

# Contents

## Section I Introduction

<b>1</b>	<b>The Various Effects of Insects on Ecosystem Functioning . . . . .</b>	<b>3</b>
	W.W. WEISSE and E. SIEMANN	
1.1	Summary . . . . .	3
1.2	Introduction . . . . .	3
1.3	A Brief Overview of Insect Effects on Ecosystem Function . . . . .	8
1.3.1	Insect Effects on Ecosystem Function	
	Via Interactions with Plants . . . . .	8
1.3.1.1	Herbivory . . . . .	8
1.3.1.2	Plant-Insect Mutualisms . . . . .	14
1.3.2	Other Direct and Indirect Effects of Insects on Ecosystem Function . . . . .	14
1.4	The Aim and Structure of this Book . . . . .	15
	References . . . . .	19

## Section II Insects and the Belowground System

<b>2</b>	<b>Insect Herbivores, Nutrient Cycling and Plant Productivity . . . . .</b>	<b>27</b>
	S.E. HARTLEY and T. H. JONES	
2.1	Summary . . . . .	27
2.2	Introduction . . . . .	28
2.3	Decomposition . . . . .	28
2.3.1	The Resources Available . . . . .	28
2.3.2	Effects of Insect Herbivory on Decomposition . . . . .	31

2.3.2.1	Herbivory and Litter Quality . . . . .	31
2.3.2.2	Herbivory, Root Exudation and Root Biomass . . . . .	32
2.4	Nutrient Cycling and Plant Productivity . . . . .	33
2.4.1	Effects on Carbon and Nitrogen Cycling . . . . .	34
2.4.1.1	Methane and Carbon Dioxide . . . . .	34
2.4.1.2	Nitrogen and Phosphorus . . . . .	35
2.4.1.3	Inputs from Aboveground Herbivores . . . . .	36
2.4.1.4	The Importance of Belowground Biota: Evidence from Controlled Environment Studies . . . . .	39
2.4.1.5	Insect Herbivory and Spatial Variation in Nutrient Availability . . . . .	40
2.4.2	Herbivory and Plant Biomass . . . . .	41
2.5	Conclusions . . . . .	45
	References . . . . .	46

3      **Indirect Effects of Invertebrate Herbivory on the Decomposer Subsystem . . . . .** 53  
D.A. WARDLE and R.D. BARDGETT

3.1	Summary . . . . .	53
3.2	Introduction . . . . .	54
3.3	Mechanistic Bases of Invertebrate Herbivore Effects . . . . .	54
3.3.1	Immediate Effects on Resource Quantity . . . . .	56
3.3.2	Longer-Term Effects on Resource Quantity . . . . .	56
3.3.3	Effects of Changed Litter Quality . . . . .	57
3.3.4	Return of Invertebrate Waste Products . . . . .	58
3.3.5	Effects of Changes in Vegetation Composition . . . . .	59
3.3.6	Feedbacks and Aboveground Consequences . . . . .	61
3.4	Significance of Invertebrate Herbivore Outbreaks . . . . .	61
3.5	Multiple Species Herbivore Communities . . . . .	62
3.6	Comparisons of Ecosystems . . . . .	64
3.7	Conclusions . . . . .	65
	References . . . . .	66

4      **Biotic Interactions in the Rhizosphere: Effects on Plant Growth and Herbivore Development . . . . .** 71  
M. BONKOWSKI and S. SCHEU

4.1	Summary . . . . .	71
4.2	The Rhizosphere – Interface of Intense Microbial and Faunal Interactions . . . . .	72

<b>Contents</b>	<b>IX</b>
4.2.1 Plants as Drivers of Rhizosphere Interactions . . . . .	73
4.3 Belowground Interactions and the Herbivore System . . . . .	74
4.3.1 Effects of Mycorrhiza and Rhizobacteria on Aboveground Herbivores . . . . .	76
4.3.2 Interactions with the Micro-Decomposer Food Web . . . . .	77
4.3.2.1 The Bacterial Loop and Herbivore Performance . . . . .	78
4.3.2.2 The Fungal Food Chain and Herbivore Performance . . . . .	79
4.3.2.3 Ecosystem Engineers and Herbivore Performance . . . . .	81
4.4 Top-Down Effects by Subsidizing Generalist Predators . . . . .	83
References . . . . .	85
<b>5 Belowground Herbivores and Ecosystem Processes . . . . .</b>	<b>93</b>
<b>G.J. MASTERS</b>	
5.1 Summary . . . . .	93
5.2 Introduction . . . . .	94
5.3 Experimenting with Belowground Insect Herbivores . . . . .	94
5.4 Belowground Herbivory and Plant Productivity: Allocation and Biomass . . . . .	97
5.5 Implications of Belowground Herbivory for Nutrient Cycling . . . . .	101
5.6 Implications of Belowground Herbivory for Multitrophic Interactions . . . . .	104
5.7 Conclusion . . . . .	109
References . . . . .	109
<b>Section III Plant-Insect Interactions and Ecosystem Processes</b>	
<b>6 Bottom-Up Effects and Feedbacks in Simple and Diverse Experimental Grassland Communities . . . . .</b>	<b>115</b>
<b>J. JOSHI, S.J. OTWAY, J. KORICHEVA, A.B. PFISTERER, J. ALPHEI, B.A. ROY, M. SCHERER-LORENZEN, B. SCHMID, E. SPEHN and A. HECTOR</b>	
6.1 Summary . . . . .	115
6.2 Introduction . . . . .	116
6.3 Effects of Plant Diversity on Herbivorous Insects Feeding Above Ground . . . . .	117

6.3.1	Hypotheses Predicting the Response of Herbivores to Higher Plant Diversity . . . . .	117
6.3.2	Responses of Specialist and Generalist Herbivores in Plant Diversity Experiments . . . . .	119
6.3.3	Concomitant Responses of Natural Enemies of Herbivores .	123
6.3.4	Insect Herbivores as Drivers of Ecosystem Processes . . . .	124
6.4	Effects of Plant Diversity on Pathogens . . . . .	125
6.5	Belowground Food Web . . . . .	126
6.5.1	Plant Biomass and Microbial Response . . . . .	126
6.5.2	Soil Animals that Feed on Microbes . . . . .	128
6.6	Conclusions . . . . .	129
	References . . . . .	130
7	<b>The Potential of Phytophagous Insects in Restoring Invaded Ecosystems: Examples from Biological Weed Control . . . . .</b>	135
	H. ZWÖLFER and H. ZIMMERMANN	
7.1	Summary . . . . .	135
7.2	Introduction . . . . .	136
7.3	Success Rates and Successes in Biological Weed Control . .	137
7.4	Weed Characteristics and Positive Traits of Insects in Biological Control . . . . .	138
7.4.1	Weed Species . . . . .	139
7.4.2	Insect Species . . . . .	139
7.5	Three Examples of Successful Weed Control . . . . .	140
7.5.1	<i>Rhinocyllus conicus</i> on <i>Carduus nutans</i> . . . . .	140
7.5.2	Interactions Between Three Weevil Species in the Biocontrol of the Invader <i>Sesbania punicea</i> in South Africa . . . . .	143
7.5.2.1	The Seed-Destroying Agents: <i>Trichapion lativentre</i> and <i>Rhyssomatus marginatus</i> . . . . .	144
7.5.2.2	The Stem-Borer: <i>Neodiplogrammus quadriguttatus</i> . . . .	145
7.5.3	Aquatic Weeds . . . . .	146
7.6	Discussion and Conclusions . . . . .	147
	References . . . . .	150
8	<b>Plant-Insect-Pathogen Interactions on Local and Regional Scales . . . . .</b>	155
	A. KRUESS, S. EBER, S. KLUTH and T. TSCHARNTKE	
8.1	Summary . . . . .	155
8.2	Introduction . . . . .	156

8.3	Biological Weed Control, Interactions and Ecosystem Processes . . . . .	157
8.3.1	Classical Biological Control . . . . .	157
8.3.2	Plant–Pathogen–Herbivore Interactions . . . . .	158
8.4	Creeping Thistle, Insects, Pathogens and Processes . . . . .	160
8.4.1	The Creeping Thistle ( <i>Cirsium arvense</i> ) . . . . .	160
8.4.2	Interactions Between Pathogens and Insect Vectors on a Local Scale . . . . .	161
8.4.3	Regional Dynamics of <i>Cirsium arvense</i> and an Associated Herbivore . . . . .	163
8.4.4	The Influence of Landscape Context at Different Spatial Scales . . . . .	165
8.5	Conclusions and Future Outlook . . . . .	168
	References . . . . .	169
<b>9</b>	<b>Food Web Interactions and Ecosystem Processes . . . . .</b>	<b>175</b>
	A. JANSSEN and M.W. SABELIS	
9.1	Summary . . . . .	175
9.2	Introduction . . . . .	175
9.3	Interactions Among Entire Trophic Levels . . . . .	178
9.4	Effects of Diversity Within Trophic Levels . . . . .	179
9.4.1	Apparent Competition . . . . .	180
9.4.2	Omnivory . . . . .	180
9.4.3	Intraguild Predation . . . . .	181
9.4.4	Plant-Mediated Indirect Interactions Between Herbivores .	181
9.4.5	Indirect Plant Defences . . . . .	182
9.4.6	Interactions Among Plants . . . . .	183
9.4.7	Behavioural Effects . . . . .	184
9.5	Conclusions and Perspectives . . . . .	184
	References . . . . .	186
<b>10</b>	<b>A General Rule for Predicting When Insects Will Have Strong Top-Down Effects on Plant Communities: On the Relationship Between Insect Outbreaks and Host Concentration . . . . .</b>	<b>193</b>
	W.P. CARSON, J. PATRICK CRONIN and Z.T. LONG	
10.1	Summary . . . . .	193
10.2	Introduction . . . . .	193
10.3	The Significance of Insect Outbreaks . . . . .	194

10.3.1	Insect Outbreaks Are Common in Numerous Community-Types Worldwide . . . . .	195
10.3.2	Insect Outbreaks Are More Common and More Devastating per Host in Large, Dense and Continuous Host Stands . . . . .	199
10.3.3	Native Outbreaking Insects Function as Keystone Species by Reducing the Abundance of the Dominant Species and Increasing Diversity . . . . .	200
10.3.4	Insect Outbreaks Are Common Relative to Host Life Span Yet May Often Go Unnoticed . . . . .	201
10.3.5	Chrysomelid Beetles and Lepidoptera Seem to be Responsible for the Majority of Outbreaks . . . . .	201
10.4	The Host Concentration Model May Predict Insect Impact on Plant Communities at Multiple Spatial Scales Better Than Resource Supply Theory . . . . .	202
10.4.1	Resource Supply Theory . . . . .	202
10.4.2	The Host Concentration Model (HCM) . . . . .	203
10.4.3	Distinguishing Between the Two Models . . . . .	204
10.5	Relationship to Other Related Processes Proposed to Promote Diversity . . . . .	204
10.5.1	Does Pathogen Impact Increase with Host Concentration? .	205
	References . . . . .	205
11	<b>The Ecology Driving Nutrient Fluxes in Forests . . . . .</b>	213
	B. STADLER, E. MÜHLENBERG and B. MICHALZIK	
11.1	Summary . . . . .	213
11.2	Introduction . . . . .	214
11.3	Life Histories of Canopy Insects . . . . .	215
11.3.1	Aphids . . . . .	215
11.3.2	Scale Insects . . . . .	215
11.3.3	Lepidopterous Larvae . . . . .	216
11.4	Population Ecological Background of Nutrient Fluxes . . . . .	217
11.4.1	Sites and Experimental Setup . . . . .	219
11.4.2	Results . . . . .	220
11.5	Trophic Effects and Organic Pathways . . . . .	224
11.6	Herbivore-Mediated Changes in Quality and Quantity of Nutrient Fluxes . . . . .	226
11.7	Synthesis and Conclusions . . . . .	230
11.7.1	Understanding the Temporal Dynamics of Energy and Nutrient Fluxes . . . . .	230
11.7.2	Understanding the Spatial Variability in Fluxes . . . . .	231

Contents	XIII
11.7.3    Understanding the Mechanics that Regulate Fluxes . . . . .	232
11.7.4    Generating Testable Hypotheses . . . . .	233
References . . . . .	235

## Section IV Methods: Reducing, Enhancing and Simulating Insect Herbivory

12	Simulating Herbivory: Problems and Possibilities . . . . .	243
	J. HJÄLTÉN	
12.1	Summary . . . . .	243
12.2	Introduction to the Problem . . . . .	244
12.3	Advantages of Simulated Herbivory . . . . .	245
12.4	Disadvantages of Simulated Herbivory . . . . .	247
12.4.1	Simple Biotic Interactions . . . . .	247
12.4.2	Complex Biotic Interactions . . . . .	249
12.4.3	Basic Ecosystem Processes . . . . .	250
12.5	Conclusions and Suggestions for the Future . . . . .	251
	References . . . . .	253
13	The Use and Usefulness of Artificial Herbivory in Plant-Herbivore Studies . . . . .	257
	K. LEHTILÄ and E. BOALT	
13.1	Summary . . . . .	257
13.2	Introduction . . . . .	258
13.3	Material and Methods . . . . .	258
13.4	Commonness of Differences Between Natural and Artificial Herbivory . . . . .	260
13.5	Strength of the Effect of Natural and Artificial Damage . . . . .	266
13.6	Responses of Different Types of Response Traits to Artificial and Natural Damage . . . . .	267
13.7	Simulations of Mammalian and Invertebrate Herbivory . . . . .	269
13.8	Attempts of Exact Simulation . . . . .	270
13.9	Conclusions . . . . .	271
	References . . . . .	273

<b>14</b>	<b>From Mesocosms to the Field: The Role and Value of Cage Experiments in Understanding Top-Down Effects in Ecosystems . . . . .</b>	<b>277</b>
O.J. SCHMITZ		
14.1	Summary . . . . .	277
14.2	Introduction . . . . .	278
14.3	Research Approach . . . . .	281
14.4	<i>In-Ecosystem Investigation Using Enclosure Experiments .</i>	282
14.4.1	Natural History: Knowing the Players in the System . . . . .	282
14.4.2	Enclosure Cages: Design and Biophysical Properties . . . . .	285
14.4.3	Considerations for the Design of Cage Experiments . . . . .	288
14.4.3.1	Artificial Complements of Populations or Communities in Enclosure Cages Are Not Realistic . . . . .	288
14.4.3.2	Experimental Outcome Could Be an Artifact of the Venue .	288
14.4.3.3	Enclosures Unrealistically Constrain Movement of Species .	289
14.4.3.4	Time Scale of Enclosure Experiments Exclude or Distort Important Features of Communities and Ecosystems . . . . .	290
14.4.4	Mechanistic Insights from Enclosure Cage Experiments . .	290
14.4.4	Identifying the Potential for Top-Down Control . . . . .	291
14.4.5	<i>Of-Ecosystem Studies: Testing the Reliability</i> of Mechanistic Insights from Cage Experiments . . . . .	297
14.4.5.1	Direct and Indirect Effects of Top Predators . . . . .	299
14.4.5.2	Top Predator Effects on Plant Diversity and Productivity .	300
	References . . . . .	300
<b>15</b>	<b>Reducing Herbivory Using Insecticides . . . . .</b>	<b>303</b>
E. SIEMANN, W.P. CARSON, W.E. ROGERS and W.W. WEISSE		
15.1	Summary . . . . .	303
15.2	Basic Concepts . . . . .	303
15.3	Using Insecticides to Infer the Role of Herbivores . . . . .	304
15.4	Ghost of Herbivory Past . . . . .	307
15.5	Artifacts of Method May Masquerade as Release from Herbivory . . . . .	308
15.5.1	What Types of Artifacts Are a Concern? . . . . .	308
15.5.2	Overview of Published Studies . . . . .	309
15.5.3	Quantification of Herbivore Damage . . . . .	310
15.5.4	Phytotoxic Effects . . . . .	311
15.5.5	Insecticides May Be Toxic to Several Groups of Insects .	313
15.5.6	Effects of Insecticides on Non-Arthropods . . . . .	314
15.5.7	Effects of Insecticides on Soil Organisms . . . . .	314

<b>Contents</b>	<b>XV</b>
15.5.8 Nutrient Inputs May Facilitate Plant Growth . . . . .	315
15.5.9 Insect-Vectored Diseases . . . . .	317
15.5.10 Community-Level Artifacts . . . . .	318
15.6 Are There Better Types of Insecticides? . . . . .	318
15.7 Conclusions . . . . .	319
<b>Appendix: Results of Surveyed Studies . . . . .</b>	<b>320</b>
<b>References . . . . .</b>	<b>324</b>
<b>16 The Role of Herbivores in Exotic Plant Invasions: Insights Using a Combination of Methods to Enhance or Reduce Herbivory . . . . .</b>	<b>329</b>
W.E. ROGERS and E. SIEMANN	
16.1 Summary . . . . .	329
16.2 Introduction . . . . .	329
16.3 The Role of Herbivores in Exotic Plant Invasions . . . . .	330
16.4 Focal Plant Species . . . . .	331
16.5 Experimental Methods for Assessing Herbivory Effects . . . . .	331
16.5.1 Common Garden/Reciprocal Transplant Studies . . . . .	332
16.5.2 Reducing Herbivory on Target Plants Using Insecticide Sprays . . . . .	336
16.5.3 Reducing Herbivory on Community Assemblages Using Insecticide Sprays . . . . .	337
16.5.4 Factorial Manipulations of Herbivory, Resources and Competition . . . . .	338
16.5.5 Simulating Herbivory Via Mechanical Leaf Damage . . . . .	339
16.5.6 Simulating Herbivory Via Mechanical Root Damage . . . . .	341
16.5.7 Simulating Herbivory Using Herbicide Sprays . . . . .	342
16.5.8 Assessing Herbivore Damage Using Exclosures and Enclosures . . . . .	344
16.6 Implications and Potential Significance . . . . .	347
References . . . . .	349
<b>17 Herbivore-Specific Transcriptional Responses and Their Research Potential for Ecosystem Studies . . . . .</b>	<b>357</b>
C. VOELCKEL and I.T. BALDWIN	
17.1 Summary . . . . .	357
17.2 The Subtle Effects of Insects on Ecosystem Function . . . . .	357
17.3 Transcriptional Regulation of Plant Responses . . . . .	358
17.4 Insect-Induced Transcriptional Changes . . . . .	362

17.5	How a Molecular Understanding of Plant–Insect Interactions Can Help Elucidate Ecosystem Function . . . . .	371
References	. . . . .	375

## Section V Synthesis

18	Testing the Role of Insects in Ecosystem Functioning . . . . .	383
	E. SIEMANN and W.W. WEISSE	
18.1	Summary . . . . .	383
18.2	Introduction . . . . .	384
18.3	Simple Models of Niche Space . . . . .	385
18.3.1	Reduced Vigour Model . . . . .	385
18.3.2	Reduced Range of Tolerance Model . . . . .	387
18.3.3	Specialist Herbivores . . . . .	388
18.4	Effects of Herbivores in Resource Competition Models . . . . .	389
18.4.1	Specialist Herbivores in Resource Competition Models . . . . .	391
18.4.2	Generalist Herbivores in Resource Competition Models . . . . .	395
18.5	Differential Impacts on Plants with Different Traits . . . . .	396
18.6	Conclusions from the Modelling Work . . . . .	396
18.7	Suggestions for Future Studies . . . . .	397
18.7.1	Exploring Below- and Aboveground Interactions in More Detail . . . . .	397
18.7.2	Measuring Herbivory Effects at Nominal Levels as Well as in Outbreak Situations . . . . .	398
18.7.3	Quantifying the Effects of Plant Resource Allocation Under Herbivory for Ecosystem Functioning . . . . .	399
18.7.4	Combining Various Methodologies to Achieve an Understanding of Insect Effects on Ecosystem Function .	399
References	. . . . .	400
<b>Subject Index</b>	. . . . .	403
<b>Taxonomic Index</b>	. . . . .	409