

# Contents

|                                                                    |         |
|--------------------------------------------------------------------|---------|
| <i>List of contributors</i>                                        | page xi |
| <i>Preface</i>                                                     | xiii    |
| <i>Photo credits</i>                                               | xvi     |
| 1 Ecological importance of ferns                                   | 1       |
| <i>Joanne M. Sharpe, Klaus Mehlreter and Lawrence R. Walker</i>    |         |
| 1.1 Introduction                                                   | 1       |
| 1.2 Advances in the study of fern ecology                          | 2       |
| 1.3 Fern ecology topics in this book                               | 5       |
| 1.4 Fern structure, life cycles, evolution and classification      | 7       |
| 1.4.1 Life cycle and alternation of generations                    | 7       |
| 1.4.2 Fern evolution                                               | 16      |
| 1.4.3 Current systematic classification of ferns and<br>lycophytes | 17      |
| 1.5 Summary                                                        | 18      |
| 2 Biogeography of ferns                                            | 22      |
| <i>Michael Kessler</i>                                             |         |
| 2.1 Introduction                                                   | 22      |
| 2.2 Dispersal and vicariance                                       | 23      |
| 2.2.1 Long distance dispersal                                      | 23      |
| 2.2.2 Dispersal to oceanic islands                                 | 24      |
| 2.2.3 Vicariance                                                   | 26      |
| 2.3 Range size: variability and spatial distribution               | 28      |
| 2.3.1 Range size and its correlates                                | 28      |
| 2.3.2 Endemism                                                     | 29      |
| 2.4 Alpha diversity                                                | 32      |
| 2.4.1 Patterns of species richness                                 | 32      |
| 2.4.2 Mountains as hot spots of fern diversity                     | 35      |
| 2.4.3 Mechanisms determining patterns of species richness          | 36      |

|       |                                                     |     |
|-------|-----------------------------------------------------|-----|
| 2.5   | Beta diversity                                      | 44  |
| 2.5.1 | Soil gradients                                      | 44  |
| 2.5.2 | Elevational gradients                               | 44  |
| 2.6   | Questions for the future                            | 46  |
| 3     | Ecological insights from fern population dynamics   | 61  |
|       | <i>Joanne M. Sharpe and Klaus Mehlreter</i>         |     |
| 3.1   | Introduction                                        | 61  |
| 3.2   | Life cycle of ferns and lycophytes                  | 63  |
| 3.3   | Fern spore banks                                    | 63  |
| 3.4   | Gametophyte growth and population structure         | 67  |
| 3.5   | Sporophyte morphology and reproduction              | 71  |
| 3.5.1 | Sporophyte rhizomes                                 | 71  |
| 3.5.2 | Juvenile leaves                                     | 76  |
| 3.5.3 | Adult leaves                                        | 77  |
| 3.5.4 | Vegetative reproduction                             | 78  |
| 3.6   | Classification of fern life history stages          | 80  |
| 3.6.1 | Age determination                                   | 80  |
| 3.6.2 | Sporophyte life history stages                      | 84  |
| 3.6.3 | Subdividing life history stages: leaf complexity    | 87  |
| 3.7   | Population structure comparisons                    | 89  |
| 3.7.1 | Siberian forest: comparing species within a habitat | 90  |
| 3.7.2 | <i>Isoetes lacustris</i> : comparing environments   | 90  |
| 3.7.3 | Long-term studies                                   | 91  |
| 3.7.4 | Summary                                             | 93  |
| 3.8   | Leaf phenology                                      | 95  |
| 3.8.1 | Leaf growth                                         | 96  |
| 3.8.2 | Leaf life span                                      | 96  |
| 3.8.3 | Leaf production rates                               | 98  |
| 3.8.4 | Summary                                             | 100 |
| 3.9   | Recommendations for future fern population studies  | 101 |
| 3.9.1 | Consistent methodologies                            | 101 |
| 3.9.2 | Expanding geographic range                          | 102 |
| 3.9.3 | Long-term monitoring                                | 102 |
| 4     | Nutrient ecology of ferns                           | 111 |
|       | <i>Sarah J. Richardson and Lawrence R. Walker</i>   |     |
| 4.1   | Introduction                                        | 111 |
| 4.2   | How do ferns acquire nutrients?                     | 112 |
| 4.2.1 | Roots and rhizomes                                  | 112 |
| 4.2.2 | Litter trapping                                     | 114 |
| 4.2.3 | Mutualisms                                          | 115 |

|       |                                                            |     |
|-------|------------------------------------------------------------|-----|
| 4.3   | Soil fertility and fern distribution                       | 117 |
| 4.3.1 | Fern biomass and cover                                     | 117 |
| 4.3.2 | Fern species richness                                      | 118 |
| 4.3.3 | Tree fern distributions and soil nutrients                 | 119 |
| 4.3.4 | Tropical fern distributions and soil cation concentrations | 121 |
| 4.3.5 | Ferns on low fertility soils                               | 121 |
| 4.4   | Nutrient concentrations in fern leaves and litter          | 123 |
| 4.4.1 | Comparisons between ferns and seed plants                  | 124 |
| 4.4.2 | Tree ferns                                                 | 128 |
| 4.4.3 | Litter quality of ferns and decomposition rates            | 129 |
| 4.5   | Nutrient limitation and consequences for ecosystems        | 130 |
| 4.5.1 | Nutrient ratios                                            | 130 |
| 4.5.2 | Nutrient additions                                         | 132 |
| 4.6   | Future research directions                                 | 133 |
| 5     | Fern adaptations to xeric environments                     | 140 |
|       | <i>Peter Hietz</i>                                         |     |
| 5.1   | Introduction                                               | 140 |
| 5.2   | Xerophytic ferns and their habitats                        | 141 |
| 5.3   | Adaptations to drought                                     | 147 |
| 5.3.1 | Water transport in ferns and lycophytes                    | 147 |
| 5.3.2 | Control of water loss                                      | 149 |
| 5.3.3 | Water uptake                                               | 150 |
| 5.3.4 | Water storage                                              | 154 |
| 5.4   | Desiccation tolerance                                      | 155 |
| 5.4.1 | Desiccation tolerance of sporophytes                       | 155 |
| 5.4.2 | Desiccation tolerance of gametophytes                      | 159 |
| 5.5   | Photoinhibition and photoprotection                        | 160 |
| 5.6   | Crassulacean acid metabolism                               | 162 |
| 5.7   | Phenology                                                  | 167 |
| 5.8   | Competitive ferns                                          | 169 |
| 5.9   | Other extreme environments                                 | 169 |
| 5.10  | Conclusions                                                | 170 |
| 6     | Ferns, disturbance and succession                          | 177 |
|       | <i>Lawrence R. Walker and Joanne M. Sharpe</i>             |     |
| 6.1   | Introduction                                               | 177 |
| 6.2   | Disturbance                                                | 185 |
| 6.2.1 | Volcanoes and landslides                                   | 186 |
| 6.2.2 | Hurricanes                                                 | 187 |
| 6.2.3 | Flooding                                                   | 189 |

|       |                                                                       |     |
|-------|-----------------------------------------------------------------------|-----|
| 6.2.4 | Fire                                                                  | 190 |
| 6.2.5 | Humans                                                                | 191 |
| 6.3   | Succession                                                            | 192 |
| 6.3.1 | Fern succession                                                       | 192 |
| 6.3.2 | Dispersal                                                             | 194 |
| 6.3.3 | Establishment, growth and longevity                                   | 198 |
| 6.3.4 | Fern impacts on ecosystem dynamics                                    | 200 |
| 6.3.5 | Interactions among ferns and other plants                             | 205 |
| 6.4   | Conclusions and future directions                                     | 208 |
| 7     | Interactions of ferns with fungi and animals                          | 220 |
|       | <i>Klaus Mehltreter</i>                                               |     |
| 7.1   | Introduction                                                          | 220 |
| 7.2   | Types of interactions                                                 | 221 |
| 7.3   | Interactions with fungi                                               | 222 |
| 7.3.1 | Saprophytic and parasitic fungi                                       | 223 |
| 7.3.2 | Mycorrhizae                                                           | 227 |
| 7.4   | Interactions with animals                                             | 231 |
| 7.4.1 | Herbivory                                                             | 232 |
| 7.4.2 | Responses of ferns to herbivory                                       | 239 |
| 7.4.3 | Mutualistic interactions of ferns and ants                            | 241 |
| 7.5   | Conclusions                                                           | 246 |
| 8     | Problem ferns: their impact and management                            | 255 |
|       | <i>Roderick C. Robinson, Elizabeth Sheffield and Joanne M. Sharpe</i> |     |
| 8.1   | Introduction                                                          | 255 |
| 8.2   | Native problem ferns                                                  | 262 |
| 8.2.1 | <i>Pteridium</i>                                                      | 262 |
| 8.2.2 | Other native problem ferns                                            | 274 |
| 8.3   | Alien terrestrial problem ferns                                       | 278 |
| 8.3.1 | <i>Lygodium</i>                                                       | 278 |
| 8.3.2 | Other alien terrestrial problem ferns                                 | 280 |
| 8.4   | Alien aquatic problem ferns                                           | 283 |
| 8.4.1 | <i>Salvinia</i>                                                       | 284 |
| 8.4.2 | <i>Azolla</i> , <i>Ceratopteris</i> and <i>Marsilea</i>               | 287 |
| 8.5   | Management of problem ferns                                           | 290 |
| 8.5.1 | Management strategies                                                 | 292 |
| 8.5.2 | Control options                                                       | 293 |
| 8.6   | Examples of socioeconomic effects of problem ferns                    | 305 |
| 8.7   | Conclusions and future prognoses                                      | 308 |
| 8.7.1 | Public awareness, the best preemptive control measure                 | 308 |
| 8.7.2 | <i>Pteridium</i>                                                      | 309 |

|        |                                                                  |     |
|--------|------------------------------------------------------------------|-----|
| 8.7.3  | New hybrid ferns and other potential invasives                   | 309 |
| 8.7.4  | International cooperation in monitoring and research             | 309 |
| 8.7.5  | The <i>Lygodium</i> menace                                       | 310 |
| 8.7.6  | Summary                                                          | 310 |
| 9      | Fern conservation                                                | 323 |
|        | <i>Klaus Mehltreter</i>                                          |     |
| 9.1    | Introduction                                                     | 323 |
| 9.2    | Ecological data needed for risk assessment                       | 327 |
| 9.2.1  | Abundance                                                        | 327 |
| 9.2.2  | Geographical range                                               | 329 |
| 9.2.3  | Habitat specificity                                              | 333 |
| 9.2.4  | Intrinsic biological factors                                     | 334 |
| 9.2.5  | Population dynamics and genetic diversity                        | 340 |
| 9.2.6  | Environmental disturbances                                       | 341 |
| 9.2.7  | Summary                                                          | 343 |
| 9.3    | Risk assessment                                                  | 343 |
| 9.3.1  | IUCN Red List criteria                                           | 343 |
| 9.3.2  | Risk categories of the IUCN Red List of<br>Threatened Species    | 345 |
| 9.3.3  | CITES                                                            | 349 |
| 9.4    | Management strategies for fern conservation                      | 350 |
| 9.4.1  | <i>Ex situ</i> conservation                                      | 350 |
| 9.4.2  | <i>In situ</i> management strategies                             | 351 |
| 9.5    | Conclusions                                                      | 352 |
| 10     | Current and future directions in fern ecology                    | 360 |
|        | <i>Lawrence R. Walker, Klaus Mehltreter and Joanne M. Sharpe</i> |     |
| 10.1   | Introduction                                                     | 360 |
| 10.2   | Biogeography: dispersal, habitats and diversity                  | 360 |
| 10.3   | Population dynamics: growth, reproduction<br>and life cycles     | 363 |
| 10.4   | Ecophysiology                                                    | 365 |
| 10.4.1 | Nutrients                                                        | 365 |
| 10.4.2 | Water                                                            | 366 |
| 10.4.3 | Light                                                            | 367 |
| 10.5   | Disturbance responses                                            | 367 |
| 10.6   | Species interactions                                             | 368 |
| 10.7   | Ferns and humans                                                 | 369 |
| 10.8   | Unresolved questions in fern ecology                             | 370 |
| 10.8.1 | Correlates of fern diversity                                     | 370 |
| 10.8.2 | Correlates of fern abundance                                     | 371 |

|        |                                                                          |     |
|--------|--------------------------------------------------------------------------|-----|
| 10.8.3 | Controls over gametophyte growth and development                         | 371 |
| 10.8.4 | Spore size and dispersal                                                 | 371 |
| 10.8.5 | Controls over life history transitions                                   | 372 |
| 10.8.6 | Ecological niches                                                        | 372 |
| 10.8.7 | Interactions                                                             | 372 |
| 10.8.8 | Roles in community and ecosystem development                             | 373 |
| 10.8.9 | Human uses of ferns                                                      | 373 |
| 10.9   | Conclusions                                                              | 373 |
| 10.9.1 | The importance of ferns                                                  | 373 |
| 10.9.2 | The future of ferns                                                      | 374 |
|        | Appendix A Classification system of ferns and lycophytes                 | 379 |
|        | Appendix B Index to genera of ferns and lycophytes in alphabetical order | 386 |
|        | <i>Alan R. Smith</i>                                                     |     |
|        | Appendix C Geological timescale                                          | 406 |
|        | <i>Glossary</i>                                                          | 407 |
|        | <i>Index</i>                                                             | 429 |

Color plates are between pages 176 and 177.