Island Biogeography

Ecology, Evolution, and Conservation

۵

ROBERT J. WHITTAKER School of Geography, University of Oxford

•

OXFORD NEW YORK TOKYO

OXFORD UNIVERSITY PRESS

Contents

1	The natural laboratory paradigm	1
2	Island environments	7
2.1	Types of islands	7
2.2	Modes of origin	8
	2.2.1 Plate boundary islands	12
	2.2.2 Islands in intra-plate locations	12
2.3	Environmental changes over long time-scales	14
	2.3.1 Changes in relative sea level-reefs, atolls, and guyots	14
	2.3.2 Eustatic changes in sea level	17
	2.3.3 Climate change on islands	19
	2.3.4 Case study of an island at sea: the environmental history of	
	Jamaica over the past 50 million years	20
2.4	Physical environment of islands	21
	2.4.1 Topographic characteristics	21
	2.4.2 Climatic characteristics	23
	2.4.3 Water resources	25
	2.4.4 Tracks in the ocean	26
2.5	Natural disturbance on islands	26
	2.5.1 Magnitude and frequency	29
	2.5.2 Continued volcanism	31
2.6	Summary	31
3	Biodiversity hot-spots	33
3.1	Introduction: the global significance of island biodiversity	33
3.2	The split between continental and oceanic islands revisited	· 33
3.3	Species poverty	34
3.4	Disharmony, filters, and regional biogeography	35
3.5	Endemicity	43
	3.5.1 Neo- and palaeo-endemicity	43
	3.5.2 Endemic plants	44
	3.5.3 Endemic animals	46
3.6	Extinct island endemics: a cautionary note	49
3.7	Summary	51
4	Speciation and the island condition	53
4.1	Introduction: first know your species	53
4.2	The species concept and its place in phylogeny	54

4.3	The geographical contexts of speciation events	56
	4.3.1 Distributional context	56
	4.3.2 Locational context—island or mainland change?	57
4.4	Mechanisms of speciation	59
	4.4.1 Allopatric or geographical speciation	59
	4.4.2 Competitive speciation	60
	4.4.3 Polyploidy	61
4.5	One more framework: tree form or phylogeny	62 63
4.6	Summary	05
5	Arrival and change	64
5.1	Founder effects, genetic drift, and bottlenecks	64
5.2	Sex on islands	67
5.3	Niche shifts	69
	5.3.1 The loss of dispersability	70
	5.3.2 Gigantism and nanism	72
	5.3.3 Character displacement	77
	5.3.4 Ecological release	78
	5.3.5 Other niche shifts and syndromes	79
5.4	Summary	82
6	Emergent models of island evolution	83
6.1	Speciation with little or no radiation: anagenesis	83
6.2	The taxon cycle	84
	6.2.1 Melanesian ants	84
	6.2.2 Caribbean birds	86
	6.2.3 Caribbean anoles	90
	6.2.4 Evaluation	92
6.3	Adaptive radiation	93
	6.3.1 Darwin's finches and the Hawaiian honeycreeper-finches	95
	6.3.2 Hawaiian crickets and drosophilids	100
	6.3.3 Adaptive radiation in plants	102
6.4	Observations on the forcing factors of island evolution	105
	6.4.1 Environmental change as a driving force 6.4.2 Rates of speciation vary through time and between taxa	105 106
	6.4.3 Dispersal ability and endemism	100
	6.4.4 Biogeographical hierarchies and island evolutionary models	107
6.5	Summary	111
_		
7	Species numbers games	113
7.1	Introduction	113
7.2	The development of the equilibrium theory of island biogeography	114

.

Contents

viii

	7.2.1 Species-area patterns	115
	7.2.2 Species abundance distributions	116
	7.2.3 The distance effect	118
	7.2.4 Turnover, the core theory (ETIB) and its immediate derivatives	118
7.3	Spatial analyses of island species number	122
	7.3.1 Area and habitat diversity	122
	7.3.2 The habitat-unit model	123
	7.3.3 Competing hypotheses for the species-area effect	123
	7.3.4 Area is not always that important	125
	7.3.5 Species-energy theory	125
	7.3.6 Isolation and distance	127
	7.3.7 Species-area relationships in remote archipelagos	128
	7.3.8 Scale effects	129
7.4	Turnover	131
	7.4.1 Pseudoturnover and cryptoturnover	131
	7.4.2 When is an island in equilibrium?	133
	7.4.3 Propagules and pools	133
	7.4.4 The rescue effect and the effect of island area on immigration rate	133
	7.4.5 The path to equilibrium	134
	7.4.6 What causes extinctions?	136
	7.4.7 Forms of equilibria and non-equilibria	137
7.5	Summary	142
8	Community assembly and dynamics	144
8.1	Introduction	144
8.2	Island assembly theory	144
	8.2.1 Assembly rules	145
	8.2.2 Incidence functions and tramps	145
	8.2.3 The dynamics of island assembly	147
	8.2.4 Checkerboard distributions	148
	8.2.5 Combination and compatibility—assembly rules for cuckoo-doves	149
	8.2.6 Criticisms, 'null' models, and responses	151
	8.2.7 Other studies of assembly structure	155
8.3	Nestedness	161
8.4	Successional island ecology: first elements	165
8.5	Krakatau—succession, dispersal structure, and hierarchies	166
	8.5.1 Background	166
	8.5.2 Community succession	168
	8.5.3 A dispersal-structured model of island recolonization 8.5.4 Colonization and turnover—the dynamics of species lists	170 173
0 4	8.5.5 The balance between stochasticism and determinism	178
8.6	8.5.5 The balance between stochasticism and determinism Disturbed island ecology revisited	178 180
8.6 8.7	8.5.5 The balance between stochasticism and determinism Disturbed island ecology revisited A general critique of island ecology theory	178 180 185
	 8.5.5 The balance between stochasticism and determinism Disturbed island ecology revisited A general critique of island ecology theory 8.7.1 Scale and the dynamics of island biotas—Haila's critique 	178 180 185 187
	8.5.5 The balance between stochasticism and determinism Disturbed island ecology revisited A general critique of island ecology theory	178 180 185

·

۵

ix

*

Contents

.

х

-

Contents

9	Island theory and conservation	192
9.1.	Habitats as islands	192
9.2	Minimum viable populations and minimum viable areas	194
	9.2.1 How many individuals are needed?	194
	9.2.2 Minimum viable populations and disturbance	195
	9.2.3 How big an area?	197
	9.2.4 Applications of incidence functions	197
9.3	Metapopulation dynamics	199
	9.3.1 The core-sink model variant	201
	9.3.2 Deterministic explanations of extinctions within metapopulations	203
9.4	Reserve configuration—the 'single large or several small' debate	204
	9.4.1 Dealing with the leftovers	205
	9.4.2 The answer depends, in part, on the type of organism	207
9.5	Physical changes consequent upon fragmentation	207
9.6	Relaxation and turnover—the evidence	209
9.7	Succession in fragmented landscapes	212
9.8	The implications of nestedness	212
9.9	Edge effects	214
9.10	Landscape effects, isolation, and corridors	216
	9.10.1 The benefits of wildlife corridors	216
	9.10.2 The benefits of isolation	218
	9.10.3 Reserve systems in the landscape	220
	9.10.4 Species that don't stay put	221
9.11	Does conservation biology need island theory?	221
	9.11.1 A non-equilibrium world?	221
	9.11.2 Ecological hierarchies and fragmented landscapes	223 225
	9.11.3 Climate change and reserve systems	225
0.10	9.11.4 Concluding remarks	-
9.12	Summary	226
10	The human impact on island ecosystems—	
	the lighthouse-keeper's cat and other stories	228
10.1	Introduction—the scale of loss	228
10.2	The agencies of destruction	230
	10.2.1 Predation by humans	230
	10.2.2 Introduced species	230
	10.2.3 Disease	231
	10.2.4 Habitat degradation and loss	232
10.3	Trends in the causes of decline	233
10.4	A record of passage—patterns of loss across island taxa	235
	10.4.1 Pacific Ocean birds	235
	10.4.2 Indian Ocean birds	239
	10.4.3 Reptiles	240
	10.4.4 Caribbean land mammals	241
	10.4.5 Island snails	242
	10.4.6 Plants in peril	242

	Contents	xi
10.5	How fragile and invasible are island ecosystems?	245
10.6	Contemporary problems and solutions	247
	10.6.1 Conservation measures	247
	10.6.2 Contemporary problems in the Galápagos	250
	10.6.3 Sustainable development on islands: constraints and remedies	251
10.7	Summary	255
Furthe	er reading	257
Refere	References	
Index		279

•

۵

.

.

-