Chapter 1
Introduction to Spatial Ecology and Its Relevance for Conservation

1.1 What Is Spatial Ecology?

"Space: The final frontier" Kareiva (1994)

All aspects of ecology play out in space. From Darwin's entangled bank to Hutchinson's ecological theater (Hutchinson 1965; Darwin 1859), space is inherent to all processes and research in ecology. The importance of space has captured the imagination of biologists interested in a wide variety of topics, such as migration, species coexistence, deforestation, and the spread of invasive species. Therefore, how space directly and indirectly affects biodiversity and ecosystem functioning is implicitly and/or explicitly the focus of several subdisciplines in the life sciences (Fig. 1.1).

All of these subdisciplines share concepts and analytical methods that stem from the field of spatial ecology: a field coined by Tilman and Karieva in 1997. Since then, the term "spatial ecology" has been used in a wide range of ways depending on each ecological subdiscipline and field. Biogeography focuses on species geographic distributions (Lomolino 2017). Landscape ecology relates spatial heterogeneity to ecological processes and species distribution (Turner and Gardner 2015). Movement ecology focuses on organismal dispersal and migration (Nathan et al. 2008). Macroecology investigates the relation of processes and species at large spatial scales (Gaston and Blackburn 2000). Metaecology considers dispersal and spatial interactions at different spatial scales to model ecological processes that affect species distribution and dynamics (i.e., metapopulations, metacommunities, metaecosystems; Massol et al. 2011). Spatial and landscape genetics relate how landscape features affect gene glow and local adaptation (Manel et al. 2003; Guillot et al. 2009). Finally, conservation biology develops and applies spatial solutions to a variety of problems, including mitigating the effects of roads, protected area networks, and spatial prioritization in conservation planning (Primack 2014) (Fig. 1.1).

Throughout this book, we use the term spatial ecology in a broad sense referring to the study and modeling of the role(s) of space on ecological processes (e.g.,

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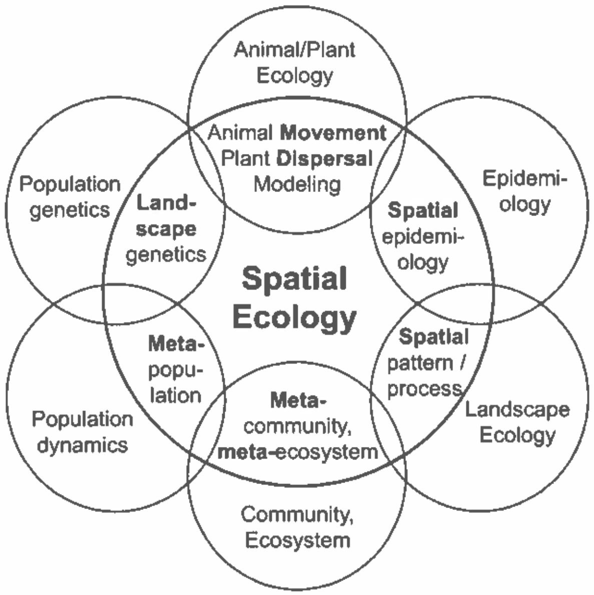


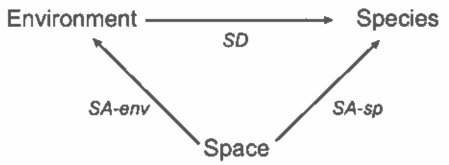
Fig. 1.1 Spatial subdisciplines derived from ecological disciplines using a spatial ecology framework to tackle current conservation issues

population dynamics, species interactions, dispersal) that in turn affects ecological patterns, such as species distributions. This definition shares similarities with some early definitions of landscape ecology (Pickett and Cadenasso 1995; Turner 1989). Yet over the years, landscape ecology evolved to include socio-economic aspects of landscapes as well (Wu 2017).

Research in spatial ecology aims to understand the processes that affect species distributions and dynamics, and how these processes play out across space. Endogenous processes are related to the dynamics of each ecological entity (e.g., movement, dispersal, and migration) and the interactions among entities within and across species (population demographics, genetic variation, behavior, competition, facilitation, trophic interactions, etc.). Exogenous processes are related to the response of organisms to environmental factors that are themselves spatially structured (climate, local habitat features, microhabitat heterogeneity, patch disturbance-succession, environmental filtering, historical contingencies, etc.). Overall, it is the combined action and feedback effects of these endogenous and exogenous processes that result in the spatial patterns observed at different levels of organization though space (e.g., metapopulations, metacommunities, and metaecosystems) (Fig. 1.2).

Spatial ecology is increasingly applied to conservation and management to help deliver more effective ways to conserve biodiversity. The rapid rate at which landscapes are altered is creating spatially heterogeneous environmental conditions that affect species ability to disperse and ultimately persist. Yet, even in homogeneous environments, endogenous processes alone can shape species spatial distributions (Okubo 1974). This is why many of the core ecological theories and analytical models used in spatial ecology are process-based ones. Therefore, one of the most important cornerstones of spatial ecology as a discipline is the way in

Fig. 1.2 How space affects both the spatial structure of the environmental conditions and species distribution. Species distribution is also affected by the spatial structure of the environmental data (adapted from Wagner and Fortin 2005)



which the challenges of understanding the processes underlying the spatial distribution of ecological entities are tackled. Spatial ecology offers concepts and tools to understand, predict, and map how biodiversity responds to environmental change.

1.2 The Importance of Space in Ecology

Species dynamics occur over space and time. Space affects species in multiple ways from how they use resources and occupy space within their home range and throughout their geographical range, how they move, disperse, and migrate through heterogeneous landscapes, as well as how they interact with other species (Table 1.1).

To determine the relative importance of space on ecological patterns and processes, both mathematical and statistical models are frequently used (Dale and Fortin 2014; Cantrell et al. 2009; Fortin et al. 2012; Ovaskainen et al. 2016). These two modeling approaches encompass stark differences from data needs, model assumptions, and epistemologies (Fig. 1.2). Both process-based (e.g., mathematical, stochastic simulations and computational models) and phenomenological approaches (e.g., statistical regression models) have a long history of contributing to our understanding of the spatial distribution of ecological entities from fine to broad scales (Levin 1976; MacArthur and Wilson 1967). Such spatial models aim to improve our understanding of the underlying processes acting on species distributions (e.g., to estimate the relative importance of environmental drivers versus dispersal to species distributions) and to perform ecological forecasting (e.g., to predict species distributions based on such processes; Pagel and Schurr 2012; Dietze 2017).

The foundation for spatial ecology can be traced largely to the seminal paper of Watt (1947) on the relationship between spatial pattern and ecological processes. Watt (1947) emphasized that plants occurred in bounded communities—patches—that form a dynamic mosaic across the landscape, what has become known as the

Table 1.1 Examples of how space can be incorporated into spatial analyses and their effects on ecological processes (adapted from Fortin et al. (2012))

Spatial aspects	Effects on ecological processes and data
x–y coordinates	Location of data according to positions of other locations (Euclidean or relative distance)
Spatial autocorrelation	The magnitude, spatial scale, and directionality of data values as a function of distances between data point locations
Spatial relationship	Locations of abiotic predictors affect the responses of biotic/ecological variables
Spatial legacy	Influence of past spatial pattern on current ecological processes and species current spatial pattern
Spatial contingency	Influence of nearby locations (local neighbors) on ecological processes and species spatial pattern
Spatial perception	How the intervening landscape features affect daily animal movement and species dispersal ability
Multiple spatial scales	Additive spatial scales influence current spatial pattern

"shifting-mosaic steady state" concept (Bormann and Likens 1979). Then, in the 1950s and 1960s, there were three key areas of research that emphasized the importance of space for ecological processes and its relevance for conservation. First, some influential experimental studies highlighted the importance of space for ecology. In a seminal experiment, Huffaker (1958) showed how predator–prey dynamics could be stable when including the potential for spatial refugia of prey, while stability was not possible in small, homogenous habitats. This result was important because prior to that time, spatial concepts had not been formally considered in theory and concepts regarding species coexistence. This experiment emphasized the role of movement in altering species interactions and community structure, a theme that has persisted and grown over time.

A second area of conceptual development came from theoretical ecology (Hastings and Gross 2012), where ecologists investigated how diffusion of organisms through space can alter population and community dynamics (Skellam 1951; Okubo and Levin 2001; Hilborn 1979). Skellam (1951) pioneered these ideas by applying reaction–diffusion models originally derived for molecular processes to the problem of dispersal and population dynamics. In this model, Skellam (1951) assumed diffusion (or random movement) of organisms. While it is clear that organisms do not move in a simple random manner, the utility of this approach is that this simple formulation can go a long way in explaining observed patterns in ecology (Kareiva 1982, 1983), and it can be extended to capture non-random issues (e.g., advection; Reeve et al. 2008). In addition, Skellam's work set the stage for modeling invasive spread, a topic of great importance to conservation biology.

The third area is the application of biogeographic concepts to our understanding of species–area relationships by Preston (1948, 1962) and later MacArthur and

Wilson (1963, 1967). This area was particularly crucial in developing the application of spatial ecology to practical issues of conservation (Higgs 1981). Indeed, many ecological theories and conservation concepts, including practical solutions, stem from island biogeography theory, where the size of islands/patches and their spatial configuration (spacing/isolation) are critical for species persistence through variation in colonization and extinction events (MacArthur and Wilson 1967; Laurance 2008).

The current era of spatial ecology has grown from island biogeography, where dispersal of individuals is key and can act as a rescue effect or spatial insurance (Loreau et al. 2003a) that protects a population from local extinction. Here, species are often considered to act as metapopulations (Hanski 1999; Levins 1969). The concept of spatial insurance has been extended to dispersal of several species to maintain species assemblages and communities as metacommunities (Leibold et al. 2017, 2004) and to maintain ecosystem functions as metaecosystems (Loreau et al. 2003b; Guichard 2017).

1.3 The Importance of Space in Conservation

Conservation biologists have increasingly embraced the importance of space in the conservation of biodiversity and ecosystem services (Schagner et al. 2013; Moilanen et al. 2009). Space is relevant for conservation in four major ways: (1) it is essential for spatial mapping of biodiversity and ecosystem services; (2) it provides guidance for mitigating effects of environmental change; (3) it facilitates effective prioritization of areas for conservation; and (4) it provides key components of tools and models used in conservation.

Several biogeography and macroecology theories provide spatial foundations for understanding and mapping biodiversity across the planet. The emphasis on spatial components first emerged in the field of biogeography, where there was interest in identifying and understanding species distributions and geographic gradients in biodiversity throughout the world. For instance, early on scientists emphasized the latitudinal gradient of diversity, where diversity was greater in the tropics than in the temperate zone (Currie and Paquin 1987). Understanding this and other biogeographic (and macroecological) patterns have been, and continue to be, of interest in conservation as it helps identify hotspots of biodiversity and endemism of conservation relevance (Myers et al. 2000; Dawson et al. 2017; Orme et al. 2005).

Many approaches to mitigating the effects of environmental change embrace spatial concepts. For example, the use of corridors in conservation explicitly emphasizes how the spatial configuration of the environment can promote biodiversity (Crooks and Sanjayan 2006). Translocations and re-introduction programs require understanding how potential release locations may inhibit or foster the success of such programs (Seddon et al. 2014). Adaptation strategies to mitigate the effects of climate change often emphasize spatial ecological concepts (Heller and Zavaleta 2009).

Conservation prioritization and planning, one of the major foci for conservation biology, also emphasizes the importance of spatial ecology. Early rules for conservation planning embraced the need to limit isolation of protected areas and maximize their area (Diamond 1975). Later work has embraced explicit mapping of conservation prioritization strategies and how issues such as complementarity of biodiversity among protected areas is essential for efficient conservation planning (Margules and Pressey 2000). More recently, conservation planning for climate change emphasizes how key areas are currently connected and how connectivity may change as climate and land use continue to change (Pressey et al. 2007; Schmitz et al. 2015; Carroll et al. 2017). Throughout, spatial concepts are essential for guiding effective strategies for both biodiversity and ecosystem service conservation (Chan et al. 2006; Moilanen and Wintle 2007).

Ecological concepts and analytical tools developed in the fields of landscape ecology, geography, and spatial statistics are now commonly used in conservation so that informed decisions about planning strategies and management can be made (e.g., Moilanen et al. 2009). Indeed, most conservation planning and management requires knowledge and the explicit spatial modeling of space and its major consequences on species spatial variation and responses to global change. The inclusion of space is therefore crucial when modeling species ecology and responses to a changing world such as (1) species dispersal, (2) species interactions, (3) disturbance dynamics, and (4) environmental change. Furthermore, as the field of conservation aims to provide better management recommendations to mitigate threats to biodiversity, implicit and explicit aspects of space need to be incorporated into applied solutions such as restoration, species reintroductions, and maintaining connectivity among habitat patches. In all these conservation applications the spatial scale of implementation is key (Wiens 1989; Levin 1992, 2000; McGarigal et al. 2016; Doak et al. 1992; Fletcher et al. 2013; Gering et al. 2003).

1.4 The Growth of Frameworks for Spatial Modeling

Before modeling species dispersal, response to environmental conditions, and species interactions, quantification of their spatial distribution is needed. This is why in ecology and conservation the first steps toward a better understanding and management of biodiversity often consist of (1) mapping species distributions, and (2) quantifying spatial patterns of both species distributions and environmental conditions (Ferrier 2002; Gaston and Blackburn 2000; Guisan and Thuiller 2005). Once such quantitative information is obtained, the next modeling steps frequently aim at relating and modeling the responses of species to environmental conditions across space and/or the species (intraspecific and interspecific) spatial interactions (Synes et al. 2017).

Modeling the processes that affect species distribution can be done using different degrees of complexity in the analytical tools used. The level of complexity depends on the processes modeled and ecological theories considered. Then, knowledge gaps about

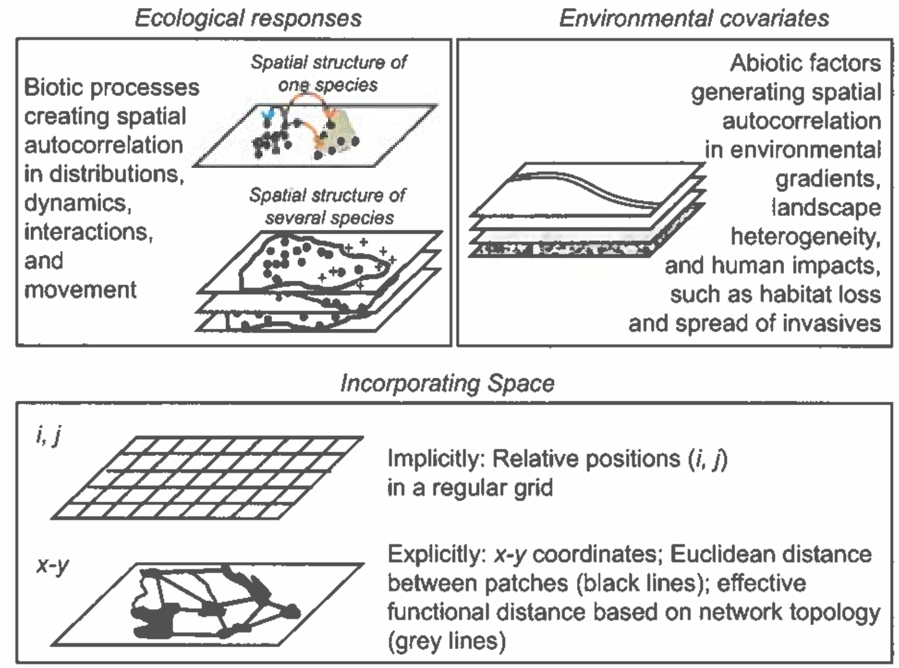


Fig. 1.3 How spatial processes affect species (response variables) and covariates (predictors), and how space can be incorporated into models

species distribution can be gained by combining data on species behavior from empirical studies and theoretical models of dispersal and related flows across space. Early dispersal models set the stage for the development of ecological theories that embrace space (Fig. 1.3), such as island biogeography (MacArthur and Wilson 1967), patch dynamics (Pickett and White 1984), hierarchical theory (Wu and Loucks 1995; Allen and Starr 1982), species coexistence (Chesson 2000), metapopulation (Hanski 1999), metacommunity (Leibold and Chase 2017), and metaecosystem theory (Guichard 2017). Although these disciplines can be seen as separate fields, spatial ecology brings them together through theory, models, and data analysis (Massol et al. 2011).

The emergence of modeling frameworks for spatial ecology was also fostered by several technological advances ranging from the availability of aerial photographs, remote sensing captors, and computing power. This allowed for conceptual and modeling developments in spatial ecology to advance more realistic ways to represent and incorporate space into statistical and modeling approaches (Fig. 1.3). Indeed, the ability to explicitly include the effects of space in ecological models was also pivotal in the explosion of novel ecological questions and analytical ways to address them over the last few decades.

The quantum leap in spatial ecology modeling frameworks involved considering and incorporating space into modeling: implicitly (kernels, moving windows, relative topological position, etc.), explicitly (*x–y*, diffusion, spread, individual/agent-based models, etc.), and realistically (explicit network structure, spatial weights, multiple spatial scales, etc.) (Fig. 1.3). It started by considering space as discrete units. Such discretization of space opened a multitude of novel ways to model ecological systems either in a spatially implicit fashion, where species occupancy and abundance are modeled considering the effects of relative neighbors based on grid topology (e.g., cellular automata models), or in a spatially explicit way, where the actual Euclidean distances among cells (quadrats, pixels, sampling locations) are used to model the spread of disturbance, disease, or species using dispersal kernels. Then space was represented by the exact *x–y* coordinates of each individual in a given area such that the spatially explicit movement of individuals could be modeled using individual/agent-based modeling approaches (Grimm et al. 2005; Matthews et al. 2007). For example, this approach enabled modeling the dynamics and succession of tree species at the tree-level using SORTIE (Pacala et al. 1996). Using *x–y* coordinates of individuals or sampling locations also allowed the spatially explicit modeling of movement and connectivity while accounting for species dispersal ability through spatially heterogeneous landscapes (Urban and Keitt 2001). Lastly, the spatially explicit representation of space permits us to model processes acting over several spatial scales using meta-models (Urban 2005; Talluto et al. 2016). The ability to model species and their responses to global change explicitly in space opens the door to investigate the effects of the spatial legacy (Wallin et al. 1994; James et al. 2007; Peterson 2002) of heterogeneity on ecological processes and species persistence.

1.5 The Path Ahead

Spatial ecology and conservation has rapidly advanced over the past 20 years. With an increasing emphasis on the use of spatial data and modeling to address both fundamental and applied problems, the topic has matured. Spatial ecology embraces spatial modeling and analysis, which is often applied to conservation issues.

In the remainder of this book, our path will be to provide an introduction to several issues in spatial ecology and conservation, with an emphasis on spatial modeling of applied ecological problems. We emphasize learning-by-doing, where we illustrate these topics with real data and the application of spatial modeling to these topics. We first cover topics regarding the quantification of spatial pattern in ecological data and we then focus more specifically on topics regarding how species respond to spatial pattern and its relevance for conservation (Table 1.2). We hope that this coverage will deliver a strong foundation for students and professionals alike to begin tackling ongoing issues of ecological and conservation importance.

Table 1.2 Examples of spatial analytical methods (and book chapter(s) where they are presented) used in spatial ecology and the quantitative components that they are estimating

Spatial analytical methods	Spatial components addressed
Multiscale analysis (Chap. 2)	Determine key spatial scales affecting the response variables
Categorical pattern analysis (Chap. 3)	Quantify land-use and land-cover patterns
Spatial point processes (Chap. 4)	Identifying the spatial pattern of points (events) and understand the potential processes generating those patterns
Spatial-, geo-statistics (Chap. 5)	Magnitude, range, and directionality of spatial variance
Spatial regressions (Chap. 6)	Accounting for spatial structure of the response (spatial nuisance) and independent variables (spatial contingency) in estimating relationships
Species distribution models (Chap. 7)	Interpolation, projections, and forecasting
Animal movement models (Chaps. 8 and 9)	Accounting for spatial heterogeneity and quantifying trajectories
Spatial network analysis (Chap. 9)	Topological network, Euclidean, and functional distances
Spatial population dynamics (Chap. 10)	Population dynamics accounting for spatial heterogeneity
Beta diversity (Chap. 11)	Spatial species turnover
Spatial community analysis (Chap. 11)	Spatial components of species interactions and environmental filtering

References

Allen TFH, Starr TB (1982) Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago
Bormann FH, Likens GE (1979) Catastrophic disturbance and the steady-state in northern hardwood forests. Am Sci 67(6):660–669
Cantrell S, Cosner C, Ruan S (2009) Spatial ecology. Chapman & Hall/CRC, Boca Raton, FL
Carroll C, Roberts DR, Michalak JL, Lawler JJ, Nielsen SE, Stralberg D, Hamann A, McRae BH, Wang TL (2017) Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. Glob Chang Biol 23(11):4508–4520. https://doi.org/10.1111/gcb.13679
Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. PLoS Biol 4(11):2138–2152. https://doi.org/10.1371/journal.pbio.0040379
Chesson PL (2000) General theory of competitive coexistence in spatially varying environments. Theor Popul Biol 58:211–237
Crooks KR, Sanjayan M (eds) (2006) Connectivity conservation. Cambridge University Press, New York
Currie DJ, Paquin V (1987) Large-scale biogeographical patterns of species richness of trees. Nature 329(6137):326–327. https://doi.org/10.1038/329326a0
Dale MRT, Fortin MJ (2014) Spatial analysis: a guide for ecologists, 2nd edn. Cambridge University Press, Cambridge
Darwin C (1859) On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life. John Murray, London

Dawson W, Moser D, van Kleunen M, Kreft H, Pergl J, Pysek P, Weigelt P, Winter M, Lenzner B, Blackburn TM, Dyer EE, Cassey P, Scrivens SL, Economo EP, Guenard B, Capinha C, Seebens H, Garcia-Diaz P, Nentwig W, Garcia-Berthou E, Casal C, Mandrak NE, Fuller P, Meyer C, Essl F (2017) Global hotspots and correlates of alien species richness across taxonomic groups. Nat Ecol Evol 1(7):0186. https://doi.org/10.1038/s41559-017-0186

Diamond JM (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biol Conserv 7(2):129–146. https://doi.org/10.1016/0006-3207(75)90052-x

Dietze M (2017) Ecological forcasting. Princeton University Press, Princeton

Doak DF, Marino PC, Kareiva PM (1992) Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theor Popul Biol 41(3):315–336. https://doi.org/10.1016/0040-5809(92)90032-o

Ferrier S (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Syst Biol 51(2):331–363. https://doi.org/10.1080/10635150252899806

Fletcher RJ Jr, Revell A, Reichert BE, Kitchens WM, Dixon JD, Austin JD (2013) Network modularity reveals critical scales for connectivity in ecology and evolution. Nat Commun 4:2572. https://doi.org/10.1038/ncomms3572

Fortin MJ, James PMA, MacKenzie A, Melles SJ, Rayfield B (2012) Spatial statistics, spatial regression, and graph theory in ecology. Spatial Stat 1:100–109. https://doi.org/10.1016/j.spasta.2012.02.004

Gaston KJ, Blackburn TM (2000) Pattern and process in macroecology. Blackwell Science, Oxford, UK

Gering JC, Crist TO, Veech JA (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conserv Biol 17 (2):488–499. https://doi.org/10.1046/j.1523-1739.2003.01465.x

Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke HH, Weiner J, Wiegand T, DeAngelis DL (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310(5750):987–991. https://doi.org/10.1126/science.1116681

Guichard F (2017) Recent advances in metacommunities and meta-ecosystem theories. F1000 Research 6:610

Guillot G, Leblois R, Coulon A, Frantz AC (2009) Statistical methods in spatial genetics. Mol Ecol 18(23):4734–4756. https://doi.org/10.1111/j.1365-294X.2009.04410.x

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8(9):993–1009

Hanski I (1999) Metapopulation ecology. Oxford University Press, Oxford

Hastings A, Gross L (eds) (2012) Encyclopedia of theoretical ecology. UC Press, Berkeley, CA

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol Conserv 142(1):14–32. https://doi.org/10.1016/j.biocon.2008.10.006

Higgs AJ (1981) Island biogeography theory and nature reserve design. J Biogeogr 8(2):117–124. https://doi.org/10.2307/2844554

Hilborn R (1979) Some long-term dynamics of predator-prey models with diffusion. Ecol Model 6 (1):23–30. https://doi.org/10.1016/0304-3800(79)90055-3

Huffaker CB (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27:343–383

Hutchinson GE (1965) The ecological theater and the evolutionary play. Yale University Press, New Haven

James PMA, Fortin MJ, Fall A, Kneeshaw D, Messier C (2007) The effects of spatial legacies following shifting management practices and fire on boreal forest age structure. Ecosystems 10 (8):1261–1277. https://doi.org/10.1007/s10021-007-9095-y

Kareiva P (1982) Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. Ecol Monogr 52(3):261–282. https://doi.org/10.2307/2937331

Kareiva PM (1983) Local movement in herbivorous insects - applying a passive diffusion-model to mark-recapture field experiments. Oecologia 57(3):322–327. https://doi.org/10.1007/bf00377175

Kareiva P (1994) Space: the final frontier for ecological theory. Ecology 75(1):1–1. https://doi.org/10.2307/1939376

Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biol Conserv 141(7):1731–1744. https://doi.org/10.1016/j.biocon.2008.05.011

Leibold MA, Chase JM (2017) Metacommunity ecology. Princeton University Press, Princeton, NJ

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7(7):601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Leibold MA, Chase JM, Ernest SKM (2017) Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. Ecology 98(4):909–919

Levin SA (1976) Population dynamic models in heterogeneous environments. Annu Rev Ecol Syst 7:287–310. https://doi.org/10.1146/annurev.es.07.110176.001443

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73(6):1943–1967. https://doi.org/10.2307/1941447

Levin SA (2000) Multiple scales and the maintenance of biodiversity. Ecosystems 3(6):498–506. https://doi.org/10.1007/s100210000044

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Lomolino MV (2017) Biogeography: biological diversity across space and time, 5th edn. Sinauer, Sunderland, MA

Loreau M, Mouquet N, Gonzalez A (2003a) Biodiversity as spatial insurance in heterogeneous landscapes. Proc Natl Acad Sci U S A 100(22):12765–12770. https://doi.org/10.1073/pnas.2235465100

Loreau M, Mouquet N, Holt RD (2003b) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecol Lett 6(8):673–679. https://doi.org/10.1046/j.1461-0248.2003.00483.x

MacArthur RH, Wilson EO (1963) Equilibrium theory of insular zoogeography. Evolution 17(4):373. https://doi.org/10.2307/2407089

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18(4):189–197. https://doi.org/10.1016/s0169-5347(03)00008-9

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405(6783):243–253. https://doi.org/10.1038/35012251

Massol F, Gravel D, Mouquet N, Cadotte MW, Fukami T, Leibold MA (2011) Linking community and ecosystem dynamics through spatial ecology. Ecol Lett 14(3):313–323. https://doi.org/10.1111/j.1461-0248.2011.01588.x

Matthews RB, Gilbert NG, Roach A, Polhill JG, Gotts NM (2007) Agent-based land-use models: a review of applications. Landsc Ecol 22(10):1447–1459. https://doi.org/10.1007/s10980-007-9135-1

McGarigal K, Wan HY, Zeller KA, Timm BC, Cushman SA (2016) Multi-scale habitat selection modeling: a review and outlook. Landsc Ecol. https://doi.org/10.1007/s10980-016-0374-x

Moilanen A, Wintle BA (2007) The boundary-quality penalty: a quantitative method for approximating species responses to fragmentation in reserve selection. Conserv Biol 21(2):355–364. https://doi.org/10.1111/j.1523-1739.2006.00625.x

Moilanen A, Wilson KA, Possingham H (eds) (2009) Spatial conservation prioritization: quantitative methods and computational tools. Oxford University Press, Oxford

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858. https://doi.org/10.1038/35002501
Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proc Natl Acad Sci U S A 105 (49):19052–19059. https://doi.org/10.1073/pnas.0800375105
Okubo A (1974) Diffusion-induced instability in model ecosystems, another possible explanation of patchiness. Technical Report 86. Chesapeake Bay Institute, MD
Okubo A, Levin SA (2001) Diffusion and ecological problems: modern perspectives. Springer, New York
Orme CDL, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson VA, Webster AJ, Ding TS, Rasmussen PC, Ridgely RS, Stattersfield AJ, Bennett PM, Blackburn TM, Gaston KJ, Owens IPF (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature 436(7053):1016–1019. https://doi.org/10.1038/nature03850
Ovaskainen O, De Knegt HJ, del Mar Delgado M (2016) Quantitative ecology and evolutionary biology: integrating models with data. Oxford University Press, Oxford
Pacala SW, Canham CD, Saponara J, Silander JA, Kobe RK, Ribbens E (1996) Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol Monogr 66 (1):1–43. https://doi.org/10.2307/2963479
Pagel J, Schurr FM (2012) Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. Glob Ecol Biogeogr 21(2):293–304. https://doi.org/10.1111/j.1466-8238.2011.00663.x
Peterson GD (2002) Contagious disturbance, ecological memory, and the emergence of landscape pattern. Ecosystems 5(4):329–338. https://doi.org/10.1007/s10021-001-0077-1
Pickett STA, Cadenasso ML (1995) Landscape ecology: spatial heterogeneity in ecological systems. Science 269(5222):331–334
Pickett STA, White PS (1984) The ecology of natural disturbance and patch dynamics. Academic Press, New York
Pressey RL, Cabeza M, Watts ME, Cowling RM, Wilson KA (2007) Conservation planning in a changing world. Trends Ecol Evol 22(11):583–592. https://doi.org/10.1016/j.tree.2007.10.001
Preston FW (1948) The commonness, and rarity, of species. Ecology 29(3):254–283. https://doi.org/10.2307/1930989
Preston FW (1962) The canonical distribution of commonness and rarity: Part I. Ecology 43 (2):185–215,431–432
Primack RB (2014) Essentials of conservation biology, 6th edn. Sinauer Associates, Sunderland, MA
Reeve JD, Cronin JT, Haynes KJ (2008) Diffusion models for animals in complex landscapes: incorporating heterogeneity among substrates, individuals and edge behaviours. J Anim Ecol 77 (5):898–904. https://doi.org/10.1111/j.1365-2656.2008.01411.x
Schagner JP, Brander L, Maes J, Hartje V (2013) Mapping ecosystem services' values: current practice and future prospects. Ecosyst Serv 4:33–46. https://doi.org/10.1016/j.ecoser.2013.02.003
Schmitz OJ, Lawler JJ, Beier P, Groves C, Knight G, Boyce DA, Bulluck J, Johnston KM, Klein ML, Muller K, Pierce DJ, Singleton WR, Strittholt JR, Theobald DM, Trombulak SC, Trainor A (2015) Conserving biodiversity: practical guidance about climate change adaptation approaches in support of land-use planning. Nat Areas J 35(1):190–203
Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP (2014) Reversing defaunation: restoring species in a changing world. Science 345(6195):406–412. https://doi.org/10.1126/science.1251818
Skellam JG (1951) Random dispersal in theoretical populations. Biometrika 28:196–218
Synes NW, Brown C, Watts K, White SM, Gilbert MA, Travis JM (2017) Emerging opportuniteis for landscape ecological modelling. Curr Landsc Ecol Rep 1:146–167
Talluto MV, Boulangeat I, Ameztegui A, Aubin I, Berteaux D, Butler A, Doyon F, Drever CR, Fortin MJ, Franceschini T, Lienard J, McKenney D, Solarik KA, Strigul N, Thuiller W, Gravel D (2016) Cross-scale integration of knowledge for predicting species ranges: a metamodelling framework. Glob Ecol Biogeogr 25(2):238–249. https://doi.org/10.1111/geb.12395
Tilman D, Kareiva P (1997) Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, NJ

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197. https://doi.org/10.1146/annurev.ecolsys.20.1.171
Turner MG, Gardner RH (2015) Landscape ecology in theory and practice, 2nd edn. Springer, New York
Urban DL (2005) Modeling ecological processes across scales. Ecology 86(8):1996–2006
Urban D, Keitt T (2001) Landscape connectivity: a graph-theoretic perspective. Ecology 82 (5):1205–1218
Wagner HH, Fortin MJ (2005) Spatial analysis of landscapes: concepts and statistics. Ecology 86 (8):1975–1987. https://doi.org/10.1890/04-0914
Wallin DO, Swanson FJ, Marks B (1994) Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. Ecol Appl 4(3):569–580. https://doi.org/10.2307/1941958
Watt AS (1947) Pattern and process in the plant community. J Ecol 35(1–2):1–22. https://doi.org/10.2307/2256497
Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3(4):385–397
Wu JG (2017) Thirty years of landscape ecology (1987–2017): retrospects and prospects. Landsc Ecol 32(12):2225–2239. https://doi.org/10.1007/s10980-017-0594-8
Wu JG, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Q Rev Biol 70(4):439–466. https://doi.org/10.1086/419172