which species range increases and species richness decreases as latitude increases.²⁹ There is active discussion as to why this should be so.
- **Dominance–diversity relation** or patterns of dominance: in temperate regions, forests tend to have ‘indicator’ or dominant species – such as oaks, beeches and pines – which may account for more than 5 per cent of the species abundance, or cover, when plotted against the species rank for the community. In tropical forests, the inverse is generally true, and as species richness increases, dominance of any one tree species decreases.
- **Species–area relations:** generally, larger areas support more species. Species numbers (S) are related to area (A) by the relation $S = cA^z$ or $\log(S) = \log(c) + z \log(A)$. The slope of the line z varies from 0.5 to 1.0 for different land masses, between 0.1 and 0.2 for non-isolated area within landmasses and between 0.2 and 0.5 for islands or isolated habitat patches.³⁰

Important links exist between these various relations, with an increasing body of ecological evidence suggesting that ecosystem stability and function are reduced when species diversity is decreased. We will consider this issues in the context of human induced global environmental change addresses in the final chapter.

²⁸ See Wikipedia at http://en.wikipedia.org/wiki/Rapport's_rule

²⁹ See Arita (2005) for a recent discussion on Rapport's rule and American mammals.

³⁰ See the discussions in Lomolino et al. (2005) and Drake et al. (2006).

Conclusions

In this chapter, we have reviewed the ways in which life on earth is spatially organised and have shown that the organisation is dependent on the way in which one approaches the question. Organisation is scale dependent and reflects the effects of both long-term and short-term environmental changes. Finally, it appears that ecosystem stability may ultimately depend on optimising species diversity.

A reminder of your learning outcomes

By the end of this chapter you should be able to:

- explain how life in the biosphere is organised on different spatial scales
- explain the nature of biomes and how they differ from plant and animal kingdoms or realms
- explain the distribution and extent of floristic and faunal kingdoms or realms

- explain and exemplify what are meant by cosmopolitan, disjunct and endemic biota
- discuss what is meant by the term 'species diversity' and the relation between species diversity and latitude, altitude and area
- discuss the hypotheses that are used to explain patterns of species diversity.

Sample examination questions

1. Critically evaluate the hypotheses that have been advanced to explain latitudinal gradients of species diversity.
2. What relations exist between the distribution of biomes and global climate and how might this relation be modelled?
3. What evidence is there to support the hypothesis that ecosystem stability is controlled by species diversity?

Notes