

JUAN J. MORRONE

---

# NEOTROPICAL BIOGEOGRAPHY

Regionalization and Evolution



CRC Press  
Taylor & Francis Group





# Taylor & Francis

Taylor & Francis Group

<http://taylorandfrancis.com>

# Neotropical Biogeography

## Regionalization and Evolution

# CRC Biogeography Series

Series Editor

**Malte C. Ebach**

*University of New South Wales  
School of Biological  
Earth and Environmental Sciences  
New South Wales  
Australia*

Handbook of Australasian Biogeography, *Malte C. Ebach*  
Biogeography and Evolution in New Zealand, *Michael Heads*



# Neotropical Biogeography

## Regionalization and Evolution

Juan J. Morrone

Professor of Biogeography, Systematics  
and Comparative Biology

Museo de Zoología “Alfonso L. Herrera”  
Facultad de Ciencias, UNAM



CRC Press

Taylor & Francis Group

Boca Raton London New York

---

CRC Press is an imprint of the  
Taylor & Francis Group, an **informa** business

**Cover photo caption:** Tropical rainforest at Los Tuxtlas, Veracruz, Mexico. Photograph courtesy of Alberto González.

CRC Press  
Taylor & Francis Group  
6000 Broken Sound Parkway NW, Suite 300  
Boca Raton, FL 33487-2742

© 2017 by Taylor & Francis Group, LLC  
CRC Press is an imprint of Taylor & Francis Group, an Informa business

No claim to original U.S. Government works

Printed on acid-free paper

International Standard Book Number-13: 978-1-138-03248-4 (Hardback)

This book contains information obtained from authentic and highly regarded sources. Reasonable efforts have been made to publish reliable data and information, but the author and publisher cannot assume responsibility for the validity of all materials or the consequences of their use. The authors and publishers have attempted to trace the copyright holders of all material reproduced in this publication and apologize to copyright holders if permission to publish in this form has not been obtained. If any copyright material has not been acknowledged please write and let us know so we may rectify in any future reprint.

Except as permitted under U.S. Copyright Law, no part of this book may be reprinted, reproduced, transmitted, or utilized in any form by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying, microfilming, and recording, or in any information storage or retrieval system, without written permission from the publishers.

For permission to photocopy or use material electronically from this work, please access [www.copyright.com](http://www.copyright.com) (<http://www.copyright.com/>) or contact the Copyright Clearance Center, Inc. (CCC), 222 Rosewood Drive, Danvers, MA 01923, 978-750-8400. CCC is a not-for-profit organization that provides licenses and registration for a variety of users. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

**Trademark Notice:** Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

---

#### Library of Congress Cataloging-in-Publication Data

---

Names: Morrone, Juan J.  
Title: Neotropical biogeography : regionalization and evolution / Juan J. Morrone.  
Description: Boca Raton : CRC Press, 2017. | Includes bibliographical references.  
Identifiers: LCCN 2016045862 | ISBN 9781138032484 (hardback : alk. paper) | ISBN 9781315390666 (ebook)  
Subjects: LCSH: Biogeography--Central America. | Biogeography--South America. | Biogeography--Tropics.  
Classification: LCC QH84.5 .M68 2017 | DDC 577.2/2--dc23  
LC record available at <https://lccn.loc.gov/2016045862>

---

Visit the Taylor & Francis Web site at  
<http://www.taylorandfrancis.com>

and the CRC Press Web site at  
<http://www.crcpress.com>

*I dedicate this book to Chico Mendes (1944–1988),  
guardian angel of the Neotropical forests.*





# Taylor & Francis

Taylor & Francis Group

<http://taylorandfrancis.com>

# Contents

List of Figures .....	xix
Preface.....	xxvii
Author .....	xxix
Chapter 1	
Theoretical Background.....	1
Evolutionary Biogeography.....	1
Steps of Evolutionary Biogeography.....	2
Biogeographic Regionalization .....	7
Nomenclatural Conventions .....	8
Format Used in the Book .....	8
Chapter 2	
Historical Background .....	9
Biogeographic Placement of the Neotropical Region .....	11
Early Regionalization of the Neotropical Region .....	12
Modern Biogeographic Regionalization .....	24
Biogeographic Regionalization in the Twenty-First Century .....	36
Chapter 3	
The Neotropical Region.....	41
Neotropical Region .....	41
Endemic and Characteristic Taxa.....	43
Biotic Relationships.....	44
Regionalization.....	47
Chapter 4	
The Mexican Transition Zone.....	49
Mexican Transition Zone .....	49
Endemic and Characteristic Taxa.....	51
Biotic Relationships.....	54
Regionalization.....	59
Cenocrons.....	59
Sierra Madre Occidental Province.....	61
Definition.....	63
Endemic and Characteristic Taxa.....	63
Vegetation.....	64
Biotic Relationships.....	64
Regionalization.....	64
Cenocrons.....	65

Sierra Madre Oriental Province .....	65
Definition.....	66
Endemic and Characteristic Taxa.....	66
Vegetation.....	67
Biotic Relationships.....	68
Regionalization.....	68
Trans-Mexican Volcanic Belt Province .....	69
Definition.....	70
Endemic and Characteristic Taxa.....	71
Vegetation.....	71
Biotic Relationships.....	71
Regionalization.....	72
Cenocrons.....	73
Sierra Madre del Sur Province.....	74
Definition.....	74
Endemic and Characteristic Taxa.....	75
Vegetation.....	75
Biotic Relationships.....	75
Regionalization.....	76
Chiapas Highlands Province.....	77
Definition.....	77
Endemic and Characteristic Taxa.....	78
Vegetation.....	78
Biotic Relationships.....	78
Regionalization.....	79
 Chapter 5	
The Antillean Subregion.....	81
Antillean Subregion .....	81
Endemic and Characteristic Taxa.....	82
Biotic Relationships.....	83
Regionalization.....	92
Cenocrons.....	92
Bahama Province .....	93
Definition.....	93
Endemic and Characteristic Taxa.....	94
Vegetation.....	94
Biotic Relationships.....	94
Regionalization.....	94
Cuban Province.....	94
Definition.....	95
Endemic and Characteristic Taxa.....	95
Vegetation.....	96
Biotic Relationships.....	96

Regionalization.....	96
Cenocrons.....	98
Cayman Islands Province.....	98
Definition.....	98
Endemic and Characteristic Taxa.....	98
Vegetation.....	98
Biotic Relationships.....	98
Regionalization.....	99
Jamaica Province .....	99
Definition.....	99
Endemic and Characteristic Taxa.....	99
Vegetation.....	99
Biotic Relationships.....	99
Regionalization.....	100
Hispaniola Province .....	100
Definition.....	100
Endemic and Characteristic Taxa.....	100
Vegetation.....	101
Biotic Relationships.....	101
Regionalization.....	102
Puerto Rico Province .....	102
Definition.....	102
Endemic and Characteristic Taxa.....	102
Vegetation.....	102
Biotic Relationships.....	103
Regionalization.....	103
Lesser Antilles Province .....	103
Definition.....	103
Endemic and Characteristic Taxa.....	104
Vegetation.....	104
Biotic Relationships.....	104
 Chapter 6	
The Brazilian Subregion .....	105
Brazilian Subregion.....	106
Endemic and Characteristic Taxa.....	107
Biotic Relationships.....	107
Regionalization.....	109
Boreal Brazilian Dominion.....	109
Definition.....	111
Endemic and Characteristic Taxa.....	111
Biotic Relationships.....	111
Regionalization.....	112

Napo Province.....	112
Definition.....	113
Endemic and Characteristic Taxa.....	113
Vegetation.....	113
Biotic Relationships.....	113
Regionalization.....	114
Imerí Province.....	114
Definition.....	114
Endemic and Characteristic Taxa.....	114
Vegetation.....	115
Biotic Relationships.....	115
Regionalization.....	115
Pantepui Province .....	115
Definition.....	116
Endemic and Characteristic Taxa.....	116
Vegetation.....	118
Biotic Relationships.....	118
Cenocrons.....	119
Guianan Lowlands Province .....	121
Definition.....	121
Endemic and Characteristic Taxa.....	121
Vegetation.....	122
Biotic Relationships.....	122
Roraima Province.....	122
Definition.....	123
Endemic and Characteristic Taxa.....	123
Vegetation.....	123
Biotic Relationships.....	123
Pará Province .....	123
Definition.....	124
Endemic and Characteristic Taxa.....	124
Vegetation.....	125
Biotic Relationships.....	125
South Brazilian Dominion .....	125
Definition.....	126
Endemic and Characteristic Taxa.....	126
Regionalization.....	126
Ucayali Province .....	126
Definition.....	127
Endemic and Characteristic Taxa.....	128
Vegetation.....	128
Biotic Relationships.....	128
Regionalization.....	128

Madeira Province .....	129
Definition.....	129
Endemic and Characteristic Taxa.....	129
Vegetation.....	130
Biotic Relationships.....	130
Rondônia Province .....	130
Definition.....	131
Endemic and Characteristic Taxa.....	131
Vegetation.....	131
Biotic Relationships.....	132
Regionalization.....	132
Yungas Province .....	132
Definition.....	133
Endemic and Characteristic Taxa.....	133
Vegetation.....	134
Biotic Relationships.....	134
Regionalization.....	134
Pacific Dominion .....	135
Definition.....	135
Endemic and Characteristic Taxa.....	135
Biotic Relationships.....	136
Regionalization.....	136
Guatuso–Talamanca Province.....	136
Definition.....	138
Endemic and Characteristic Taxa.....	138
Vegetation.....	138
Biotic Relationships.....	139
Puntarenas–Chiriquí Province.....	139
Definition.....	139
Endemic and Characteristic Taxa.....	140
Vegetation.....	140
Biotic Relationships.....	140
Chocó–Darién Province.....	140
Definition.....	141
Endemic and Characteristic Taxa.....	141
Vegetation.....	142
Biotic Relationships.....	143
Regionalization.....	143
Guajira Province .....	143
Definition.....	143
Endemic and Characteristic Taxa.....	144
Vegetation.....	144
Biotic Relationships.....	144
Regionalization.....	145

Venezuelan Province.....	145
Definition.....	145
Endemic and Characteristic Taxa.....	146
Vegetation.....	146
Biotic Relationships.....	146
Trinidad Province.....	146
Definition.....	147
Endemic and Characteristic Taxa.....	147
Vegetation.....	147
Biotic Relationships.....	147
Magdalena Province.....	147
Definition.....	148
Endemic and Characteristic Taxa.....	148
Vegetation.....	149
Biotic Relationships.....	149
Regionalization.....	149
Sabana Province.....	149
Definition.....	149
Endemic and Characteristic Taxa.....	150
Vegetation.....	150
Biotic Relationships.....	150
Regionalization.....	151
Cauca Province.....	151
Definition.....	151
Endemic and Characteristic Taxa.....	152
Vegetation.....	152
Biotic Relationships.....	152
Galapagos Islands Province.....	152
Definition.....	153
Endemic and Characteristic Taxa.....	154
Vegetation.....	154
Biotic Relationships.....	155
Western Ecuador Province.....	156
Definition.....	156
Endemic and Characteristic Taxa.....	157
Vegetation.....	157
Ecuadorian Province.....	157
Definition.....	158
Endemic and Characteristic Taxa.....	158
Vegetation.....	158
Mesoamerican Dominion.....	158
Definition.....	159
Endemic and Characteristic Taxa.....	162
Biotic Relationships.....	162



Regionalization.....	163
Cenocrons.....	164
Pacific Lowlands Province.....	166
Definition.....	167
Endemic and Characteristic Taxa.....	167
Vegetation.....	167
Biotic Relationships.....	167
Regionalization.....	169
Balsas Basin Province.....	170
Definition.....	171
Endemic and Characteristic Taxa.....	171
Vegetation.....	171
Biotic Relationships.....	171
Regionalization.....	173
Veracruzán Province.....	173
Definition.....	174
Endemic and Characteristic Taxa.....	174
Vegetation.....	174
Biotic Relationships.....	175
Regionalization.....	175
Yucatán Peninsula Province.....	175
Definition.....	176
Endemic and Characteristic Taxa.....	176
Vegetation.....	176
Biotic Relationships.....	178
Regionalization.....	178
Mosquito Province.....	179
Definition.....	179
Endemic and Characteristic Taxa.....	180
Vegetation.....	180
Biotic Relationships.....	180
Regionalization.....	180
 Chapter 7	
The Chacoan Subregion.....	181
Chacoan Subregion.....	181
Endemic and Characteristic Taxa.....	182
Biotic Relationships.....	182
Regionalization.....	182
Southeastern Amazonian Dominion.....	182
Definition.....	183
Endemic and Characteristic Taxa.....	183
Regionalization.....	184
Biotic Relationships.....	184

Xingu–Tapajós Province .....	184
Definition.....	184
Endemic and Characteristic Taxa.....	184
Vegetation.....	185
Biotic Relationships.....	185
Chacoan Dominion .....	185
Definition.....	185
Endemic and Characteristic Taxa.....	185
Biotic Relationships.....	186
Regionalization.....	186
Caatinga Province .....	186
Definition.....	188
Endemic and Characteristic Taxa.....	189
Vegetation.....	189
Biotic Relationships.....	190
Regionalization.....	190
Cerrado Province .....	190
Definition.....	192
Endemic and Characteristic Taxa.....	192
Vegetation.....	192
Biotic Relationships.....	193
Regionalization.....	194
Chaco Province .....	195
Definition.....	196
Endemic and Characteristic Taxa.....	196
Vegetation.....	196
Biotic Relationships.....	197
Regionalization.....	197
Pampean Province.....	199
Definition.....	200
Endemic and Characteristic Taxa.....	200
Vegetation.....	200
Biotic Relationships.....	201
Regionalization.....	201
Paraná Dominion .....	203
Definition.....	203
Endemic or Characteristic Taxa .....	204
Biotic Relationships.....	205
Regionalization.....	205
Atlantic Province.....	205
Definition.....	206
Endemic and Characteristic Taxa.....	206
Vegetation.....	207
Biotic Relationships.....	208
Regionalization.....	208

Paraná Province .....	208
Definition.....	209
Endemic and Characteristic Taxa.....	209
Vegetation.....	209
Biotic Relationships.....	210
Regionalization.....	210
<i>Araucaria</i> Forest Province.....	211
Definition.....	211
Endemic and Characteristic Taxa.....	212
Vegetation.....	212

## Chapter 8

The South American Transition Zone .....	213
South American Transition Zone.....	213
Endemic and Characteristic Taxa.....	214
Biotic Relationships.....	215
Regionalization.....	215
Cenocrons.....	217
Páramo Province.....	217
Definition.....	218
Endemic and Characteristic Taxa.....	218
Vegetation.....	218
Biotic Relationships.....	221
Regionalization.....	221
Cenocrons.....	222
Desert Province.....	222
Definition.....	223
Endemic and Characteristic Taxa.....	223
Vegetation.....	223
Biotic Relationships.....	224
Regionalization.....	224
Cenocrons.....	224
Puna Province.....	225
Definition.....	226
Endemic and Characteristic Taxa.....	226
Vegetation.....	227
Biotic Relationships.....	227
Regionalization.....	227
Atacama Province.....	227
Definition.....	228
Endemic and Characteristic Taxa.....	228
Vegetation.....	228
Biotic Relationships.....	230

Regionalization..... 230  
Cenocrons..... 230  
Cuyan High Andean Province ..... 230  
    Definition..... 231  
    Endemic and Characteristic Taxa..... 231  
    Vegetation..... 231  
    Biotic Relationships..... 232  
Monte Province ..... 232  
    Definition..... 233  
    Endemic and Characteristic Taxa..... 233  
    Vegetation..... 234  
    Biotic Relationships..... 234  
    Regionalization..... 234  
    Cenocrons..... 235  
  
Epilogue ..... 237  
References ..... 239  
Index ..... 277

## List of Figures

<b>Frontispiece</b>	Biogeographic regionalization of the Neotropical region	
<b>Figure 1.1</b>	Flow chart showing the steps of evolutionary biogeography .....	3
<b>Figure 1.2</b>	Steps of parsimony analysis of endemism used to identify generalized tracks. (a) Map with an individual track represented; (b) data matrix; (c) cladogram obtained; and (d) map with two generalized tracks and one node .....	4
<b>Figure 1.3</b>	Steps of parsimony analysis of paralogy-free subtrees used to identify a general area cladogram. (a) Two taxon-area cladograms; (b) four paralogy-free subtrees derived from the area cladograms; (c) data matrix; and (d) general area cladogram obtained .....	6
<b>Figure 2.1</b>	Map of the Neotropical region and its subregions.....	10
<b>Figure 2.2</b>	Map of the world biogeographic regionalization, indicating transition zones.....	12
<b>Figure 2.3</b>	Map of the zoogeographic regionalization of South America .....	14
<b>Figure 2.4</b>	Map of the zoogeographic regionalization of Mexico .....	16
<b>Figure 2.5</b>	Map of the zoogeographic regionalization of Argentina .....	17
<b>Figure 2.6</b>	Map of the zoogeographic regionalization of Central America Mexico according to Ryan (1963) .....	18
<b>Figure 2.7</b>	Map of the zoogeographic regionalization of Mexico .....	19
<b>Figure 2.8</b>	Map showing the boundaries between the Guianan–Brazilian and Andean–Patagonian subregions .....	20
<b>Figure 2.9</b>	Map of the zoogeographic regionalization of South America .....	21
<b>Figure 2.10</b>	Map of the zoogeographic regionalization of South America .....	22
<b>Figure 2.11</b>	Map of the phytogeographic regionalization of Argentina .....	23
<b>Figure 2.12</b>	Map of the biogeographic regionalization of North and Central America .....	24
<b>Figure 2.13</b>	Map of the biogeographic regionalization of South America .....	25
<b>Figure 2.14</b>	Map showing the dispersal centers of Neotropical vertebrates.....	27
<b>Figure 2.15</b>	Map of the regionalization of South America.....	28
<b>Figure 2.16</b>	Map of the provinces of Latin America .....	29
<b>Figure 2.17</b>	Map of the phytogeographic regionalization of Mexico .....	30

<b>Figure 2.18</b>	Map of the regionalization of South America.....	31
<b>Figure 2.19</b>	Map of the phytogeographic regionalization of the Caribbean.....	33
<b>Figure 2.20</b>	Map of the regionalization of Latin America .....	34
<b>Figure 2.21</b>	Map showing the bioregions of Latin America and the Caribbean.....	35
<b>Figure 2.22</b>	Map of the biogeographic regionalization of Mexico .....	37
<b>Figure 2.23</b>	Map of the biogeographic regionalization of Morrone (2014b) .....	38
<b>Figure 3.1</b>	Map with the individual track of the Neotropical genus <i>Rhinacloa</i> (Miridae).....	44
<b>Figure 3.2</b>	Map with the individual track of the Neotropical genus <i>Ptychoderes</i> (Anthribidae) .....	45
<b>Figure 3.3</b>	General area cladogram depicting the relationships of the biogeographic regions of the world.....	45
<b>Figure 3.4</b>	Map of the subregions and transition zones of the Neotropical region.....	46
<b>Figure 4.1</b>	Map showing the main mountains of the Mexican transition zone .....	50
<b>Figure 4.2</b>	Map with the distribution of the species of <i>Elliptoleus</i> in the Mexican transition zone .....	52
<b>Figure 4.3</b>	Map with the distribution of the species of the <i>Platynus</i> <i>degallieri</i> species group in the Mexican transition zone .....	53
<b>Figure 4.4</b>	Maps with generalized tracks in the Mexican transition zone.....	56
<b>Figure 4.5</b>	Map with nodes identified in the Mexican transition zone .....	57
<b>Figure 4.6</b>	General area cladograms evaluated by Míguez-Gutiérrez et al. (2013). (a) Marshall and Liebherr's (2000) areas, assumption 0; (b) Marshall and Liebherr's (2000) areas, assumption 1; (c) Flores-Villela and Goyenechea's (2001) areas, assumption 0; (d) Flores-Villela and Goyenechea's (2001) areas, assumption 1; (e) Morrone's (2006) areas, assumption 0; (f) Morrone's (2006) areas, assumption 1 .....	58
<b>Figure 4.7</b>	Map of the provinces of the Mexican transition zone .....	59
<b>Figure 4.8</b>	Diagrammatic representation of the development of the Mexican transition zone .....	62
<b>Figure 4.9</b>	Map with the individual track of <i>Pinus engelmanni</i> (Pinaceae) in the Sierra Madre Occidental province .....	63

<b>Figure 4.10</b>	Map of the subprovinces of the Sierra Madre Oriental physiographic province.....	67
<b>Figure 4.11</b>	Map with the individual track of <i>Pterourus palamedes leontis</i> (Papilionidae) in the Sierra Madre Oriental province.....	68
<b>Figure 4.12</b>	Map with the individual track of <i>Onthophagus hippopotamus</i> (Scarabaeidae) in the Trans–Mexican Volcanic Belt province.....	71
<b>Figure 4.13</b>	Map of the districts of the Trans–Mexican Volcanic Belt province.....	73
<b>Figure 4.14</b>	Map with the individual track of <i>Bursera aloexylon</i> (Burseraceae) in the Sierra Madre del Sur province.....	75
<b>Figure 4.15</b>	Map with the individual track of <i>Sceloporus malachitichus</i> (Phrynosomatidae) in the Chiapas Highlands province.....	78
<b>Figure 5.1</b>	Map with the distribution of the species of <i>Cyclura</i> (Iguanidae) in the Antilles, with their phylogenetic relationships indicated.....	83
<b>Figure 5.2</b>	Dispersal–vicariance model for the Caribbean basin.....	84
<b>Figure 5.3</b>	Map with the general area cladogram for freshwater fishes of the Greater Antilles.....	85
<b>Figure 5.4</b>	General area cladogram for several taxa of the Greater Antilles.....	86
<b>Figure 5.5</b>	Map with the main geographic and tectonic features of the Caribbean basin.....	87
<b>Figure 5.6</b>	Map of the regionalization of the Caribbean basin islands and continental portions, based on a parsimony analysis of endemicity of bird distributions.....	89
<b>Figure 5.7</b>	Consensus of the general area cladograms.....	90
<b>Figure 5.8</b>	General area cladogram depicting the relationships of the biogeographic subregions and dominions of the Neotropical region.....	91
<b>Figure 5.9</b>	Map of the provinces of the Antillean subregion.....	92
<b>Figure 5.10</b>	Map with the individual track of <i>Polycentropus nigriceps</i> (Polycentropidae) in the Cuban province.....	95
<b>Figure 5.11</b>	Map of the biogeographic districts of the Cuban province.....	97
<b>Figure 5.12</b>	Map with the individual track of <i>Ardistomis hispaniolensis</i> (Carabidae) in the Hispaniola province.....	101
<b>Figure 6.1</b>	Map with the individual track of <i>Calyptrion</i> (Violaceae) in the Brazilian subregion.....	107



- Figure 6.2** Dispersal events of the *Crotalus durissus* complex (Viperidae), estimated by the phylogeographic analysis of Wüster et al. (2005)... 108
- Figure 6.3** Map of the dominions and provinces of the Brazilian subregion .... 110
- Figure 6.4** Aspect of a typical tepui. (a) Lowland forest; (b) talus slope; (c) escarpment; (d) talus slope; (e) escarpment; and (f) summit..... 117
- Figure 6.5** Map with the individual track of *Naupactus viloriai* (Curculionidae) in the Pantepui province ..... 118
- Figure 6.6** Schematic representation of Rull's (2005) model explaining the diversification in the Pantepui. (a) Glacial period; (b) interglacial period. HL: highlands; LW: lowlands; SL: slopes. Events represented in cross sections (top) and their corresponding aerial views (bottom). Straight dotted lines indicate the 1,100 meters altitudinal limit, above which the tepui summits have been isolated from lowlands, even during glacial phases. Solid arrows indicate the sense of biotic migration in each case..... 120
- Figure 6.7** Map with the individual track of *Sicoderus nodieri* (Curculionidae) in the Guianan Lowlands province ..... 122
- Figure 6.8** Map with the individual track of *Caprimulgus longirostris roraimae* (Caprimulgidae) in the Roraima province..... 124
- Figure 6.9** Map with the individual track of *Geotrigona aequinoctialis* (Apidae) in the Pará province..... 125
- Figure 6.10** Map with the individual track of *Cyphocharax spiluropsis* (Curimatidae) in the South Brazilian dominion ..... 127
- Figure 6.11** Map with the individual track of *Proechimys brevicauda* (Echimyidae) in the Ucayali province ..... 128
- Figure 6.12** Map with the individual track of *Conopophaga melanogaster* (Conopophagidae) in the Madeira province ..... 130
- Figure 6.13** Map with the individual track of *Steindachnerina fasciata* (Curimatidae) in the Rondônia province ..... 132
- Figure 6.14** Maps with individual tracks in the Pacific dominion. (a) *Cecropia angustifolia* (Cecropiaceae); (b) *Transandinomys talamancae* (Cricetidae) ..... 137
- Figure 6.15** Map with the individual track of *Dendropsophus phlebodes* (Hylidae) in the Guatuso–Talamanca province ..... 138
- Figure 6.16** Map with the individual track of *Tikuna atramentum* (Leptophebiidae) in the Puntarenas–Chiriquí province..... 140

<b>Figure 6.17</b>	Maps with individual tracks in the Chocó–Darién province. (a) <i>Aristolochia trianae</i> (Aristolochiaceae); (b) <i>Androdon aequatorialis</i> (Trochilidae).....	142
<b>Figure 6.18</b>	Map with the individual track of <i>Micrurus dissolculus nigristrotris</i> (Elapidae) in the Guajira province .....	144
<b>Figure 6.19</b>	Map with the individual track of <i>Clivina oblita</i> (Carabidae) in the Venezuelan province .....	146
<b>Figure 6.20</b>	Map with the individual track of <i>Proechimys magdalenae</i> (Echymidae) in the Magdalena province .....	148
<b>Figure 6.21</b>	Map with the individual track of <i>Forsteria venezuelensis</i> (Trichodactylidae) in the Sabana province.....	150
<b>Figure 6.22</b>	Map with the individual track of <i>Cecropia megastachya</i> (Cecropiaceae) in the Cauca province.....	152
<b>Figure 6.23</b>	Map of the Galapagos Islands .....	153
<b>Figure 6.24</b>	Vegetation zones in the Galapagos Islands .....	155
<b>Figure 6.25</b>	Map with the individual track of <i>Galapaganus</i> (Curculionidae) in the Galapagos Islands, Ecuador, and Peru.....	156
<b>Figure 6.26</b>	Map with the individual track of <i>Proechimys decumanus</i> (Echimyidae) in the Western Ecuador province .....	157
<b>Figure 6.27</b>	Map with the individual track of <i>Fuchsia ayavacensis</i> (Onagraceae) in the Ecuadorian province.....	158
<b>Figure 6.28</b>	Map with the tectonic blocks recognized in Mesoamerica.....	161
<b>Figure 6.29</b>	Map with the individual track of <i>Ptychoderes bivittatus</i> (Anthribidae) in the Mesoamerican dominion.....	162
<b>Figure 6.30</b>	Map indicating the number of bird species associated to seasonally dry forests of Mesoamerica.....	163
<b>Figure 6.31</b>	Maps with individual tracks in the Pacific Lowlands province. (a) <i>Bursera excelsa</i> (Burseraceae); (b) <i>Cyclocephala capitata</i> (Scarabaeidae) .....	168
<b>Figure 6.32</b>	Vegetation of the Pacific Lowlands province. (a) <i>Brosimum alicastrum</i> ; (b) <i>Celtis monoica</i> ; (c) <i>Chamaedorea</i> sp.; (d) <i>Enterolobium cyclocarpum</i> ; (e) <i>Orbignya cohune</i> ; (f) <i>Canna indica</i> ; (g) <i>Tectaria heracleifolia</i> ; (h) <i>Tradescantia zebrina</i> ; and (i) <i>Bursera simaruba</i> .....	169
<b>Figure 6.33</b>	Maps with individual tracks in the Balsas Basin province. (a) <i>Montanoa liebmanni</i> (Asteraceae); (b) <i>Cotinis pueblensis</i> (Scarabaeidae) .....	172

- Figure 6.34** Vegetation of the Balsas Basin province. (a) *Bursera morelensis*; (b) *Neobuxbaumia* sp.; (c) *Euphorbia* sp.; (d) *Stenocereus weberi*; (e) *Bursera longipes*; (f) *Lysiloma microphylla*; (g) *Ceiba parvifolia*; (h) *Pachycereus* sp.; (i) *Bursera fagaroides*; and (j) *Bursera copalifera* ..... 172
- Figure 6.35** Map with the individual track of *Troilides torquatus tolus* (Papilionidae) in the Veracruz province..... 174
- Figure 6.36** Maps with individual tracks in the Yucatán Peninsula province. (a) *Caesalpinia gaumeri* (Fabaceae); (b) *Priamides rogeri* (Papilionidae) ..... 177
- Figure 6.37** Vegetation of the Yucatán Peninsula province. (a) *Bursera simaruba*; (b) *Zexmania frutescens*; (c) *Lysiloma bahamensis*; (d) *Piscidia piscipula*; (e) *Cydista heterophylla*; (f) *Lonchocarpus rugosus*; (g) *Bixa orellana*; (h) *Pileus mexicanus*; and (i) *Cedrela odorata* ..... 177
- Figure 6.38** Maps with biogeographic zones recognized by Espadas Manrique et al. (2003) in the Yucatán Peninsula province. (a) Yucatán Dry; (b) Yucatán; (c) El Petén; and (d) Belize ..... 178
- Figure 6.39** Map with the individual track of *Lithachne humilis* (Poaceae) in the Mosquito province ..... 180
- Figure 7.1** Map of the dominions and provinces of the Chacoan subregion ..... 183
- Figure 7.2** Maps with individual tracks in the Chacoan dominion. (a) *Enterolobium contortisiliquum* (Fabaceae); (b) *Astronium urundeuva* (Anacardiaceae)..... 187
- Figure 7.3** Maps showing the superposition of distributional areas of Chacoan bird species. (a) Pampean province; (b) Chaco province; (c) Cerrado province; and (d) Caatinga province..... 188
- Figure 7.4** Map with the individual track of *Stygnus polyacanthus* (Stygnidae) in the Caatinga province ..... 189
- Figure 7.5** Map of the districts of the Caatinga province ..... 191
- Figure 7.6** Maps with individual tracks in the Cerrado province. (a) *Stygnus multispinosus* (Stygnidae); (b) *Acanthoscurria* aff. *gomesiana* (Theraphosidae)..... 193
- Figure 7.7** Map of the districts of the Cerrado province..... 194
- Figure 7.8** Maps with individual tracks in the Chaco province. (a) *Tytius confluens* (Buthidae); (b) *Furnarius cristatus* (Furnariidae) ..... 197

<b>Figure 7.9</b>	Vegetation types in the Chaco province. (a) Xeric forest or <i>quebrachal</i> ; (b) savanna or <i>espartillar</i> ; (c) gallery forest; and (d) vegetation sequence in a humid area.....	198
<b>Figure 7.10</b>	Map of the districts of the Chaco province.....	199
<b>Figure 7.11</b>	Map with the individual track of <i>Criscia</i> (Asteraceae) in the Pampean province .....	201
<b>Figure 7.12</b>	Sequence of biotic impoverishment from the Chaco to the Espinal, Prepuna, Monte, and Pampean provinces .....	202
<b>Figure 7.13</b>	Map with the individual track of <i>Homalocerus</i> (Belidae) in the Paraná dominion.....	204
<b>Figure 7.14</b>	Map with the individual track of <i>Leucopternis lacernulata</i> (Accipitridae) in the Atlantic province .....	207
<b>Figure 7.15</b>	Maps with individual tracks in the Paraná province. (a) <i>Fuchsia regia</i> subsp. <i>regia</i> (Onagraceae); (b) <i>Cyphocharax modestus</i> (Curimatidae).....	210
<b>Figure 7.16</b>	Map with the individual track of <i>Cyphocharax nagelii</i> (Curimatidae) in the <i>Araucaria</i> forest province .....	211
<b>Figure 8.1</b>	General area cladogram obtained by Urtubey et al. (2010). Asterisks indicate the provinces of the South American transition zone .....	215
<b>Figure 8.2</b>	Map of the provinces of the South American transition zone .....	216
<b>Figure 8.3</b>	Maps with individual tracks in the Páramo province. (a) Strengerianini (Pseudothelphusidae); (b) <i>Gigantodax cervicornis</i> (Simuliidae).....	219
<b>Figure 8.4</b>	Páramo vegetation. (a) Schematic representation of the vegetational zonation; (b) detail of the grass páramo. (i) <i>Chusquea tessellata</i> ; (ii) <i>Diplostephium schultzii</i> ; (iii) <i>Blechnum loxense</i> ; (iv) <i>Espeletia hartwegiana</i> ; (v) <i>Neurolepis cf. aperta</i> ; and (vi) <i>Puya</i> sp.....	220
<b>Figure 8.5</b>	Map with the individual track of <i>Conepatus rex inca</i> (Mephitidae) in the Desert province .....	224
<b>Figure 8.6</b>	Map with the individual track of <i>Epilobium pedicelare</i> (Onagraceae) in the Puna province .....	226
<b>Figure 8.7</b>	Map with the individual track of <i>Listroderes robustior</i> (Curculionidae) in the Atacama province .....	229

- Figure 8.8** Vegetation in the scrub desert of the Atacama province.  
 (a) Scrub; (b) xeric forest with *Acacia caven*; and (c) ravine  
 forest with *Salix humboldtiana* ..... 229
- Figure 8.9** Maps with individual tracks in the Cuyan High Andean  
 province. (a) *Azorella cryptantha* (Apiaceae); (b) *Cyanoliseus*  
*patagonus andinus* (Psittacidae) ..... 231
- Figure 8.10** Maps with individual tracks in the Monte province.  
 (a) *Enoplopactus lizeri* (Curculionidae); (b) *Bothrops*  
*ammodytoides* (Viperidae) ..... 233

## Preface

The Neotropics comprise the tropical areas of the Americas, from Mexico to Argentina. Hundreds of biogeographic studies of plant and animal taxa from this region have been published for more than 150 years, producing a basic knowledge that is synthesized into regionalization schemes. In this book, I address two central questions of evolutionary biogeography: which areas are recognized within the Neotropical region and how did their biotas evolve? In the last few decades, molecular phylogenetics and parametric model-based biogeography have allowed the postulation of complex biogeographic scenarios for particular taxa, and the search for biotic patterns has been somewhat neglected. However, I feel that biogeographic regionalizations based on the distributional patterns of plant and animal taxa are still relevant in the twenty-first century because they constitute the background knowledge of systematic, ecological, evolutionary, and other kinds of studies.

The biogeographic regionalization of the Neotropical region presented herein consists of three subregions, two transition zones, seven dominions, and 53 provinces. For each unit, I provide the valid name according to the International Code of Area Nomenclature (ICAN) followed by a list of citations and synonyms, a brief characterization, and some endemic and characteristic taxa. In order to deal with biotic evolution, I refer to the identification of biotas through areas of endemism and generalized tracks, their relationships based on track and cladistic biogeographic analyses, and, when possible, the cenocrons or biotic subsets that have been identified within them. This attempt of synthesis is based on a vast bibliography that I have compiled for more than two decades. I feel grateful to many authors who have provided insights on the regionalization and evolution of the Neotropical region. Particularly inspirational for my work were Jorge Artigas, Ángel L. Cabrera, Joel Cracraft, León Croizat, Philip Darlington, Gonzalo Halffter, Michael Heads, René Jeannel, Guillermo Kuschel, Emilio Maury, Ernst Mayr, Paul Müller, Eduardo Rapoport, Osvaldo Reig, Raúl Ringuelet, Donn E. Rosen, Jerzy Rzedowski, Jay Savage, George G. Simpson, Arne Takhtajan, Alfred R. Wallace, and Abraham Willink.

I thank Lone Aagesen, Tania Escalante, Cecilia Ezcurra, Livia León-Paniagua, Isolda Luna, Silvio Nihei, Sergio Roig-Juñent, and Luis Sánchez-González for providing useful comments on a preliminary version of the manuscript. Many friends and colleagues provided useful discussions, helped with the bibliography, provided data, and shared their ideas with me: Lone Aagesen, Dalton de Sousa Amorim, Marcelo Arana, Fabrizio Cecca, Jorge Crisci, Guadalupe del Río, Malte C. Ebach, Amparo Echeverry, Tania Escalante, Celene Espadas, David Espinosa, Cecilia Ezcurra, Ignacio Ferro, Ismael Ferrusquía-Villafranca, Gustavo Flores, Oscar Flores-Villela, Jorge Fontenla, Irene Goyenechea-Mayer, Gonzalo Halffter, Michael

Heads, Liliana Katinas, Analía Lanteri, Livia León-Paniagua, Jonathan Liria, Jorge Llorente-Bousquets, Peter Löwenberg-Neto, Isolda Luna-Vega, Juan Márquez-Luna, Andrés Moreira-Muñoz, Adolfo Navarro-Sigüenza, Paula Posadas, Alejandra Ribichich, Gerardo Rodríguez-Tapia, Sergio Roig-Juñent, Adriana Ruggiero, Luis Sánchez-González, Claudia Szumik, Estrella Urtubey, and Mario Zunino.

**Juan J. Morrone**

*Mexico City*



## Author

**Juan J. Morrone** is full professor of biogeography, systematics, and comparative biology at the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Mexico. He works on phylogenetic systematics of weevils (Coleoptera: Curculionidae) and evolutionary biogeography and regionalization of the Neotropical and Andean regions.

He joined the Museo de Zoología “Alfonso L. Herrera” of the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Mexico, in 1998, after working for some years at the Museo de La Plata, Universidad Nacional de La Plata (UNLP), Argentina, where he obtained his PhD degree. He is a Member of the Academia Mexicana de Ciencias, Fellow of the Willi Hennig Society, and Research Associate of the American Museum of Natural History and the Buffalo Museum of Science. He has authored 270 scientific papers and has authored, or edited, 29 books on evolutionary biogeography, phylogenetic systematics, biogeographic regionalization, biodiversity conservation, and evolution.



# Taylor & Francis

Taylor & Francis Group

<http://taylorandfrancis.com>

# Theoretical Background

Evolutionary biogeography integrates distributional, phylogenetic, molecular, and paleontological data in order to discover biogeographic patterns exhibited by plant and animal taxa, and assess the historical changes that have shaped biotic assembly (Morrone, 2009). Biogeographic regionalizations are hierarchical classifications categorizing geographic areas in terms of their endemic taxa and their relationships. They represent the syntheses of different evolutionary biogeographic analyses and, at the same time, constitute the background knowledge of other studies (e.g., systematic, ecological, or evolutionary).

### EVOLUTIONARY BIOGEOGRAPHY

Evolutionary biogeography is the integrative study of distributional, phylogenetic, molecular, and paleontological data, aimed to discover biogeographic patterns and assess the historical changes that have shaped them (Morrone, 2009). It follows a stepwise approach. First, areas of endemism or generalized tracks are identified and considered as hypotheses about biotic identity based on the distributional congruence exhibited by different plant and animal taxa. Second, cladistic biogeographic analyses test these hypotheses, based on the available phylogenetic evidence on the taxa analyzed. Third, biogeographic regionalization is achieved based on cladistic biogeographic hypotheses. Fourth, the molecular dating of divergences between lineages and fossil data allows the identification of cenocrons, which represent subsets of taxa within a biota, identified by their common origin and evolutionary history. Cenocrons incorporate a temporal dimension that implies a time frame of the dispersal of sets of taxa into the biota. Finally, after the biotas and cenocrons have been identified, one may construct a geobiotic scenario by accounting biological and non-biological data to explain the episodes of vicariance/biologic divergence and dispersal/biologic convergence that have shaped the evolution of the biotas analyzed.

The dispersal–vicariance model followed herein assumes that the relationship between earth history and life is more complex than what is assumed in simpler models, because biotic history is reticulate. It treats vicariance as the default explanation for general biogeographic patterns and dispersal as the process that shapes the