

Human activity during the Anthropocene has transformed landscapes worldwide on a scale that rivals or exceeds even the largest of natural forces. Landscape ecology has emerged as a science to investigate the interactions between natural and anthropogenic landscapes and ecological processes across a wide range of scales and systems: from the effects of habitat or resource distributions on the individual movements, gene flow, and population dynamics of plants and animals; to the human alteration of landscapes affecting the structure of biological communities and the functioning of entire ecosystems; to the sustainable management of natural resources and the ecosystem goods and services upon which society depends. This novel and comprehensive text presents the principles, theory, methods, and applications of landscape ecology in an engaging and accessible format that is supplemented by numerous examples and case studies from a variety of systems, including freshwater and marine 'scapes'.

Essentials of Landscape Ecology is suitable for upper-level undergraduate and graduate courses in landscape ecology. This textbook can also be used as a supplemental text in other ecology courses, as well as courses in forestry, resource and wildlife management, conservation and restoration biology, sustainable land-use and environmental planning. For the professional landscape ecologist, it provides an authoritative overview of the latest research and developments.

Cover image: © Linda Gass, 2007. *Fields of Salt*. Art quilt (stitched painting) depicting a landscape in the San Francisco Bay Area (California, USA) where the natural wetlands have been converted to salt ponds for industrial salt production.

OXFORD
UNIVERSITY PRESS

www.oup.com

ISBN 978-0-19-883839-5



9 780198 838395

Contents

Chapter 1	An Introduction to Landscape Ecology: Foundations and Core Concepts	1
<hr/>		
Why Study Landscape Ecology?		2
Birth of a Discipline		4
Regional Perspectives on Landscape Ecology		5
European Perspective		5
North American Perspective		7
Globalization of Landscape Ecology		8
Core Concepts of Landscape Ecology		9
Organization of this Book		11
Chapter Summary Points		12
Discussion Questions		13
<hr/>		
Chapter 2	Scaling Issues in Landscape Ecology	14
<hr/>		
Why is Scale so Important in Ecology?		14
Uses (and Misuses) of Scale in Ecology		16
Ecological Scale		16
Relationship between Grain and Extent		16
Effect of Changing Grain and Extent		18
Choosing the 'Right' Scale of Study		21
Hierarchy Theory and Landscape Ecology		24
Hierarchical Organization of Biological Systems		27
Structure of a Hierarchical System		28
Landscape Scale or Landscape Level?		29
Implications of Hierarchy Theory for Landscape Ecology		32
Extrapolating Across Scales		33
Extrapolating Within Domains of Scale		34
Extrapolating Across Domains of Scale		34
Uncertainty, Predictability, and Ecological Forecasting		36
Future Directions		39
Chapter Summary Points		40
Discussion Questions		41
<hr/>		
Chapter 3	Landscape Heterogeneity and Dynamics	42
<hr/>		
Heterogeneity and Disturbance Dynamics as Core Concepts in Landscape Ecology		42
Emergence of Heterogeneity and Dynamical Concepts in Ecology		44
Heterogeneity at Broad Geographic Scales: Biogeography and Life Zones		44
Dynamics of Plant Community Assembly: Climax State or Independent Assembly?		45
Patch Dynamics: A Paradigm Shift in Ecology		47
Toward a Non-Equilibrium View of Ecology		48
Homogeneity: The Frictionless Plane of Ecological Theory		49

Patch-Based Theory in Ecology	50
Toward a Landscape-Mosaic View of Environmental Heterogeneity	52
How is Heterogeneity Defined?	54
Spatial Heterogeneity	54
Temporal Heterogeneity	55
How are Disturbances Defined?	56
The Disturbance Regime	56
The Intermediate Disturbance Hypothesis	58
Large Infrequent Disturbances	59
Implications of the Disturbance Regime for Landscape Dynamics	61
Formation and Evolution of Landscapes: Geomorphological Processes	63
Formation of Montane Landscapes	63
Formation of River Networks	68
Formation and Diversity of Soils	69
Landscape Dynamics: Abiotic Disturbances	73
Volcanic Eruptions	73
Landsliding	76
Flooding and the Natural Flow Regime	78
Windstorms, Hurricanes, and Storm Surges	85
Drought	89
Fire	94
Landscape Dynamics: Biotic Agents of Landscape Formation and Disturbance	101
Organisms as Geomorphic Agents	102
Organisms as Ecosystem Engineers	102
The Keystone Role of Species	105
Relative Impact of Species on Landscapes	107
Humans as the Primary Driver of Landscape Change	107
Stages of Anthropogenic Landscape Transformation	108
Types of Human Land Use	110
Land-Use Legacy Effects	120
Future Directions	122
Chapter Summary Points	123
Discussion Questions	125
 Chapter 4 Landscape Pattern Analysis	 127
On the Importance of Landscape Pattern Analysis in Landscape Ecology	127
Sources of Landscape Data	128
Historical Land Surveys	129
Remote Sensing	131
From Landscape Data to Landscape Data Analysis	153
Geographical Information Systems	156
Data Input Subsystem	157
Data Processing and Database Management Subsystem	158
Data Manipulation and Analysis Subsystem	159
Data Output Subsystem	165
Landscape Metrics	165
Measures of Landscape Composition	167
Measures of Landscape Configuration	168
Effects of Pattern and Scale on Landscape Metrics	178
Use and Misuse of Landscape Metrics	184
Spatial Analysis	186
A Primer to Spatial Statistics	186
Spatial Statistics	189

Future Directions (and Some Caveats)	202
Chapter Summary Points	203
Discussion Questions	205

Chapter 5 Landscape Connectivity 206

What is Landscape Connectivity and Why is it Important?	206
Elements of Landscape Connectivity	208
Structural versus Functional Connectivity	209
Patch Connectivity versus Landscape Connectivity	210
Patch-Based Connectivity Measures	210
Which Patch-Connectivity Measure to Use and When?	212
From Patches to Landscapes	213
Methods for Assessing Landscape Connectivity	214
Neutral Landscape Models	214
Graph-Theoretic Approaches	221
Assessing Connectivity in Heterogeneous Landscapes	227
Assessing Connectivity in River Networks	232
Which Landscape Connectivity Approach to Use and When?	235
Beyond Landscape Connectivity	236
Should Landscape Connectivity be a Dependent or Independent Variable?	236
Future Directions	237
Chapter Summary Points	237
Discussion Questions	238

Chapter 6 Landscape Effects on Individual Movement and Dispersal: Behavioral Landscape Ecology 239

Why are Movement and Dispersal Important from a Landscape Ecological Perspective?	240
Scales of Movement	241
Movement Responses to Hierarchical Patch Structure	242
Allometric Scaling of Movement	245
Movement Responses to Patch Structure	245
Movement out of Patches (Emigration)	246
Movement Between Patches	256
Movement into Patches (Immigration)	260
Analysis of Movement Pathways	264
Tracking Animal Movements	265
Scaling Issues in Tracking Animal Movements	268
Measuring Movement Pathways	269
Models of Animal Movement	272
Mathematical Models of Animal Movement	272
Spatially Explicit Models of Animal Movement	277
Space Use and Home-Range Analysis	280
Methods of Home-Range Estimation	280
Measuring Plant Dispersal	284
Future Directions	286
Chapter Summary Points	287
Discussion Questions	289

Why Should Landscape Ecologists Study Population Distributions and Dynamics?	292
Overview: Effects of Habitat Loss and Fragmentation on Populations	292
Habitat Loss versus Fragmentation	293
Patch Area and Isolation Effects	294
Fragmentation and Edge Effects	294
Species Distribution Patterns	299
Spatial Pattern Analysis of Species Distributions	300
Patch versus Landscape Effects on Species Distributions	302
Species Distribution Models	303
Resource-Selection Functions	303
Ecological Niche Models	306
Climate Envelope Models	308
Summary	309
A Primer to Population Models	310
Basic Population Growth Model	310
Matrix Population Models	310
Source–Sink Population Dynamics	312
How Best to Identify Population Sources and Sinks?	313
Are Habitat Sinks a Drain on Habitat Sources?	314
Metapopulation Dynamics	315
Classical Metapopulation Models	316
Incidence Function Model	318
Source–Sink Metapopulations	319
Metapopulation Viability and Extinction Thresholds	321
Spatially Explicit Population Simulation Models	329
Which Population Model to Use and When?	332
Future Directions	334
Chapter Summary Points	334
Discussion Questions	335

Chapter 8 Landscape Effects on Population Spatial Spread: Range Shifts, Biological Invasions, and Landscape Epidemiology 337

Spatial Spread: The Good, the Bad, and the Ugly	337
Landscape Effects on Species' Range Shifts	339
Modeling Species Distributions in Response to Climate Change	340
Range Shifts in Fragmented Landscapes	343
Landscape Effects on Invasive Spread	344
Landscape Ecology of Invasive Spread	344
Spatial Models of Invasive Spread	349
Landscape Connectivity and the Potential for Invasive Spread	353
Source–Sink Metapopulation Dynamics and Invasive Spread	355
Species Distribution Models of Invasive Spread	356
Landscape Epidemiology	357
Landscape Ecology of Disease Spread	358
Spatial Models of Disease Spread	362
Metapopulation Models of Disease Spread	364
Landscape Connectivity and the Potential for Disease Spread	366
Disease Risk Mapping	370
Evolutionary Landscape Epidemiology	371

Future Directions	373
Chapter Summary Points	374
Discussion Questions	375

Chapter 9 Landscape Genetics: Landscape Effects on Gene Flow and Population Genetic Structure 377

What is Landscape Genetics?	378
A Primer to Population Genetics	380
Types of Genetic Markers	380
Estimating Genetic Variation and Divergence	383
Measuring Gene Flow and Population Connectivity	390
From Population Genetics to Landscape Genetics	393
Bayesian Genetic Clustering	393
Multivariate Ordination Techniques	396
Landscape Genetics	398
Landscape Correlates of Population Genetic Structure	399
Functional Connectivity	399
Identification of Movement Corridors and Barriers to Gene Flow	404
Habitat Area versus Fragmentation Effects	409
Source–Sink Population Dynamics	411
Current versus Historical Landscape Effects on Population Genetic Structure	413
Evolutionary Landscape Genetics	415
Beyond Strong Selection: Other Mechanisms of Microgeographic Divergence	416
Toward a Landscape-Genomic Approach to the Study of Adaptive Genetic Variation	421
Adaptive Responses to Future Climate and Landscape Changes	425
Future Directions	429
Chapter Summary Points	431
Discussion Questions	432

Chapter 10 Landscape Effects on Community Structure and Dynamics 434

A Landscape Perspective on the Structure and Dynamics of Communities	435
Measures of Community Structure	436
Species Richness	437
Species Diversity	437
Spatial Partitioning of Diversity	439
Patterns of Species Diversity	446
Latitudinal Gradients in Species Richness	447
Elevational Gradients in Species Richness	451
Species–Area Relationships	455
Island Biogeography and the Habitat Fragmentation Paradigm	467
Effects of Habitat Loss and Fragmentation on Species Diversity	474
Habitat-Amount Hypothesis	475
Interdependence of Habitat Loss and Fragmentation	477
Landscape Effects on Species Interactions	478
Competitive Coexistence	478
Predator–Prey Dynamics	484
Parasite–Host and Host–Parasitoid Dynamics	489
Plant–Pollinator Interactions	495

Metacommunity Structure and Dynamics	502
Future Directions	505
Chapter Summary Points	507
Discussion Questions	511

Chapter 11 Landscape Effects on Ecosystem Structure and Function	512
---	------------

Why is a Landscape Ecology of Ecosystems Needed?	512
Ecosystem Processes in a Landscape Context	514
Topographic and Land-Management Effects on Nutrient Availability and Ecosystem Productivity	516
Effects of Land-Cover Change on Nutrient Dynamics	521
The Metaecosystem: Interacting Ecosystems in a Landscape Context	524
Spatial Subsidies	525
Mobile-Link Species	527
Source–Sink Metaecosystem Dynamics	529
From Ecosystem Function to Landscape Function	530
Landscape Function and ‘Dysfunctional’ Landscapes	530
Assessing and Monitoring Landscape Function	532
Managing for Landscape Multifunctionality and Sustainability	539
Future Directions	541
Chapter Summary Points	542
Discussion Questions	545
Glossary	547
References	573
Index	623