



International Institute for
Applied Systems Analysis
Schlossplatz 1
A-2361 Laxenburg, Austria

Tel: +43 2236 807 342
Fax: +43 2236 71313
E-mail: publications@iiasa.ac.at
Web: www.iiasa.ac.at

Interim Report

IR-04-004

**Evolution Restricts the Coexistence of Specialists and
Generalists – the Role of Trade-off Structure**

Martijn Egas (egas@science.uva.nl)
Ulf Dieckmann (dieckmann@iiasa.ac.at)
Maurice W. Sabelis (sabelis@science.uva.nl)

Approved by

Leen Hordijk
Director, IIASA

January 2004



The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

Scientific progress within the network is collected in the IIASA Studies in Adaptive Dynamics series.

- No. 1 Metz JAJ, Geritz SAH, Meszéna G, Jacobs FJA, van Heerwaarden JS: *Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction*. IIASA Working Paper WP-95-099 (1995). van Strien SJ, Verduyn Lunel SM (eds): *Stochastic and Spatial Structures of Dynamical Systems*, Proceedings of the Royal Dutch Academy of Science (KNAW Verhandelingen), North Holland, Amsterdam, pp. 183-231 (1996).
- No. 2 Dieckmann U, Law R: *The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes*. IIASA Working Paper WP-96-001 (1996). *Journal of Mathematical Biology* 34:579-612 (1996).
- No. 3 Dieckmann U, Marrow P, Law R: *Evolutionary Cycling of Predator-Prey Interactions: Population Dynamics and the Red Queen*. IIASA Preprint (1995). *Journal of Theoretical Biology* 176:91-102 (1995).
- No. 4 Marrow P, Dieckmann U, Law R: *Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective*. IIASA Working Paper WP-96-002 (1996). *Journal of Mathematical Biology* 34:556-578 (1996).
- No. 5 Law R, Marrow P, Dieckmann U: *On Evolution under Asymmetric Competition*. IIASA Working Paper WP-96-003 (1996). *Evolutionary Ecology* 11:485-501 (1997).
- No. 6 Metz JAJ, Mylius SD, Dieckmann O: *When Does Evolution Optimize? On the Relation Between Types of Density Dependence and Evolutionarily Stable Life History Parameters*. IIASA Working Paper WP-96-004 (1996).
- No. 7 Ferrière R, Gatto M: *Lyapunov Exponents and the Mathematics of Invasion in Oscillatory or Chaotic Populations*. *Theoretical Population Biology* 48:126-171 (1995).
- No. 8 Ferrière R, Fox GA: *Chaos and Evolution*. IIASA Preprint (1996). *Trends in Ecology and Evolution* 10:480-485 (1995).
- No. 9 Ferrière R, Michod RE: *The Evolution of Cooperation in Spatially Heterogeneous Populations*. IIASA Working Paper WP-96-029 (1996). *The American Naturalist* 147:692-717 (1996).
- No. 10 van Dooren TJM, Metz JAJ: *Delayed Maturation in Temporally Structured Populations with Non-Equilibrium Dynamics*. IIASA Working Paper WP-96-070 (1996). *Journal of Evolutionary Biology* 11:41-62 (1998).
- No. 11 Geritz SAH, Metz JAJ, Kisdi É, Meszéna G: *The Dynamics of Adaptation and Evolutionary Branching*. IIASA Working Paper WP-96-077 (1996). *Physical Review Letters* 78:2024-2027 (1997).
- No. 12 Geritz SAH, Kisdi É, Meszéna G, Metz JAJ: *Evolutionary Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree*. IIASA Working Paper WP-96-114 (1996). *Evolutionary Ecology* 12:35-57 (1998).
- No. 13 Heino M, Metz JAJ, Kaitala V: *Evolution of Mixed Maturation Strategies in Semelparous Life-Histories: The Crucial Role of Dimensionality of Feedback Environment*. IIASA Working Paper WP-96-126 (1996). *Philosophical Transactions of the Royal Society of London Series B* 352:1647-1655 (1997).
- No. 14 Dieckmann U: *Can Adaptive Dynamics Invade?* IIASA Working Paper WP-96-152 (1996). *Trends in Ecology and Evolution* 12:128-131 (1997).
- No. 15 Meszéna G, Czibula I, Geritz SAH: *Adaptive Dynamics in a 2-Patch Environment: A Simple Model for Allopatric and Parapatric Speciation*. IIASA Interim Report IR-97-001 (1997). *Journal of Biological Systems* 5:265-284 (1997).
- No. 16 Heino M, Metz JAJ, Kaitala V: *The Enigma of Frequency-Dependent Selection*. IIASA Interim Report IR-97-061 (1997). *Trends in Ecology and Evolution* 13:367-370 (1998).
- No. 17 Heino M: *Management of Evolving Fish Stocks*. IIASA Interim Report IR-97-062 (1997). *Canadian Journal of Fisheries and Aquatic Sciences* 55:1971-1982 (1998).
- No. 18 Heino M: *Evolution of Mixed Reproductive Strategies in Simple Life-History Models*. IIASA Interim Report IR-97-063 (1997).
- No. 19 Geritz SAH, van der Meijden E, Metz JAJ: *Evolutionary Dynamics of Seed Size and Seedling Competitive Ability*. IIASA Interim Report IR-97-071 (1997). *Theoretical Population Biology* 55:324-343 (1999).
- No. 20 Galis F, Metz JAJ: *Why Are There So Many Cichlid Species? On the Interplay of Speciation and Adaptive Radiation*. IIASA Interim Report IR-97-072 (1997). *Trends in Ecology and Evolution* 13:1-2 (1998).
- No. 21 Boerlijst MC, Nowak MA, Sigmund K: *Equal Pay for all Prisoners/ The Logic of Contrition*. IIASA Interim Report IR-97-073 (1997). *American Mathematical Society Monthly* 104:303-307 (1997). *Journal of Theoretical Biology* 185:281-293 (1997).

- No. 22 Law R, Dieckmann U: *Symbiosis Without Mutualism and the Merger of Lineages in Evolution*. IIASA Interim Report IR-97-074 (1997). Proceedings of the Royal Society of London Series B 265:1245-1253 (1998).
- No. 23 Klinkhamer PGL, de Jong TJ, Metz JAJ: *Sex and Size in Cosexual Plants*. IIASA Interim Report IR-97-078 (1997). Trends in Ecology and Evolution 12:260-265 (1997).
- No. 24 Fontana W, Schuster P: *Shaping Space: The Possible and the Attainable in RNA Genotype-Phenotype Mapping*. IIASA Interim Report IR-98-004 (1998). Journal of Theoretical Biology 194:491-515 (1998).
- No. 25 Kisdi É, Geritz SAH: *Adaptive Dynamics in Allele Space: Evolution of Genetic Polymorphism by Small Mutations in a Heterogeneous Environment*. IIASA Interim Report IR-98-038 (1998). Evolution 53:993-1008 (1999).
- No. 26 Fontana W, Schuster P: *Continuity in Evolution: On the Nature of Transitions*. IIASA Interim Report IR-98-039 (1998). Science 280:1451-1455 (1998).
- No. 27 Nowak MA, Sigmund K: *Evolution of Indirect Reciprocity by Image Scoring/ The Dynamics of Indirect Reciprocity*. IIASA Interim Report IR-98-040 (1998). Nature 393:573-577 (1998). Journal of Theoretical Biology 194:561-574 (1998).
- No. 28 Kisdi É: *Evolutionary Branching Under Asymmetric Competition*. IIASA Interim Report IR-98-045 (1998). Journal of Theoretical Biology 197:149-162 (1999).
- No. 29 Berger U: *Best Response Adaptation for Role Games*. IIASA Interim Report IR-98-086 (1998).
- No. 30 van Dooren TJM: *The Evolutionary Ecology of Dominance-Recessivity*. IIASA Interim Report IR-98-096 (1998). Journal of Theoretical Biology 198:519-532 (1999).
- No. 31 Dieckmann U, O'Hara B, Weisser W: *The Evolutionary Ecology of Dispersal*. IIASA Interim Report IR-98-108 (1998). Trends in Ecology and Evolution 14:88-90 (1999).
- No. 32 Sigmund K: *Complex Adaptive Systems and the Evolution of Reciprocation*. IIASA Interim Report IR-98-100 (1998). Ecosystems 1:444-448 (1998).
- No. 33 Posch M, Pichler A, Sigmund K: *The Efficiency of Adapting Aspiration Levels*. IIASA Interim Report IR-98-103 (1998). Proceedings of the Royal Society London Series B 266:1427-1435 (1999).
- No. 34 Mathias A, Kisdi É: *Evolutionary Branching and Coexistence of Germination Strategies*. IIASA Interim Report IR-99-014 (1999).
- No. 35 Dieckmann U, Doebeli M: *On the Origin of Species by Sympatric Speciation*. IIASA Interim Report IR-99-013 (1999). Nature 400:354-357 (1999).
- No. 36 Metz JAJ, Gyllenberg M: *How Should We Define Fitness in Structured Metapopulation Models? Including an Application to the Calculation of Evolutionarily Stable Dispersal Strategies*. IIASA Interim Report IR-99-019 (1999). Proceedings of the Royal Society of London Series B 268:499-508 (2001).
- No. 37 Gyllenberg M, Metz JAJ: *On Fitness in Structured Metapopulations*. IIASA Interim Report IR-99-037 (1999). Journal of Mathematical Biology 43:545-560 (2001).
- No. 38 MeszÉna G, Metz JAJ: *Species Diversity and Population Regulation: The Importance of Environmental Feedback Dimensionality*. IIASA Interim Report IR-99-045 (1999).
- No. 39 Kisdi É, Geritz SAH: *Evolutionary Branching and Sympatric Speciation in Diploid Populations*. IIASA Interim Report IR-99-048 (1999).
- No. 40 Ylikarjula J, Heino M, Dieckmann U: *Ecology and Adaptation of Stunted Growth in Fish*. IIASA Interim Report IR-99-050 (1999). Evolutionary Ecology 13:433-453 (1999).
- No. 41 Nowak MA, Sigmund K: *Games on Grids*. IIASA Interim Report IR-99-038 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 135-150 (2000).
- No. 42 Ferrière R, Michod RE: *Wave Patterns in Spatial Games and the Evolution of Cooperation*. IIASA Interim Report IR-99-041 (1999). Dieckmann U, Law R, Metz JAJ (eds): The Geometry of Ecological Interactions: Simplifying Spatial Complexity, Cambridge University Press, Cambridge, UK, pp. 318-332 (2000).
- No. 43 Kisdi É, Jacobs FJA, Geritz SAH: *Red Queen Evolution by Cycles of Evolutionary Branching and Extinction*. IIASA Interim Report IR-00-030 (2000). Selection 2:161-176 (2001).
- No. 44 MeszÉna G, Kisdi É, Dieckmann U, Geritz SAH, Metz JAJ: *Evolutionary Optimisation Models and Matrix Games in the Unified Perspective of Adaptive Dynamics*. IIASA Interim Report IR-00-039 (2000). Selection 2:193-210 (2001).
- No. 45 Parvinen K, Dieckmann U, Gyllenberg M, Metz JAJ: *Evolution of Dispersal in Metapopulations with Local Density Dependence and Demographic Stochasticity*. IIASA Interim Report IR-00-035 (2000). Journal of Evolutionary Biology 16:143-153 (2003).
- No. 46 Doebeli M, Dieckmann U: *Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions*. IIASA Interim Report IR-00-040 (2000). The American Naturalist 156:S77-S101 (2000).
- No. 47 Heino M, Hanski I: *Evolution of Migration Rate in a Spatially Realistic Metapopulation Model*. IIASA Interim Report IR-00-044 (2000). The American Naturalist 157:495-511 (2001).
- No. 48 Gyllenberg M, Parvinen K, Dieckmann U: *Evolutionary Suicide and Evolution of Dispersal in Structured Metapopulations*. IIASA Interim Report IR-00-056 (2000). Journal of Mathematical Biology 45:79-105 (2002).
- No. 49 van Dooren TJM: *The Evolutionary Dynamics of Direct Phenotypic Overdominance: Emergence Possible, Loss Probable*. IIASA Interim Report IR-00-048 (2000). Evolution 54: 1899-1914 (2000).
- No. 50 Nowak MA, Page KM, Sigmund K: *Fairness Versus Reason in the Ultimatum Game*. IIASA Interim Report IR-00-57 (2000). Science 289:1773-1775 (2000).
- No. 51 de Feo O, Ferrière R: *Bifurcation Analysis of Population Invasion: On-Off Intermittency and Basin Riddling*. IIASA Interim Report IR-00-074 (2000). International Journal of Bifurcation and Chaos 10:443-452 (2000).
- No. 52 Heino M, Laaka-Lindberg S: *Clonal Dynamics and Evolution of Dormancy in the Leafy Hepatic Lophozia Silvicola*. IIASA Interim Report IR-01-018 (2001). Oikos 94:525-532 (2001).
- No. 53 Sigmund K, Hauert C, Nowak MA: *Reward and Punishment in Minigames*. IIASA Interim Report IR-01-031 (2001). Proceedings of the National Academy of Sciences of the USA 98:10757-10762 (2001).

- No. 54 Hauert C, De Monte S, Sigmund K, Hofbauer J: *Oscillations in Optional Public Good Games*. IIASA Interim Report IR-01-036 (2001).
- No. 55 Ferrière R, Le Galliard J: *Invasion Fitness and Adaptive Dynamics in Spatial Population Models*. IIASA Interim Report IR-01-043 (2001). Clobert J, Dhondt A, Danchin E, Nichols J (eds): *Dispersal*, Oxford University Press, pp. 57-79 (2001).
- No. 56 de Mazancourt C, Loreau M, Dieckmann U: *Can the Evolution of Plant Defense Lead to Plant-Herbivore Mutualism*. IIASA Interim Report IR-01-053 (2001). *The American Naturalist* 158: 109-123 (2001).
- No. 57 Claessen D, Dieckmann U: *Ontogenetic Niche Shifts and Evolutionary Branching in Size-Structured Populations*. IIASA Interim Report IR-01-056 (2001). *Evolutionary Ecology Research* 4:189-217 (2002).
- No. 58 Brandt H: *Correlation Analysis of Fitness Landscapes*. IIASA Interim Report IR-01-058 (2001).
- No. 59 Dieckmann U: *Adaptive Dynamics of Pathogen-Host Interactions*. IIASA Interim Report IR-02-007 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 39-59 (2002).
- No. 60 Nowak MA, Sigmund K: *Super- and Coinfection: The Two Extremes*. IIASA Interim Report IR-02-008 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 124-137 (2002).
- No. 61 Sabelis MW, Metz JAJ: *Perspectives for Virulence Management: Relating Theory to Experiment*. IIASA Interim Report IR-02-009 (2002). Dieckmann U, Metz JAJ, Sabelis MW, Sigmund K (eds): *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, Cambridge University Press, Cambridge, UK, pp. 379-398 (2002).
- No. 62 Cheptou P, Dieckmann U: *The Evolution of Self-Fertilization in Density-Regulated Populations*. IIASA Interim Report IR-02-024 (2002). *Proceedings of the Royal Society of London Series B* 269:1177-1186 (2002).
- No. 63 Bürger R: *Additive Genetic Variation Under Intraspecific Competition and Stabilizing Selection: A Two-Locus Study*. IIASA Interim Report IR-02-013 (2002). *Theoretical Population Biology* 61:197-213 (2002).
- No. 64 Hauert C, De Monte S, Hofbauer J, Sigmund K: *Volunteering as Red Queen Mechanism for Co-operation in Public Goods Games*. IIASA Interim Report IR-02-041 (2002). *Science* 296:1129-1132 (2002).
- No. 65 Dercole F, Ferrière R, Rinaldi S: *Ecological Bistability and Evolutionary Reversals under Asymmetrical Competition*. IIASA Interim Report IR-02-053 (2002). *Evolution* 56:1081-1090 (2002).
- No. 66 Dercole F, Rinaldi S: *Evolution of Cannibalistic Traits: Scenarios Derived from Adaptive Dynamics*. IIASA Interim Report IR-02-054 (2002). *Theoretical Population Biology* 62:365-374 (2002).
- No. 67 Bürger R, Gimelfarb A: *Fluctuating Environments and the Role of Mutation in Maintaining Quantitative Genetic Variation*. IIASA Interim Report IR-02-058 (2002). *Genetical Research* 80:31-46 (2002).
- No. 68 Bürger R: *On a Genetic Model of Intraspecific Competition and Stabilizing Selection*. IIASA Interim Report IR-02-062 (2002). *Amer. Natur.* 160:661-682 (2002).
- No. 69 Doebeli M, Dieckmann U: *Speciation Along Environmental Gradients*. IIASA Interim Report IR-02-079 (2002). *Nature* 421:259-264 (2003).
- No. 70 Dercole F, Irisson J, Rinaldi S: *Bifurcation Analysis of a Prey-Predator Coevolution Model*. IIASA Interim Report IR-02-078 (2002). *SIAM Journal on Applied Mathematics* 63:1378-1391 (2003).
- No. 71 Le Galliard J, Ferrière R, Dieckmann U: *The Adaptive Dynamics of Altruism in Spatially Heterogeneous Populations*. IIASA Interim Report IR-03-006 (2003). *Evolution* 57:1-17 (2003).
- No. 72 Taborsky B, Dieckmann U, Heino M: *Unexpected Discontinuities in Life-History Evolution under Size-Dependent Mortality*. IIASA Interim Report IR-03-004 (2003). *Proceedings of the Royal Society of London Series B* 270:713-721 (2003).
- No. 73 Gardmark A, Dieckmann U, Lundberg P: *Life-History Evolution in Harvested Populations: The Role of Natural Predation*. IIASA Interim Report IR-03-008 (2003). *Evolutionary Ecology Research* 5:239-257 (2003).
- No. 74 Mizera F, Meszéna G: *Spatial Niche Packing, Character Displacement and Adaptive Speciation Along an Environmental Gradient*. IIASA Interim Report IR-03-062 (2003). *Evolutionary Ecology Research* 5: 363-382 (2003).
- No. 75 Dercole F: *Remarks on Branching-Extinction Evolutionary Cycles*. IIASA Interim Report IR-03-075 (2003). *Journal of Mathematical Biology* 47: 569-580 (2003).
- No. 76 Hofbauer J, Sigmund K: *Evolutionary Game Dynamics*. IIASA Interim Report IR-03-078 (2003). *Bulletin of the American Mathematical Society* 40: 479-519 (2003).
- No. 77 Ernande B, Dieckmann U, Heino M: *Adaptive Changes in Harvested Populations: Plasticity and Evolution of Age and Size at Maturation*. IIASA Interim Report IR-03-058 (2003).
- No. 78 Hanski I, Heino M: *Metapopulation-Level Adaptation of Insect Host Plant Preference and Extinction-Colonization Dynamics in Heterogeneous Landscapes*. IIASA Interim Report IR-03-028 (2003). *Theoretical Population Biology* 63:309-338 (2003).
- No. 79 van Doorn G, Dieckmann U, Weissing FJ: *Sympatric Speciation by Sexual Selection: A Critical Re-Evaluation*. IIASA Interim Report IR-04-003 (2004).
- No. 80 Egas M, Dieckmann U, Sabelis MW: *Evolution Restricts the Coexistence of Specialists and Generalists - the Role of Trade-off Structure*. IIASA Interim Report IR-04-004 (2004).

Contents

Introduction	1
Model description	2
Population dynamics	2
Foraging rules	2
Trade-off structure	3
Evolutionary analysis	5
Coexistence in the absence of evolution.....	7
Coexistence under gradual evolution	9
The crucial importance of trade-off structure for the evolution of specialization.....	10
Effects of temporal variability and foraging behavior on the evolution of specialization	11
Coexistence under gradual evolution after generalist immigration.....	12
Discussion.....	13
Limitations of our study	13
Challenges for future study.....	14
References	16

Abstract

Environmental variability and adaptive foraging behavior have been shown to favor coexistence of specialists and generalists on an ecological time scale. This leaves unaddressed the question whether such coexistence can also be expected on an evolutionary time scale. In this article we study the attainability, through gradual evolution, of specialist-generalist coexistence, as well as the evolutionary stability of such communities when allowing for immigration. Our analysis shows that the potential for specialist-generalist coexistence is much more restricted than originally thought, and strongly depends on the trade-off structure assumed. We establish that ecological coexistence is less likely for species facing a trade-off between *per capita* reproduction in different habitats than when the trade-off acts on carrying capacities alone. We also demonstrate that coexistence is evolutionarily stable whenever it is ecologically stable, but that in most cases such coexistence cannot be reached through gradual evolution. We conclude that an evolutionarily stable community of specialists and generalists may only be created through immigration from elsewhere or through mutations of large effect. Our results highlight that trade-offs in fitness-determining traits can have counterintuitive effects on the evolution of specialization.

About the Authors

Martijn Egas
Institute for Biodiversity and Ecosystem Dynamics
University of Amsterdam
P.O. Box 94084
1090 GB Amsterdam
The Netherlands
and
Adaptive Dynamics Network
International Institute for Applied Systems Analysis
Schlossplatz 1
2361 Laxenburg
Austria

Ulf Dieckmann
Adaptive Dynamics Network
International Institute for Applied Systems Analysis
Schlossplatz 1
2361 Laxenburg
Austria

Maurice W. Sabelis
Institute for Biodiversity and Ecosystem Dynamics
University of Amsterdam
P.O. Box 94084
1090 GB Amsterdam
The Netherlands

Acknowledgments

We thank Éva Kisdi and Claus Rueffler for discussions of our results, Steph Menken and two anonymous reviewers for comments on the manuscript, and Jan Bruin for advice on the manuscript's title.

Martijn Egas gratefully acknowledges support by a travel grant from the European Science Foundation programme on the Theoretical Biology of Adaptation.

Ulf Dieckmann gratefully acknowledges financial support by the Austrian Science Fund; by the Austrian Federal Ministry of Education, Science, and Cultural Affairs; and by the European Research Training Network ModLife (Modern Life-History Theory and its Application to the Management of Natural Resources), funded through the Human Potential Programme of the European Commission.

Evolution Restricts the Coexistence of Specialists and Generalists – the Role of Trade-off Structure

Martijn Egas
Ulf Dieckmann
Maurice W. Sabelis

Introduction

One of the major challenges in ecology and evolutionary biology is to achieve a better link between evolutionary and ecological dynamics. Do fast selection responses add new properties to ecosystem dynamics? And, perhaps more importantly, does ecological feedback affect selection pressures in unexpected ways? The various ways through which evolutionary and ecological dynamics interact are only beginning to be explored. For example, including natural selection in metapopulation models can lead to predictions of selection-driven metapopulation extinction (Gyllenberg et al. 2002; Parvinen 2002, Parvinen et al. 2003). Also, ecological feedback is increasingly viewed as a widespread source of frequency-dependent selection that may favor sympatric speciation through selection for assortative mating (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000, 2003; Geritz and Kisdi 2000).

A topic where such questions are particularly pertinent is species coexistence. Here the aim is to pinpoint conditions under which n species can live together on less than n resources, violating the principle of competitive exclusion (Hardin 1960). On the one hand, the ecological dynamics are well explored (e.g., Hutchinson 1961; Stewart and Levin 1973; Koch 1974; Armstrong and McGehee 1976a; Levins 1979; Chesson and Warner 1981; Abrams 1984; Chesson 1985; Brown 1989; Huisman and Weissing 1999; Anderlies and Beisner 2000; Richards *et al.* 2000; Wilson and Richards 2000; review in Chesson 2000), and the evolutionary dynamics of coexisting species have been well studied in the context of ecological character displacement (e.g., MacArthur and Levins 1967; Roughgarden 1972; May and MacArthur 1972; Slatkin 1980; Case 1981; Taper and Case 1985, 1992a,b; Drossel and McKane 1999, 2000; Abrams and Chen 2002). On the other hand, we do not know whether natural selection with ecological feedback will restrict or broaden conditions for species coexistence.

Questions concerning species coexistence have been related to specialization in resource utilization (e.g., Kotler and Brown 1988; Wilson and Yoshimura 1994; McPeck 1996; Morris 1996). Wilson and Yoshimura (1994) studied the ecological coexistence of one generalist and two specialists on two resources. They concluded that such coexistence is likely, assuming some degree of optimal foraging and environmental variability. However, evolutionary change in the strategies of specialists

and generalists was not considered, leaving open the question whether such coexistence may occur or persist at an evolutionary time scale. Specifically, evolution may restrict conditions for coexistence of specialists and generalists for two reasons. First, the coexistence of two specialists and a generalist may not be evolutionarily stable, implying that evolution would change their degree of specialization which may even lead to extinction of one or more species. Second, such coexistence may not be evolutionarily attainable, implying that the trimorphic state cannot be reached through gradual evolution. To what extent these factors restrict species coexistence is the topic of this article.

Model description

This section extends the model by Wilson and Yoshimura (1994) and explains how to analyze the evolutionary attainability and stability of community states involving both generalists and specialists.

Population dynamics

We consider the population dynamics of up to three species in two habitats, described by the following discrete-time Ricker equations,

$$N_{i,t+1} = \sum_{j=1}^2 N_{ij,t} \exp \left[r \left(1 - \frac{N_{1j,t} + N_{2j,t} + N_{3j,t}}{e_{ij} \cdot K_j} \right) \right]. \quad (1)$$

Here, the basic reproduction ratios of populations in each habitat are described by an exponential function, where r is the intrinsic growth rate (assumed to be equal for all species), $N_{ij,t}$ is the abundance of species i in habitat j at time t , K_j is the carrying capacity of a species in habitat j when maximally specialized on that habitat, and e_{ij} is the level of specialization, or relative efficiency, of species i in habitat j . Throughout this paper we focus on symmetric habitats, $K_1 = K_2$.

Temporal variability among generations is introduced by randomly varying the values of K_1 and K_2 symmetrically around their mean, according to a uniform distribution. The relative variation v_j for habitat j is defined by $(K_{j,max} - K_{j,min})/K_j$. Both carrying capacities are varied independently among generations.

Foraging rules

Complementing the dynamics described by eq. (1), at the start of each generation individuals are redistributed over the two habitats based on their ideal free distribution (IFD; Fretwell and Lucas 1970). For the three species studied here, the IFD cannot be obtained analytically and thus has to be derived numerically. Departures from the IFD, which itself is biologically unrealistic, are considered as follows. Wilson and Yoshimura (1994) distributed a fraction g according to the IFD while the remaining fraction $1 - g$ was distributed randomly, i.e., with a probability $K_i/(K_1+K_2)$ of entering habitat i . The fraction g allowed for the distribution of a consumer population over the two habitats to be continuously varied between fully optimal ($g = 1$) and completely

random ($g = 0$). This rule, however, results in discontinuous foraging behavior: the proportion foragers in a habitat exhibits large jumps even if efficiencies are being varied only gradually. To avoid such unrealistic foraging behavior we consider an alternative, continuous, foraging rule, assuming that foragers necessarily make some foraging errors relative to the IFD. In reality such errors will be more pronounced when the foragers experience a smaller fitness difference $f_2 - f_1$ (defined below) between the two habitats. According to this rule the probability p_1 of using habitat 1 is

$$p_1 = \frac{1}{1 + \exp[a(f_2 - f_1)]}, \quad (2)$$

where the parameter a determines the foraging accuracy. By varying a in the range $[0, +\infty)$, we can vary the distribution of consumers from random to IFD (figure 1a). When there is no fitness difference, foragers are randomly distributed over the two habitats. For $a > 0$, an increasing fitness difference results in an increasing proportion of foragers entering the habitat they are best adapted to.

Trade-off structure

Specialization on one habitat is assumed to go at the expense of specialization on another. Extreme specialists have efficiency 1 in one habitat and efficiency 0 in the other habitat, whereas generalists have intermediate efficiencies in both habitats. The trade-off constraining the levels of specialization on the two habitats is given by

$$(e_{i1})^{1/s} + (e_{i2})^{1/s} = 1. \quad (3)$$

The strength of the trade-off is determined by the parameter s (figure 1b): the trade-off is called weak when $s < 1$ (convex relation between e_{i1} and e_{i2}) and strong when $s > 1$ (concave relation between e_{i1} and e_{i2}).

In addition to varying the trade-off's strength, different impacts of the trade-off can be considered. Individual-based derivations of the (population-level) Ricker model show how r and K depend on more mechanistic parameters. All these derivations agree in three conclusions: (i) r and K are not independent, (ii) they are linearly related, and (iii) K depends on mechanistic parameters not affecting r (Royama 1992; Dieckmann and Law 2000; Van Dooren 2000; Sumpter and Broomhead 2001). Two examples are $r = \ln[\rho/(1 - 1/n)]$, $K = \ln[\rho/(1 - 1/n)] / (-\ln[(1 - 1/n)])$, where ρ is the density-independent *per capita* reproduction, and n is the population's maximal size (Sumpter and Broomhead 2001), and $r = \gamma$, $K = \gamma / s(1 - k)$, where γ is again density-independent *per capita* reproduction, s is the neighborhood area of one individual and k measures competition intensity (Royama 1992).

These dependences of the population-level parameters r and K on individual-based traits have implications for the trade-off structures considered in our model. When individual traits determining density-independent reproduction (i.e., ρ or γ) in the two habitats trade off, this results - at the population level - in a trade-off affecting both r and K equally. A trade-off in K alone (i.e., a trade-off between K_1 and K_2 for habitats 1 and 2 respectively), is also possible, because K depends on parameters that do not affect

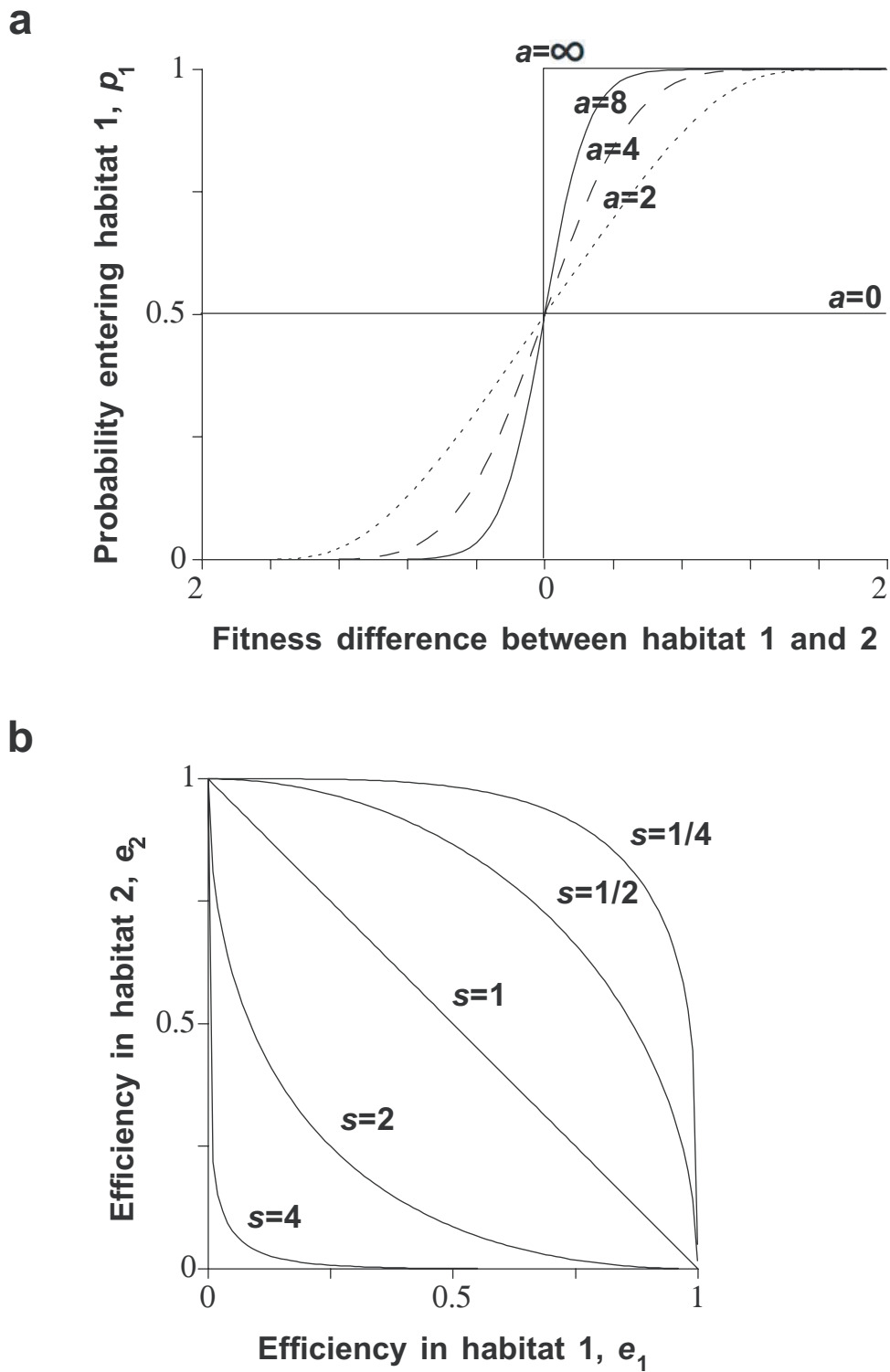


Figure 1 Functions used for specifying foraging behavior and trade-offs. (a) Continuous foraging rule (eq. 2) for various values of foraging accuracy a . The case $a = 0$ corresponds to random foraging. (b) Trade-off function (eq. 3) for different values of the trade-off strength s . Trade-offs are called strong for $s > 1$, and weak for $s < 1$.

r . This trade-off structure occurs when individual traits that determine the maximum population size in the two habitats trade off (see eq. 1). By contrast, assuming a trade-off in r alone (i.e., a trade-off between r_1 and r_2 for habitats 1 and 2 respectively) is impossible, because any parameter affecting r will likewise affect K .

Thus, we analyze two alternative trade-off structures: a trade-off in K as described by eq. (1), and a trade-off in both K and r as described in the following equation,

$$N_{i,t+1} = \sum_{j=1}^2 N_{ij,t} \exp \left[r \left(e_{ij} - \frac{N_{1j,t} + N_{2j,t} + N_{3j,t}}{K_j} \right) \right]. \quad (4)$$

Notice that in eq. (4) both r and K_j are multiplied with e_{ij} , whereas in eq. (1) this multiplication is applied to K_j only.

Evolutionary analysis

For the evolutionary analysis, we use the framework of adaptive dynamics (Metz et al. 1996; Dieckmann and Law 1996; Dieckmann 1997; Geritz et al. 1998). One of the advantages of this approach is that it provides tools for analyzing conditions for the build-up of polymorphisms through gradual evolution.

Such build-up is related to processes of evolutionary branching, through which a population under frequency-dependent selection evolves toward a fitness minimum. Under the resulting regime of disruptive selection, phenotypically similar species straddling the fitness minimum, when they occur, are predicted to diverge. Applying such analysis of frequency-dependent selection regimes sequentially yields the conditions for evolutionarily attainable coexistence, as illustrated below. In a population with only a single species, evolution may initially converge on the generalist strategy (figure 2a), even though this strategy may not be evolutionarily stable under all conditions. If evolutionary branching can occur in that situation, two very similar generalist species will be able to coexist around the branching point; these generalists will gradually diverge by specializing on one of the two habitats (figure 2b). Subsequently, these two species may end up at an evolutionary attractor that allows for secondary evolutionary branching, potentially resulting in two extreme specialists and two more generalist species (figure 2c). The two generalist species may then converge towards each other, to the extent that one of them may go extinct, leaving the other generalist in a state of evolutionarily stable coexistence with the two specialist species (figure 2d). Whereas evolutionary branching points will lead to the adaptive radiation of asexual morphs, the evolutionary processes that allow sexual species to differentiate have been investigated elsewhere (Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000, 2003; Geritz and Kisdi 2000; Matessi et al. 2001). Such extension to sexual species is beyond the scope of this article.

Complementing the analysis of evolutionary attainability, we analyze the evolutionary stability of specialist-generalist coexistence in two steps: first, we delineate the conditions required for the generalist to invade a community of two extreme specialists (e.g., through immigration), and second, we check whether the ensuing gradual evolutionary change results in the extinction of one or more of the three species.

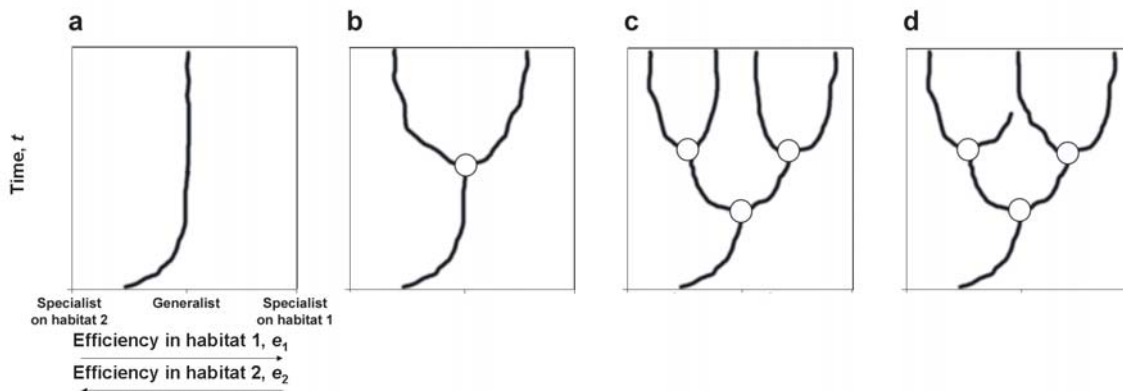


Figure 2 Sketch of the potential pathway by which coexistence of two specialists and one generalist species may be established through gradual evolution. (a) Evolution converges to the generalist strategy. (b) Primary evolutionary branching may allow for the coexistence of two similar generalist species, which subsequently diverge. The white circle atop the branching point indicates that we explicitly do not deal with the detailed genetic processes through which the two species might emerge. Secondary evolutionary branching may produce four species, all of which may coexist (c) or two of which may converge to the generalist strategy whereby one goes extinct (d). Our results ascertain the specific ecological settings for which outcomes (a), (b), and (d) occur in our model, whereas option (c), coexistence of four species, is shown to occur in our model only as a transient phenomenon.

The evolutionary analyses described above are based on evaluating the invasion fitness of rare phenotypes, defined as their long-term *per capita* growth rate in a population dominated by a given resident strategy (Metz et al. 1992). In this way, the residents determine the environment in which the rare phenotype under consideration either succeeds or fails. If the rare phenotype can grow in the resident population, its invasion fitness is positive, whereas mutants that are deleterious in the resident's environment have negative invasion fitness. To calculate invasion fitness in the above model, we numerically analyze the population dynamics of rare phenotypes: after sampling for 50,000 generations, a rare phenotype's invasion fitness is calculated as the logarithm of the geometric average of its reproduction ratio over all generations.

We use pairwise invasibility plots (PIPs) to show the sign structure of invasion fitness for different combinations of common and rare phenotypes (Matsuda 1985; Van Tienderen and De Jong 1986; Geritz et al. 1998; see also figure 3 for examples). In such plots, each point represents a combination (pair) of considered rare and common trait values (commonly called mutant and resident trait values, respectively) and gives the sign of the rare phenotype's invasion fitness. Hence, a PIP shows areas of positive and negative invasion fitness. Along the plot's main diagonal (where the two considered trait values equal each other) invasion fitness is necessarily zero; usually there is at least one other contour line of zero invasion fitness. Where this line intersects the main diagonal, an evolutionarily singular point is located, corresponding to an equilibrium of the considered evolutionary dynamics. Whether gradual evolution leads towards such a point or away from it is easily determined from the PIP (Geritz et al. 1998): for instance, if we start left of the singular point and invasion fitness above the diagonal is positive, phenotypes with a value closer to that of the singular point can invade and replace the resident phenotype. Also the evolutionary stability of singular points is readily

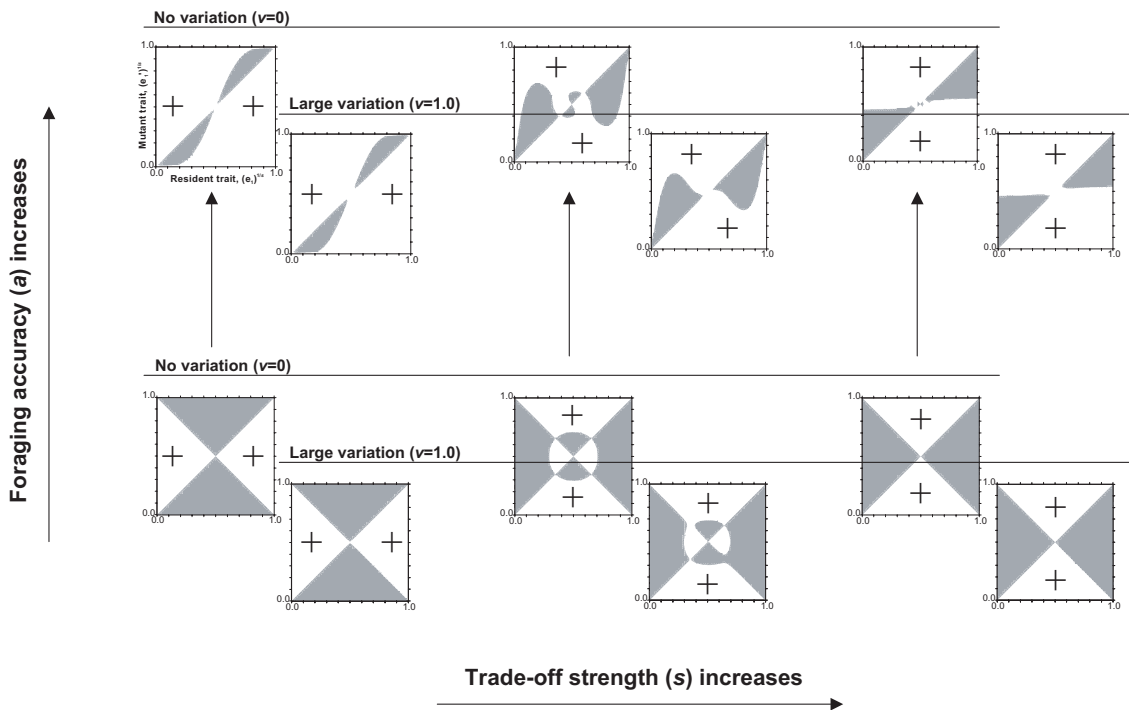


Figure 3 Representative gallery of pairwise invasibility plots (PIPs) for the case when the trade-off acts on K only. The effects of varying trade-off strength s (horizontal), foraging accuracy a (vertical), and temporal variability v (stacked) thus become visible. White areas indicate positive invasion fitness, grey areas negative. Other parameters: $r = 1.3$ and $K_1 = K_2 = 100$.

established from the PIP (Geritz et al. 1998) by checking whether the vertical line through the singular point lies within an area of negative invasion fitness (no phenotypes can invade the singular one) or positive invasion fitness (phenotypes on both sides can invade a resident population with the singular phenotype). In the latter case, the singular phenotype is an evolutionary branching point: phenotypes narrowly straddling this point can then invade each other, allowing them to coexist (Geritz et al. 1998).

Coexistence in the absence of evolution

In this section we analyze the potential for coexistence of specialists and generalists on an ecological time scale, based on the continuous foraging rule and considering the two alternative trade-off structures identified above. That is, we chart the parameter ranges for foraging accuracy, a , and trade-off strength, s , in which the extreme specialists can invade a population of generalists and, *vice versa*, the generalist can invade the community of two extreme specialists. The overlap between these two ranges characterizes the conditions for the ecological coexistence of specialists and generalists in a protected polymorphism.

It turns out that the potential for ecological coexistence strongly depends on the assumed trade-off structure. With the trade-off in K only, such coexistence is possible under a wide range of conditions (figure 4a). The extreme specialists are always able to invade a population of generalists, and, at least under weak trade-offs, the generalist can

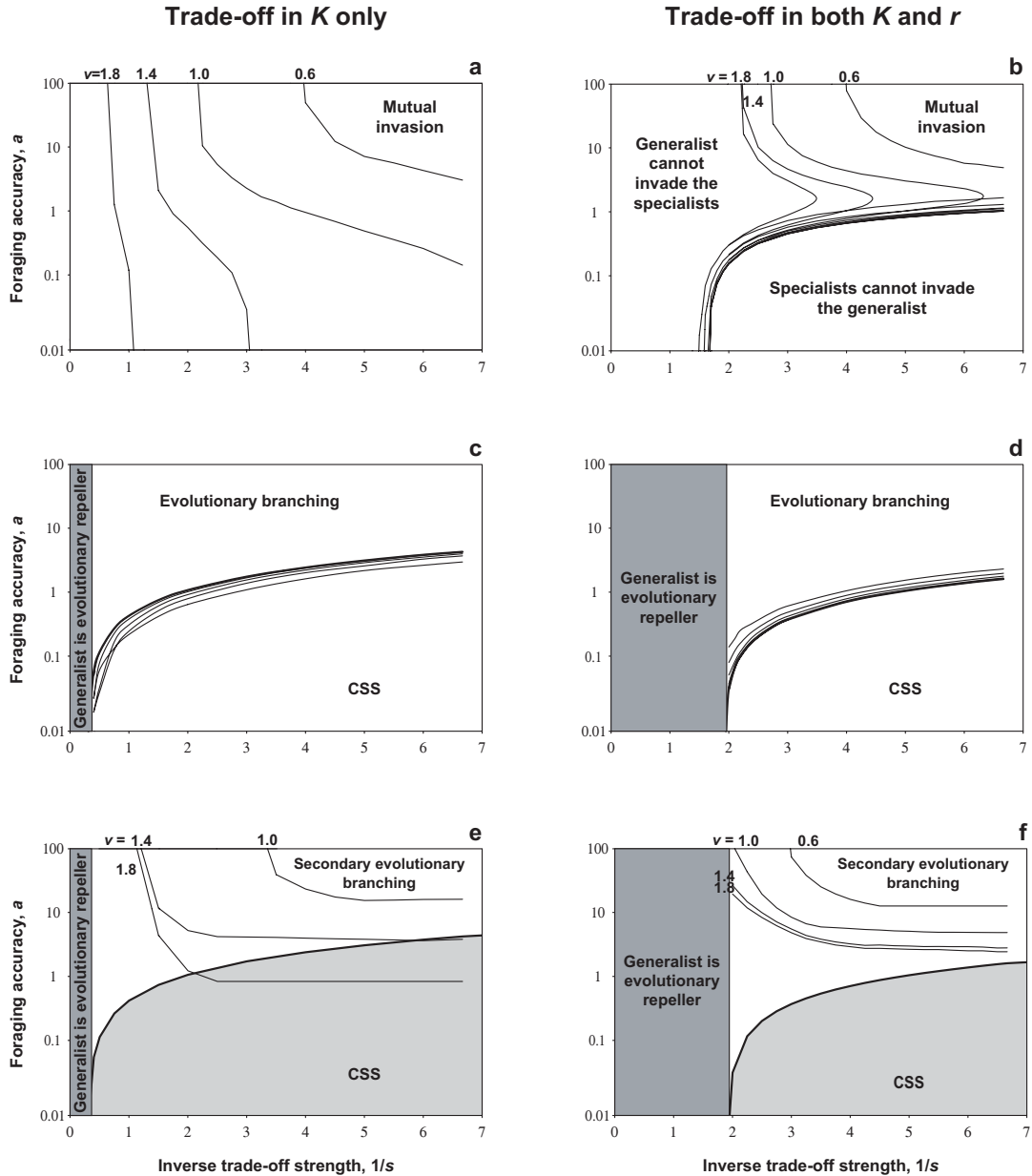


Figure 4 Conditions for ecological and evolutionary coexistence of specialists and generalists, with the trade-off in K only (left column) or in both K and r (right column). (a-b) Critical combinations of foraging accuracy a and trade-off strength s for the generalist to invade the community of two extreme specialists and *vice versa*. Coexistence of specialists and generalists is possible in the mutual invasibility areas (to the right and above the curves indicating various levels of temporal variability: $v = 0.6$, $v = 1.0$, $v = 1.4$, $v = 1.8$). Note that the extreme specialists can always invade the generalist population in panel a (as explained in the text). (c-d) Critical combinations of foraging accuracy a and trade-off strength s to result in specialization through evolutionary branching or, alternatively, in a continuously stable generalist strategy (CSS). (c) Thick curve: no variability ($v = 0$); curves below, from top to bottom $v = 0.2$, $v = 0.6$, $v = 1.0$, $v = 1.4$, $v = 1.8$. (d) Thick curve: no variability ($v = 0$); other curves, from top to bottom $v = 1.8$, $v = 1.4$, $v = 1.0$, $v = 0.6$, $v = 0.2$. (e-f) Critical combinations of foraging accuracy a and trade-off strength s for the existence of an interior pair of specialist singular strategies that are branching points (above the curves), leading to secondary branching and hence to the coexistence of specialists and generalists through gradual evolution. The thick curves delineating the grey areas indicate, according to panels (c-d), where primary evolutionary branching cannot happen in the absence of temporal variability. Other parameter values as in figure 3.

also invade the community of specialists, provided the temporal variability in the environment is sufficiently high ($v_1 = v_2 \geq 0.2$). In contrast, with the trade-off in both K and r , the potential for coexistence is much more restricted (figure 4b). Specifically, there are many settings (roughly, whenever foraging accuracy is below 1) in which the specialists cannot invade a population of generalists.

The reason for this difference lies in the way trade-offs involving carrying capacities and growth rates translate into trade-offs in fitness. With the trade-off in K only, fitness approaches minus infinity for an extreme specialist in the habitat it is not adapted to, because a carrying capacity approaching zero means instant death. Accordingly, K appears in the denominator of fitness (see Appendix). Hence, for any degree of foraging accuracy, an extreme specialist will always choose to live in the habitat it is adapted to. Because the generalist has a lower carrying capacity for that habitat, the invading extreme specialist will always attain a positive growth rate. With the trade-off in both K and r (i.e., between reproduction ratios in the two habitats) fitness does not reduce so drastically for an extreme specialist in the unfavorable habitat (see Appendix). This results in a wide range of settings in which an extreme specialist cannot invade a population of generalists because (given the strength of the trade-off) the specialist cannot forage accurately enough for the habitat it is specialized on. This large difference in coexistence between the two trade-off structures remains when we consider less extreme specialists, which never experience a fitness of minus infinity: even with an efficiency of 0.1 in one habitat (instead of 0), a specialist still has such a low fitness in that habitat that, through its foraging behavior, it concentrates completely on the habitat it is adapted to.

In their analysis, Wilson and Yoshimura (1994) considered a trade-off in K only. They found coexistence of specialists and generalists even (a) for moderately low variation in carrying capacities, (b) for a wide range of efficiency of the generalist (between 0.99 and 0.4, when variability is high), and (c) for moderate departures from optimal foraging ($g \geq 0.75$, i.e., up to a quarter of the individuals distributed randomly across habitats). Our findings for a trade-off in K only (figure 4a) agree with these earlier results. We can thus conclude that, while the choice of foraging rule (discontinuous or continuous) is immaterial for the ecological coexistence of specialists and generalists, the assumed trade-off structure has a dramatic impact on the potential for ecological coexistence.

Coexistence under gradual evolution

In this section we analyze the effects of temporal variability and foraging accuracy on the evolution of specialization, thus establishing how the coexistence of specialists and generalists can come about through gradual evolution. We start by examining the baseline case with random foraging and without temporal variation. Taking advantage of the resulting overview regarding the impact of the trade-off structure, we then explore the effects of non-random foraging and temporal variability.

As we explained above, the discontinuous foraging rule suggested by Wilson and Yoshimura (1994) involves an unrealistic jump in foraging behavior: phenotypes arbitrarily close to the resident phenotype are assumed to detect the diminutive

differentials in their relative fitness unflinchingly and to select their habitat accordingly. As long as the considered phenotypes are kept sufficiently apart, this shortcoming is not critical. Gradual evolution, however, is driven by competition between similar phenotypes and thus turns out to be structurally unstable when the discontinuous foraging rule is applied (results not shown). Since biologically meaningful conclusions must never be based on structurally unstable models, we only use the continuous foraging rule for the evolutionary analyses below.

The crucial importance of trade-off structure for the evolution of specialization

As a starting point for the evolutionary analysis, we consider the baseline case without temporal variability ($v_1 = v_2 = 0$) and with random foraging ($a = 0$). Under these conditions, the model has a one-dimensional feedback loop (through total population size), which implies that evolution is optimizing (Mylius and Dieckmann 1995; Meszena *et al.* 2001; Meszena and Metz 2003).

When the trade-off acts on K only, even the baseline case offers some surprises. For rather weak trade-offs ($s < s_1 < 1$), evolution converges to the generalist strategy (figure 3, bottom left). This is just what would be expected from classical theory (e.g., Levins 1962, 1968; Lawlor and Maynard Smith 1976). However, for moderately weak or moderately strong trade-offs ($s_1 < s < s_2$) the system becomes evolutionarily tristable (figure 3, bottom middle): depending on the initial phenotype, the population evolves either to full specialization on either habitat or to full generalization. When the trade-off is strengthened well beyond the linear case ($1 < s_2 < s$), the tristability disappears, giving way to the traditionally expected bistability: there is now always selection for increased specialization on the habitat the initial phenotype is best adapted to (figure 3, bottom right), which is in line with classical theory again.

The pattern summarized above is based on a pitchfork bifurcation occurring at $s = s_2$: when the trade-off strength is lowered beyond that threshold, the generalist repeller (figure 3, bottom right) is replaced by a generalist attractor surrounded by two repellers (figure 3, bottom middle). As s is further decreased, these new repellers move apart, until they collide, at $s = s_1$, with the boundaries of trait space. For trade-offs weaker than the latter threshold, only the generalist attractor remains (figure 3, bottom left). (When habitats are asymmetric, $K_1 \neq K_2$, the pitchfork bifurcation at $s = s_2$ is replaced by a fold bifurcation, and the two evolutionary repellers collide with the boundaries of trait space at two different trade-off strengths, $s = s_{10}, s_{11}$.) In a further departure from classical theory, the thresholds for the strength of the trade-off at which the described transitions occur depend on the value of the intrinsic growth rate r . In particular, the generalist strategy is always selected against, and hence tristability gives way to bistability, when $s > s_2 = 1/(r - 1)$ (see Appendix).

When the trade-off is in both K and r , results are more similar to the classical theory in that there are only two evolutionary regimes: for this trade-off structure, we have not found any tristability. Evolution converges to the generalist when $r < (1/s - 1)2^s$ (see Appendix). To satisfy this condition for positive r , s must be smaller than 1, $s < s_3 < 1$.

Notice, however, that in contrast to classical theory a moderately weak trade-off, $s_3 < s < 1$, will still select for full specialization. Also, the evolutionary outcome again depends on the growth rate r .

Effects of temporal variability and foraging behavior on the evolution of specialization

We now move to the general case, first considering foraging behavior and then temporal variability as well. The analysis follows the outline in figure 2.

Our investigations show that the only attracting singular point of single-species evolution is the generalist strategy. It is therefore only at this point that gradual evolution can transform the single-species community into a two-species community. If a resident population of generalists cannot be invaded by nearby strategies, the generalist strategy is continuously stable (a CSS; Eshel 1983; see figure 3 bottom left); if, instead, such invasion is possible, the generalist strategy is an evolutionary branching point (an EBP; see figure 3 top row). Investigating the evolutionary stability of the generalist strategy with foraging behavior but without temporal variability, we find that for both trade-off structures the generalist strategy changes from a CSS to an EBP when foraging accuracy is increased beyond a threshold (figure 4c,d; note that each point in these panels corresponds to a PIP as shown in figure 3). When the trade-off acts only on K , there is – for each value of the intrinsic growth rate r – a linear relationship between the foraging accuracy and the strength of the trade-off for which the CSS-EBP transition takes place (see Appendix). Also when the trade-off acts on both K and r , such a relationship exist, but for this trade-off structure the relation is nonlinear (see Appendix).

Our numerical results show that the boundary of generalist evolutionary stability is only slightly affected by considering different levels of temporal variability in the carrying capacities ($v_1 = v_2$ ranging from 0.2 to 1.8). Therefore, up to this stage in the analysis, temporal variability hardly affects the evolutionary outcome (see, e.g., figure 3). However, again there is a remarkable difference between the two trade-off structures (figure 4c,d). When the trade-off is in both K and r , higher temporal variability slightly increases the critical foraging accuracy (figure 4d). This is what we expected, based on the traditional notion that higher variability favors the generalist. By contrast, with the trade-off in K only, the reverse is true: higher temporal variability causes the generalist's evolutionary stability to be lost already at a lower foraging accuracy (figure 4c).

For the parameter values that allow for evolutionary branching in a single-species community, we numerically analyzed gradual evolution in the resulting two-species community. For the resulting evolutionary attractors, we again assessed whether evolutionary branching can occur, As explained above, such secondary evolutionary branching could transform the two-species community into a four-species community (figure 2c,d). In absence of temporal variability, evolution always leads to two extreme specialists – transitions to higher degrees of polymorphism are then precluded (figure 4e,f). With temporal variability, the outcome of gradual two-species evolution is also

often a pair of extreme specialists. Only when temporal variability is high and foraging accuracy is very high, we find singular points of two-species evolution inside the trait space of our model; these points always are secondary branching points (figure 4e,f).

For the parameter values that allow for secondary evolutionary branching, we numerically analyzed gradual evolution in the resulting four-species community. For the parameter space considered in figure 4, these four-species communities always collapsed to three-species communities involving two extreme specialists and one generalist, as sketched in figure 2d. That is to say, two of the four species evolved towards extreme specialization, and the other two species evolved towards the generalist strategy whereby one of the latter went extinct.

In summary, gradual evolution in this model can result in coexistence of specialists and generalists, but only for consumers whose foraging accuracy is very high and who live in an environment affected by strong temporal variability. In this limited parameter range, even when one or several species accidentally go extinct, evolution is predicted to reconstitute the coexistence of specialists and generalist.

Coexistence under gradual evolution after generalist immigration

Finally, we investigate the evolutionary stability of ecologically stable three-species communities. Evolutionarily stability of the community of specialists and generalist is already ensured in the parameter region where we predict secondary evolutionary branching. However, the region of parameter space where the generalist can invade a community of two extreme specialists is larger. It is quite possible that the generalist, after invading, is also able to stably coexist with the two extreme specialists on an evolutionary time scale. One possibility for such an invasion scenario is that a generalist phenotype is created through a mutation with large effect. However, genes of large effect leading to viable phenotypes do not commonly occur (for an exception, see De Jong et al. 2000). A more likely possibility therefore is invasion of a generalist into the two-specialist community by immigration from another geographic location.

For the parameter region where the generalist can invade a community of two extreme specialists (figure 4a,b), we numerically assessed whether this invasion leads to selection on the specialists to become generalist. We find that, over the entire parameter space considered, invasion of the generalist always results in stronger divergent selection on the specialists (which must remain inconsequential since the specialists are already maximally specialized). Hence, the three-species community is indeed always evolutionarily stable once created through invasion of the generalist.

We can thus conclude that, after immigration, the stable coexistence of specialists and generalist can be attained under a wider range of ecological settings than with gradual evolution alone (compare figure 4a,b with 4e,f) – allowing for community construction through migration relaxes the conditions for stable coexistence. Note that the extra parameter region allowing for coexistence is small when the trade-off acts on both K and r (compare figure 4b with 4f) because ecological coexistence is already restricted in this case, but it is much larger when the trade-off acts on K only (compare figure 4a with 4e) because in that case ecological coexistence is widely possible.

Discussion

In this article, we have shown that the potential for coexistence between specialists and generalists crucially depends on the specific trade-off structure assumed (figure 4). Ecological coexistence is much more feasible with the trade-off in K only than with the trade-off in K and r . However, under gradual evolution without immigration, conditions for the establishment of specialist-generalist coexistence become equally restricted. Specifically, coexistence of two specialists and one generalist is only attainable through gradual evolution if foraging accuracy is very high and if temporal variability is strong. When the generalist can invade a community of two specialists through immigration (or through a mutation of large effect), conditions for the evolutionarily stable coexistence of specialists and generalists are less restricted when the trade-off acts on K only, but not when the trade-off acts on both K and r . Considerable environmental variation still remains necessary. Overall, specialist-generalist coexistence turns out to be less likely than a purely ecological analysis (Wilson and Yoshimura 1994) had previously suggested.

Limitations of our study

This article is based on a relatively simple model; three of the simplifications we had to make are scrutinized below. First, we have not explicitly modeled the dynamics of resources determining the carrying capacities in the two considered habitats. This is not critical as long as resource dynamics occur on a shorter time scale than consumer dynamics; resources can then be assumed to be in a quasi-steady state depending on consumer abundances. Since the discrete-time population dynamics investigated here would often operate on an annual basis, within-season equilibration of resources may indeed be likely. However, including resource dynamics may sometimes result in non-equilibrium dynamics, creating internally driven temporal variability for the consumer. This could have interesting ecological and evolutionary implications, as discussed in the next section.

Second, one may prefer to investigate trade-offs between ecological parameters that are more mechanistic than the intrinsic growth rates and carrying capacities considered in this study. A wide range of specific studies will then be required. Although the Ricker model can be derived from individual-based descriptions, it will often be difficult to decide on the specific trait(s) traded off between habitats. As shown by Matessi and Gatto (1984), descriptions of r and K can be derived from resource-consumer models using the quasi-steady state assumption. For example, there could be a trade-off between attack rates on one resource and the other (or between conversion efficiencies of resource biomass into consumer biomass): Matessi and Gatto (1984) show that this results in a trade-off acting on both K and r , just as described in eq. (4). They also find, for various model formulations, that K is linearly related to r , again as described in eq. (4).

Third, we have assumed that consumers can partially attain an ideal free distribution (limited by their foraging accuracy), without modeling the dynamics of foraging behavior in detail. If foraging behavior occurs at the same time scale as population

dynamics, complex dynamics may result (Abrams 1999). However, the Ricker model assumes discrete time steps, whereas foraging behavior normally takes place on a much shorter time scale. Alternatively, consumers may use various other foraging strategies, such as fixed preference, and ideal free foragers then do not necessarily perform best (e.g., Fryxell 1997, Richards and De Roos 2001). Specialists and generalists may differ in the foraging strategy they adopt. It is presently unclear how such a suite of different foraging strategies would affect coexistence.

Challenges for future study

Our results have revealed surprising effects of the trade-off structure on the evolution of specialization, emphasizing two points. First, theoretical predictions based on a trade-off in fitness (e.g., Levins 1962, 1968) do not easily carry over to models (or, for that matter, experimental systems) where such a trade-off is assumed in a fitness component such as carrying capacity. Recently, Rueffler et al. (2003) have extended Levins' (1962, 1968) 'fitness set' approach to include frequency-dependent selection, presenting a framework which can deal with all possible types of trade-offs. Their results show that the way the trade-offs enter the fitness function (i.e., which components of fitness are really traded off) crucially determines the evolutionary dynamics and predictions – including selection for specialists under a weak trade-off, or selection for generalists under a strong trade-off. Second, we have shown that models (or, again, experimental systems) with trade-offs in one or several fitness components that do not linearly translate into a fitness trade-off can yield more complex predictions for the evolution of specialization than previously thought, including evolutionary tristability. Since it is generally very difficult to measure the fitness of individuals in experimental systems, evolutionary biologists usually restrict their experiments to measuring one or several components of fitness. For instance, in insect-plant biology these are oviposition rate, juvenile mortality rate, juvenile body mass increase or rate of development (i.e., traits affecting *per capita* reproduction rate; see, e.g., Futuyma and Moreno 1988; Jaenike 1990) – but typically never the maximum number of individuals a habitat can sustain (i.e., carrying capacity).

It is an interesting open question to assess which additional assumptions are needed to cause the loss of evolutionary robustness of three-species communities comprising of two specialists and one generalist. One such scenario is that the two specialist species are selected to become less specialized, to a degree where they “squeeze out” the generalist species. We suggest that separate trade-offs for both *per capita* reproduction and maximum population size – and thus more complex trade-offs in r and K than we considered – might be necessary and sufficient. Such trade-offs will translate into more complex fitness gradients which might lead to a situation where invasion of a generalist species may actually result in evolution of the specialists towards generalization, and the eventual extinction of the generalist. Another scenario is that the two specialist species are selected to become increasingly specialized, to a degree where they are outcompeted by the generalist species. This scenario seems to be more likely, since the effect of the generalist species is to dampen the variation in growth rate of the

specialists (by occupying a habitat in higher numbers if it is relatively empty and the other habitat is relatively full). This dampening effect favors increased specialization in our model, but does not lead to extinction. In a fully stochastic individual-based model, extinction may occur over a wider area of parameter space than in our current model (where population growth is deterministic). For instance, the generalist species may force the two specialist species to forage only in the habitat they are specialized on. If the density of a specialist species is low, and carrying capacity is low for several generations, this species may readily go extinct. When, in addition, coexistence can be restored relatively easily through the immigration of specialist and generalist species, our model predicts continuous change in both the number of species and the degree of specialization in the system over time – due to a complex interplay of ecological and evolutionary dynamics.

Temporal variability in model systems can be internally driven (instead of externally imposed), when the dynamics consist of sustained cycles or deterministic chaos (May 1973), which can also promote coexistence (Armstrong and McGehee 1976b, 1980; Adler 1990; Huisman and Weissing 1999). In the Ricker model for one population living on a single resource, unstable population dynamics ensue for high values of the intrinsic growth rate r (cycles for $r > 2$, chaos for $r > 2.692$; May 1975). Choosing r in our model such that the generalist species would have stable population dynamics, but a specialist species would undergo cycles (or maybe even show chaotic behavior), promises to yield complex evolutionary dynamics. A generalist species would then create a stable environment that may result in evolutionary branching leading to two specialized species. However, these would create an unstable environment which subsequently allows a generalist species to coexist, if it is able to immigrate or arise from the odd major-effect mutation. This leads to the same questions as discussed above with regard to the evolutionary robustness of specialist-generalist coexistence. Hence, studying the evolutionary dynamics of coexistence in systems with internally driven fluctuations promises to give intriguing and potentially counterintuitive new insights.

References

- Abrams, P. 1984. Variability in resource consumption rates and the coexistence of competing species. *Theoretical Population Biology* 25: 106-124.
- Abrams, P.A. 1999. The adaptive dynamics of consumer choice. *American Naturalist* 153: 83-97.
- Abrams, P.A., and X. Chen. 2002. The evolution of traits affecting resource acquisition and predator vulnerability: character displacement under real and apparent competition. *American Naturalist* 160: 692-704.
- Adler, F. 1990. Coexistence of two types on a single resource in discrete time. *Journal of Mathematical Biology* 28: 695-713.
- Anderlies, J.M., and B.E. Beisner. 2000. Fluctuating environments and phytoplankton community structure: a stochastic model. *American Naturalist* 155: 556-569.
- Armstrong, R.A., and R. McGehee 1976a. Coexistence of species competing for shared resources. *Theoretical Population Biology* 9: 317-328.
- Armstrong, R.A., and R. McGehee 1976b. Coexistence of two competitors on one resource. *Journal of Theoretical Biology* 56: 499-502.
- Armstrong, R.A., and R. McGehee 1980. Competitive exclusion. *American Naturalist* 115: 151-170.
- Brown, J.S. 1989. Coexistence on a seasonal resource. *American Naturalist* 133: 168-182.
- Brown, J.S., and N.B. Pavlovic. 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evolutionary Ecology* 6: 360-382.
- Case, T.J. 1981. Niche packing and coevolution in competition communities. *Proceedings of the National Academy of Sciences of the USA* 78: 5021-5025.
- Chesson, P.L. 1985. Coexistence of competitors in spatially and temporally varying environments: a closer look at the combined effects of different sorts of variability. *Theoretical Population Biology* 28: 263-287.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.
- Chesson, P.L., R.R. Warner 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117: 923-943.
- De Jong P.W., H.O. Frandsen, L. Rasmussen, and J.K. Nielsen 2000. Genetics of resistance against defences of the host plant *Barbarea vulgaris* in a Danish flea beetle population. *Proceedings of the Royal Society London B* 267: 1663-1670.
- Dieckmann, U. 1997. Can adaptive dynamics invade? *Trends in Ecology and Evolution* 12: 128-131.
- Dieckmann, U. and R. Law. 1996. The dynamical theory of coevolution: A derivation from stochastic ecological processes. *Journal of Mathematical Biology* 34: 579-612.

- Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. *Nature* 400: 354-357.
- Dieckmann, U. and R. Law. 2000. Relaxation projections and the method of moments. In: *The geometry of ecological interactions* (eds. Dieckmann, U, R. Law, and J.A.J. Metz). Cambridge: Cambridge University Press. p 450.
- Doebeli, M., and U. Dieckmann. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *American Naturalist* 156: S77-S101.
- Doebeli, M., and U. Dieckmann. 2003. Speciation along environmental gradients. *Nature* 421: 259-264.
- Drossel, B., and A. McKane. 1999. Ecological character displacement in quantitative genetic models. *Journal of Theoretical Biology* 196: 363-376.
- Drossel, B., and A. McKane. 2000. Competitive speciation in quantitative genetic models. *Journal of Theoretical Biology* 204: 467-478.
- Eshel, I. 1983. Evolutionary and continuous stability. *Journal of Theoretical Biology*. 103: 99-111.
- Fretwell, S.D. and H.L. Lucas Jr.. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36.
- Fryxell, J.M. 1997. Evolutionary dynamics of habitat use. *Evolutionary Ecology* 11: 687-701.
- Futuyma, D.J., and G. Moreno 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* 19: 207-233.
- Geritz S.A.H., J.A.J. Metz, É. Kisdi, and G. Meszéna .1997. Dynamics of adaptation and evolutionary branching. *Physical Review Letters* 78: 2024–2027.
- Geritz, S.A.H., É. Kisdi, G. Meszéna, and J.A.J. Metz. 1998. Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12: 35-57.
- Geritz, S.A.H., and É. Kisdi. 2000. Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proceedings of the Royal Society of London B, Biological Sciences* 267: 1671-1678.
- Gyllenberg, M., K. Parvinen, and U. Dieckmann. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *Journal of Mathematical Biology* 45: 79-105.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131: 1292-1298.
- Huisman, J., and F.J. Weissing. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402: 407-410.
- Hutchinson, G.E. 1961. The paradox of the plankton. *American Naturalist* 95: 137-145.
- Jaenike, J. 1990. Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics* 21: 243-273.

- Kisdi, É. 2002. Dispersal: risk spreading versus local adaptation. *American Naturalist* 159: 579-596.
- Koch, A. L. 1974. Coexistence resulting from an alternation of density dependent and density independent growth. *Journal of Theoretical Biology* 44: 373-386.
- Kotler, B.P., and J.S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* 19: 281-307.
- Lawlor, L.R., and J. Maynard Smith. 1976. The coevolution and stability of competing species. *American Naturalist* 110: 79-99.
- Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. *American Naturalist* 96: 361-373.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton.
- Levins, R. 1979. Coexistence in a variable environment. *American Naturalist* 114: 765-783.
- MacArthur, R.H., and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the USA* 51: 1207-1210.
- MacArthur, R.H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. *American Naturalist* 101: 377-385.
- Matessi, C., and M. Gatto. 1984. Does K-selection imply prudent predation? *Theoretical Population Biology* 25: 347-363.
- Matessi, C., A. Gimelfarb, and S. Gavrilets. 2001. Long term buildup of reproductive isolation promoted by disruptive selection: how far does it go? *Selection* 2: 41-64.
- Matsuda, H. 1985. Evolutionarily stable strategies for predator switching. *Journal of Theoretical Biology* 115: 351-366.
- May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton: Princeton University Press.
- May, R.M. 1975. Biological populations obeying difference equations: stable points, stable cycles, and chaos. *Journal of Theoretical Biology* 51: 511-524.
- May, R.M., and R.H. MacArthur. 1972. Niche overlap as a function of environmental variability. *Proceedings of the National Academy of Sciences of the USA* 69: 1109-1113.
- McPeck, M.A. 1996. Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. *American Naturalist* 148: S124-S138.
- Meszéna, G., É. Kisdi, U. Dieckmann, S.A.H. Geritz, and J.A.J. Metz 2001. Evolutionary optimisation models and matrix games in the unified perspective of adaptive dynamics. *Selection* 2: 193-210.
- Meszéna, G., and J.A.J. Metz 2003. Species diversity and population regulation: the importance of environmental feedback dimensionality. In: *Elements of Adaptive Dynamics* (eds. Dieckmann, U., and J.A.J. Metz) Cambridge: Cambridge University Press, in press.

available as IIASA Studies in Adaptive Dynamics IR-99-045 at <http://www.iiasa.ac.at/Research/ADN/Series.html>

- Metz, J.A.J., R.M. Nisbet, and S.A.H. Geritz. 1992. How should we define 'fitness' for general ecological scenarios? *Trends in Ecology and Evolution* 7: 198-202.
- Metz, J.A.J., S.A.H. Geritz, G. Meszéna, F.J.A. Jacobs, and J.S. van Heerwaarden. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: *Stochastic and Spatial Structures of Dynamical Systems* (eds: Van Strien, S.J., and S.M. Verduyn Lunel), Elsevier Amsterdam, The Netherlands, pp. 183-231.
- Morris, D.W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology* 77: 2352-2364.
- Mylius, S.D., and O. Dieckmann. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. *Oikos* 74: 218-224.
- Nisbet, R.M., E. McCauley, A.M. de Roos, W.W. Murdoch, and W.S.C. Gurney. 1991. Population-dynamics and element recycling in an aquatic plant herbivore system. *Theoretical Population Biology* 40: 125-147.
- Parvinen, K. 2002. Evolutionary branching of dispersal strategies in structured metapopulations. *Journal of Mathematical Biology* 45: 106-124.
- Parvinen, K., U. Dieckmann, M. Gyllenberg and J.A.J. Metz. 2003. Evolution of dispersal in metapopulations with local density dependence and demographic stochasticity. *Journal of Evolutionary Biology* 16: 143-153.
- Richards, S.A., R.M. Nisbet, W.G. Wilson, and H.P. Possingham. 2000. Grazers and diggers: exploitation competition and coexistence among foragers with different feeding strategies on a single resource. *American Naturalist* 155: 266-279.
- Richards, S.A., and A.M. de Roos. 2001. When is habitat assessment an advantage when foraging? *Animal Behaviour* 61: 1101-1112.
- Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology* 62: 327-335.
- Rosenzweig, M.L. 1987. Habitat selection as a source of biological diversity. *Evolutionary Ecology* 1: 315-330.
- Roughgarden, J. 1972. Evolution of niche width. *American Naturalist* 106: 683-718.
- Royama, T. 1992. *Analytical Population Dynamics*. London: Chapman & Hall. pp. 140-165.
- Rueffler, C., T.J.M. van Dooren, and J.A.J. Metz. 2003. Adaptive walks on changing landscapes: Levins' approach revised. *Theoretical Population Biology*, in press.
- Stewart, F.M., and B.R. Levin. 1973. Partitioning of resources and the outcome of interspecific competition: a model and some general considerations. *American Naturalist* 107: 171-198.
- Sumpter, D.J.T., and D.S. Broomhead. 2001. Relating individual behaviour to population dynamics. *Proceedings of the Royal Society London B* 268: 925-932.

- Taper, M.L., and T.J. Case. 1985. Quantitative genetic models for the coevolution of character displacement. *Ecology* 66: 355-371.
- Taper, M.L., and T.J. Case. 1992a. Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* 46: 317-333.
- Taper, M.L., and T.J. Case. 1992b. Coevolution among competitors. *Oxford Surveys in Evolutionary Biology* 8: 63-109.
- Van Dooren, T.J.M. 2000. The evolutionary dynamics of direct phenotypic overdominance: emergence possible, loss probable. *Evolution* 54: 1899-1914.
- Van Tienderen, P.H., and G. de Jong. 1986. Sex ratio in the haystack model: polymorphism may occur. *Journal of Theoretical Biology* 122: 69-81.
- Wilson, D.S., and J. Yoshimura. 1994. On the coexistence of specialists and generalists. *American Naturalist* 144: 692-707.
- Wilson, W.G., and S.A. Richards. 2000. Evolutionarily stable strategies for consuming a structured resource. *American Naturalist* 155: 83-100.