

# Contents

<b>1 A brief introduction to phylogenetics in R</b>	<b>1</b>
1.1 Introduction	1
1.2 Preliminaries	3
1.3 R phylogenetics	5
1.4 <i>ape</i> and the "phylo" object in R	7
1.5 The internal structure of a tree in R	11
1.6 Reading and writing phylogenetic trees	15
1.7 Plotting and manipulating trees	16
1.8 Multiple trees in a single object	24
1.9 Managing trees and comparative data	25
1.10 A simple comparative analysis: Phylogenetic principal components analysis	29
1.11 Practice problems	32
<b>2 Phylogenetically independent contrasts</b>	<b>35</b>
2.1 Introduction	35
2.2 Phylogenetic nonindependence	36
2.3 Phylogenetically independent contrasts	38
2.4 What happens if we ignore the tree?	47
2.5 Practice problems	58
<b>3 Phylogenetic generalized least squares</b>	<b>59</b>
3.1 Introduction	59
3.2 Statistical nonindependence of phylogenetic data	60
3.3 Equivalence of contrasts regression and PGLS	61
3.4 Assumptions of PGLS	67
3.5 Phylogenetic ANOVA and ANCOVA	71
3.6 Practice problems	74



<b>4</b>	<b>Modeling continuous character evolution on a phylogeny</b>	<b>75</b>
4.1	Introduction	75
4.2	The Brownian motion model	75
4.3	Brownian motion on a phylogeny	79
4.4	Properties of Brownian motion	80
4.5	Fitting a Brownian model to data	82
4.6	Phylogenetic signal	90
4.7	Other models of continuous character evolution on phylogenies	98
4.8	Fitting and comparing alternative continuous character models	100
4.9	Practice problems	105
<b>5</b>	<b>Multi-rate, multi-regime, and multivariate models for continuous traits</b>	<b>107</b>
5.1	Multi-rate Brownian evolution	108
5.2	Multi-optimum Ornstein–Uhlenbeck evolution	112
5.3	Multivariate Brownian evolution	122
5.4	Exploring evolutionary heterogeneity	129
5.5	Practice problems	144
<b>6</b>	<b>Modeling discrete character evolution on a phylogeny</b>	<b>145</b>
6.1	Introduction	145
6.2	The Mk model	145
6.3	Fitting the Mk model to data	149
6.4	Comparing alternative discrete character models	161
6.5	Practice problems	165
<b>7</b>	<b>Other models of discrete character evolution</b>	<b>167</b>
7.1	Introduction	167
7.2	Correlated binary traits	167
7.3	Modeling heterogeneity in the evolutionary rate for a discrete trait	177
7.4	Modeling rate variation using the hidden-rates model	185
7.5	A polymorphic trait model	201
7.6	The threshold model for studying discrete and continuous character traits	209
7.7	Practice problems	219
<b>8</b>	<b>Reconstructing ancestral states</b>	<b>221</b>
8.1	Introduction	221
8.2	Ancestral states for continuous characters	222
8.3	Properties of ancestral state estimation for continuous traits	228
8.4	Discrete characters	235
8.5	Joint ancestral state reconstruction	238
8.6	Marginal ancestral state reconstruction	241
8.7	Stochastic character mapping	243
8.8	What about parsimony?	251
8.9	Practice problems	254
<b>9</b>	<b>Analysis of diversification with phylogenies</b>	<b>255</b>
9.1	Introduction	255
9.2	Lineage-through-time plots and the $\gamma$ statistic	256
9.3	Estimating speciation and extinction rates from a reconstructed phylogeny	262
9.4	The effect of incomplete sampling on diversification rates	269
9.5	Likelihood surface of a birth-death model	272



9.6	Analyzing diversification using <i>diversitree</i>	273
9.7	Practice problems	280
<b>10</b>	<b>Time- and density-dependent diversification</b>	<b>281</b>
10.1	Introduction	281
10.2	Time-varying diversification	282
10.3	Fitting time-variable diversification models to data	284
10.4	Diversity-dependent diversification	300
10.5	Testing for variation in diversification rates among clades	305
10.6	Practice problems	308
<b>11</b>	<b>Character-dependent diversification</b>	<b>309</b>
11.1	Introduction	309
11.2	Binary-state speciation and extinction (BiSSE) model	310
11.3	Multi-state speciation and extinction (MuSSE) model	321
11.4	Hidden-state speciation and extinction (HiSSE) model	328
11.5	Quantitative-trait speciation and extinction (QuaSSE) model	344
11.6	Practice problems	354
<b>12</b>	<b>Biogeography and phylogenetic community ecology</b>	<b>357</b>
12.1	Introduction	357
12.2	Ancestral area reconstruction	358
12.3	Phylogenetic community ecology	370
12.4	Practice problems	382
<b>13</b>	<b>Plotting phylogenies and comparative data</b>	<b>383</b>
13.1	Introduction	383
13.2	Phylogenies in the R plotting environment	384
13.3	Plotting phylogenies without actually plotting them	399
13.4	Algorithms for drawing trees	401
13.5	Practice problems	412
	References	413
	Index	421
	Index of R functions	425