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-05-016**

Understanding Mutualism When There is Adaptation to the Partner

Claire de Mazancourt (c.mazancourt@imperial.ac.uk)
Michel Loreau (loreau@ens.fr)
Ulf Dieckmann (dieckmann@iiasa.ac.at)

Approved by

Leen Hordijk
Director, IIASA

March 2005

IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 90

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, Diekmann 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 Interacations.* 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). Proceedings of the Royal Society of London Series B-Biological Sciences, 271: 415-423 (2004).

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). American Naturalist 163: 709-725 (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). American Naturalist 163: 518-531 (2004).

No. 81 Ernande B, Dieckmann U: *The Evolution of Phenotypic Plasticity in Spatially Structured Environments: Implications of Intraspecific Competition, Plasticity Costs, and Environmental Characteristics.* IIASA Interim Report IR-04-006 (2004). Journal of Evolutionary Biology 17 (3): 613-628 (2004).

No. 82 Cressman R, Hofbauer J: *Measure Dynamics on a One-Dimensional Continuous Trait Space: Theoretical Foundations for Adaptive Dynamics.* IIASA Interim Report IR-04-016 (2004).

No. 83 Cressman R: *Dynamic Stability of the Replicator Equation with Continuous Strategy Space.* IIASA Interim Report IR-04-017 (2004).

No. 84 Ravigné V, Olivieri I, Dieckmann U: *Implications of Habitat Choice for Protected Polymorphisms.* IIASA Interim Report IR-04-005 (2004). Evolutionary Ecology Research 6: 125-145 (2004).

No. 85 Nowak MA, Sigmund K: *Evolutionary Dynamics of Biological Games.* IIASA Interim Report IR-04-013 (2004). Science 303: 793-799 (2004).

No. 86 Vukics A, Asbóth J, Meszéna G: *Speciation in Multidimensional Evolutionary Space.* IIASA Interim Report IR-04-028 (2004). Physical Review E 68 4 (2003).

No. 87 de Mazancourt C, Dieckmann U: *Trade-off Geometries and Frequency-dependent Selection.* IIASA Interim Report IR-04-039 (2004).

No. 88 Cadet CR, Metz JAJ, Klinkhamer PGL: *Size and the Not-So-Single Sex: disentangling the effects of size on sex allocation.* IIASA Interim Report IR-04-084 (2004). American Naturalist, 164: 779-792 (2004).

No. 89 Rueffler C, van Dooren TJM, Metz JAJ: *Adaptive Walks on Changing Landscapes: Levins' Approach Extended.* IIASA Interim Report IR-04-083 (2004). Theoretical Population Biology, 65: 165-178 (2004).

No. 90 de Mazancourt C, Loreau M, Dieckmann U: *Understanding Mutualism When There is Adaptation to the Partner.* IIASA Interim Report IR-05-016 (2005).

Issues of the IIASA Studies in Adaptive Dynamics series can be obtained at www.iiasa.ac.at/Research/ADN/Series.html or by writing to adn@iiasa.ac.at.

Contents

Understanding mutualism
when there is adaptation to the partner

Claire de Mazancourt[1], Michel Loreau[2], and Ulf Dieckmann[3]

[1]**Corresponding author**. Department of Biological Sciences and NERC Centre for Population Biology,
Imperial College London, Silwood Park campus, Ascot, Berkshire, SL5 7PY United Kingdom
tel: +44 207 59 42 222
fax: +44 207 59 42 339
email: c.mazancourt@imperial.ac.uk

[2] Laboratoire d'Ecologie, UMR 7625, Ecole Normale Supérieure, 46, rue d'Ulm, F-75230 Paris Cedex
05, France
tel: +33 1 44 32 37 09
fax: +33 1 44 32 38 85
email: loreau@ens.fr

[3] Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361
Laxenburg, Austria
tel: +43 2236 807 386
fax: +43 2236 71313
email: dieckmann@iiasa.ac.at

Running title: mutualism and adaptation

Type of article: Essay review in Journal of Ecology

Summary

1- A mutualism is a mutually beneficial interaction between individuals of two species. Using the ongoing debate about plant-herbivore interactions as a springboard, we show that different measures of benefit arise depending on whether adaptation within the mutualism is considered.

2- A species' *proximate response* measures the short-term effect of addition or removal of the partner species, without allowing for any adaptation. We define a *proximate mutualism* as an interaction in which removal of each partner results in a decreased performance of the other, i.e., both species show a positive proximate response to the presence of the partner.

3- Almost all empirical studies use the proximate response criterion. However, a proximate mutualism might only reflect evolved dependence (implying that, through adaptation to the partner, a species has lost its ability to perform well without the partner). Therefore, some authors discard the proximate definition of mutualism, to prefer what we define as ultimate mutualism.

4- A species' *ultimate response* measures the long-term effect of adding or removing the partner species, thus allowing for the focal species to adapt to the absence or presence of its partner. We define an *ultimate mutualism* as an interaction in which each partner could never have performed as well without the other, even if it was adapted to the absence of the partner. In other words, a mutualism is called ultimate if both species show a positive ultimate response to the presence of the partner. Despite the conceptual attractiveness of this definition, ultimate responses are difficult to measure, rendering the notion of ultimate mutualism operationally problematic.

5- Using examples from the literature, we demonstrate the counterintuitive result that even obligate mutualisms are not necessarily ultimate mutualisms.

6- Finally, we define mutualistic evolution as evolution of a trait that is costly to the bearer but beneficial to its partner in a proximate mutualism and show that, paradoxically, neither proximate nor ultimate mutualisms necessarily result in mutualistic evolution.

7- We conclude that the proximate response is the only criterion for mutualism that is operational in empirical research. A possible key mechanism that can generate a benefit in such mutualisms, evolved dependence, has to be further investigated empirically and seriously taken into account in theoretical studies, if our understanding of mutualism is to evolve.

8- More than a semantic case of hair splitting, our paper reveals a naive view of mutualism that needs revision. We need to recognise that in most if not all interactions now considered as mutualisms, measured benefits to at least one partner are likely to be partly or even completely the result of adaptation to the partner, leading to evolved dependence, rather than to what we would like to consider as "real" or ultimate benefits.

Keywords: adaptation, coevolution, evolved dependence, mutualism, overcompensation, plant-herbivore interaction, proximate response, ultimate responseisms.

Introduction

Mutualisms are widespread in nature (Boucher et al., 1982; Bronstein, 1994b; Menge, 2000; Richardson et al., 2000; Stachowicz, 2001). Although about a quarter of ecological studies are devoted to mutualism (Bronstein, 1994b), our understanding of and theoretical insights into this type of interaction are limited (Bronstein, 1994b). One factor that might critically contribute to this gap is an ambiguity in the concept of mutualism when there is, as is usual in a mutualistic interaction, adaptation to the partner species. Here we focus on an interaction in a given environment and ask how to determine whether or not it is mutualistic; of course, the same interaction might be classified differently in a different environment (conditional mutualism; see Box 1 and Bronstein, 1994a).

We would like to start with a short example to set the scene for our argument. Jeon (1972) witnessed the emergence of an obligate mutualism in the lab, evolving all the way from parasitism. *Amoeba discoides* was infected with bacteria that initially caused heavy mortality, small size, slow growth, and slow clone formation, and a high sensitivity to adverse conditions. The amoeba and the bacteria coevolved, and after 5 years of infection, the adverse effects of the bacteria had disappeared. Moreover, after this coevolution, neither the amoebae nor the bacteria would survive without the other. This interaction is thus a clear example of a mutualism: since both organisms need their partner to survive, they clearly derive a benefit from their partner's presence. However, is it possible that the amoeba would have been better off had the bacteria never been there? Does the bacterium provide a "real" benefit to the amoeba? Hence, should this interaction really be viewed as a mutualism?

In the following sections, we explain and define different criteria used to test for mutualism: proximate response, ultimate response, and mutualistic evolution. We show that there is a conflict between what is actually measured when testing for mutualism, resulting in what we call proximate mutualism, and what many of us would like a mutualism to mean, resulting in what we call ultimate mutualism. Each criterion presented here has been used previously by a number of different authors – yet these criteria have never been named, clearly defined, and properly contrasted. Filling this lacuna provides the platform for a thought-provoking discussion about what mutualism means. Several counterintuitive results will be demonstrated along the way.

This study is motivated by a debate about plant-herbivore interactions. Some plants have been shown to overcompensate, in the sense that their fitness was increased by herbivore damage. The controversy in the literature that ensued from this observation tried to clarify whether such a result implies that these plants actually benefit from herbivory, so that the plant–herbivore interaction would have to be considered mutualistic. After a general presentation of the ideas underlying this debate, we discuss specific applications as well as their broader implication for other systems. We suggest that effects like overcompensation should be taken as valid evidence that herbivory benefits plants. However, the mechanism that is likely to generate this benefit, evolved dependence, requires to be further investigated empirically and to be seriously taken into account in empirical and theoretical studies, if our understanding of mutualism is to evolve.

All key technical terms introduced in this study are defined in Box 1.

I. Theoretical basis

Proximate mutualism

Definition of proximate mutualism

One classical approach to test for mutualism experimentally is to evaluate the performance of a species before and after its partner has been removed, or has been kept at low density (Bender et al., 1984; Krebs, 1985; Schoener, 1983). This comparison defines what we call the *proximate response* of a species to the removal of its partner, and is the defining criterion for a *proximate mutualism* (Figure 1 and Box 1). It is important to stress that, in this definition, the performance of the *same genotype* (or group thereof) is compared with and without the partner species. The proximate response might depend on the genotype considered, and, notably, on its status of adaptation to the partner (Figure 1).

The proximate response criterion is used in most empirical studies of mutualisms. Bronstein (1994b), reviewing the underlying experiments, described them as follows: “mutualists were excluded or added… For example, many pollination studies examined plant success after all but a single visitor species were excluded (Herrera, 1987)… Nearly all experimental studies of plant-ant protector mutualisms involved excluding the ants in order to measure their benefit to the plant (Koptur & Lawton, 1988; Smiley, 1986).” Also mutualistic or parasitic effects of mycorrhizal associations or of leaf endophytes have been assessed by comparing plant proximate response, i.e., the performance of a plant genotype or population with and without these partners (Faeth & Sullivan, 2003; Klironomos, 2003).

Proximate mutualism can result from evolved dependence

However, an observed decrease of performance when a focal species’ partner is removed might result from the fact that the focal species was adapted to the presence of its partner, and had thus *compromised its ability to perform well in the partner's absence*. In the context of endosymbioses, such an effect has been called *evolved dependence* (Douglas & Smith, 1989).

It is important to emphasize that evolved dependence can occur independently of whether or not an association is obligate; it is likely to happen in any type of association where there is adaptation. Evolved dependence is in principle quantifiable as the performance difference between the genotype that is adapted to the partner's absence and the genotype that is adapted to its presence, both measured in the absence of the partner (Figure 1, Box 1). It comprises the cost of traits evolving as an adaptation to the partner's presence, as well as the "cost" of having lost some traits that were adaptive in the absence of the partner (the latter cost appears in quotes because it only is a cost when the partner is removed). Operationally, a very rough indicator of the expected degree of mutual adaptation is the length of time that partners have been in ecological contact with each other or, alternatively, the length of time these partners have been separated.

In conclusion, the proximate response of a genotype is bound to depend on its status of adaptation to the partner. A low performance when the partner is removed can occur simply because the genotype is not adapted to this situation: its low performance stems from evolved dependence. This is not the type of "real benefit" we have in mind when assessing a mutualistic interaction.

Ultimate mutualism

Definition of ultimate mutualism

To understand whether evolved dependence is responsible for an observed proximate mutualism between two species, or whether, instead, there is a "real benefit" from the interaction, it is important to introduce a second criterion for mutualism. Here we have to ask whether the focal species performs better than it would ever have without the other species. We thus have to consider the *ultimate response* of a species to its partner, measured by comparing the performance of *two different genotypes* (or groups thereof): the performance of the one genotype adapted to the partner, in the partner's presence, is compared to the performance of the other genotype adapted to the absence of the partner, in the partner's absence. This criterion, of course, is not without practical difficulties, which we will discuss in detail below. The criterion leads to defining an *ultimate mutualism* as an interaction in which each partner shows a positive ultimate response to the presence of the other (Figure 1, Box 1).

The proximate response of a population adapted to its partner is equal to its ultimate response plus evolved dependence. Therefore, if a population derives an ultimate benefit from a partner species, it is also likely to derive a proximate benefit from this interaction. However, the reverse is not true: a population adapted to the partner that shows a proximate benefit from the interaction might derive no ultimate benefit from the association whatsoever, if evolved dependence is the only cause of the proximate benefit.

The existence of *evolved dependence* is one reason for discrepancies between *proximate* and *ultimate responses*. Dependence of this sort is likely to be important for partners with a long history of coevolution, and we must thus expect some such interactions to be proximate but not ultimate mutualisms.

Accounting for ultimate responses in the literature

In studies of mutualism, a few authors adopted the ultimate response to measure the benefit of an interaction. Examples from the plant-herbivore literature are described below in the sections “*Theoretical argument for plant’s ultimate benefit*” and “*Measurement of plant’s ultimate responses*”.

Another example of an author defining mutualism based on ultimate responses is Roughgarden (1975) in a model for the evolution of a symbiosis between fish and anemones. Assuming the ancestral state of fish to be free-living, Roughgarden assessed the benefit of the symbiosis as the difference between the fitness of the free-living genotype and the fitness of the symbiotic genotype with an anemone. The model assumes a strong evolved dependence in the system: when the symbiotic genotype cannot find a host anemone, or when its host anemone dies, its reproductive output is much reduced.

Measurement of ultimate responses

Measuring ultimate responses requires tests both on a genotype that is adapted to the presence of the partner and on a genotype that is adapted to the absence of the partner. Since there is no point in defining quantities that are not measurable in practice, the status of adaptation to the partner must be assessed pragmatically. In particular cases, it would be impossible to assess whether adaptation had reached an evolutionary endpoint; these might not even exist (Dieckmann et al., 1995; Gomulkiewicz et al., 2000; Thompson & Cunningham, 2002). However, this should not prevent evaluation of an ultimate response based on the current status of adaptation, which can be very roughly assessed based on the length of coevolutionary history experienced by the partners. Note that in this context the strength of selection imposed by a species on its partner is likely to be more important that the length of their coevolutionary history, and would be a better proxy to the status of adaptation if it could be quantified. For assessing ultimate responses, four cases can be distinguished:

- We may have access to an ancestral state that is not adapted to the partner. Performance measurements for the two genotypes under the appropriate conditions can then be undertaken.
- The organism is fast evolving and viable without the partner, so that experimental adaptation to the partner’s absence can be selected for on a feasible timescale. Performance differences can then be measured as in the first case. Unfortunately, the population experimentally adapted to the partner’s absence might also inadvertently be subjected to other selective pressures, besides those arising from the partner’s absence.
- Even though there may be no access to a suitable ancestral state, there may yet exist separate populations of the focal organism with histories of evolution with and without the partner. Measurements can then be carried out comparing such populations, provided that sufficient replicates exist. This is not as satisfactory a situation as in the preceding cases, because other factors are likely to co-vary with the partner’s presence or absence.
- There may be no access to an ancestral state, the organism may not be viable without the partner, or, even if it is viable, its generation time may be too long for experimental adaptation to the partner’s absence to be feasible. Ultimate responses then cannot be measured. However, if there is sufficient genetic variation in the species, it may still be possible to search for genetic trade-offs between the focal species’ performance with and without the partner to establish indirect evidence for evolved dependence.

Douglas and Smith (1989) discuss in detail the difficulties of measuring ultimate responses in endosymbioses.

To summarize, the concept of ultimate mutualism is very satisfactory conceptually, but in many cases might prove unrealistic in terms of measurements. Unfortunately, some authors seem to accept only this definition of mutualism and discard any alternative based on proximate responses, thus apparently overlooking the difficulties of measuring ultimate responses as well as the fact that most empirical work has only measured proximate responses.

An obligate mutualism is not necessarily an ultimate mutualism

We would like to draw attention to the slightly counterintuitive fact that an obligate mutualism is not necessarily an ultimate mutualism. We presented the case described by Jeon (1972) in the introduction. *Amoeba discoides* was infected with a parasitic bacterium. After adaptation took place, the adverse effects of the bacteria had disappeared, suggesting a neutral ultimate response of the amoebae to the bacteria. Moreover, both organisms had become dependent on the other for survival, resulting in a mutualism that was both proximate and obligate. Importantly, however, the proximate benefit derived by the amoeba from the interaction was probably due to evolved dependence: the amoeba lost traits that made it adapted to the absence of the bacteria, and there is no evidence for the interaction providing an ultimate benefit to the amoeba.

Other examples involves *Wolbachia*, intracellular bacteria infecting a number of invertebrates. In arthropods, these bacteria are rarely found to be beneficial to their hosts and thus provide a striking example of selfish cytoplasmic elements. Despite physiological costs or even virulence, they are able to maintain themselves through induced modifications to host reproductive biology. Dedeine et al. (2001) report a case of obligate mutualism with the parasitoid wasp *Asobara tabida* Nees (Hymenoptera, Braconidae). Female wasps could not reproduce after removal of

Wolbachia because they could not produce mature oocytes. Dedeine et al. (2001) suggest that the wasp or its ancestor became associated with a *Wolbachia* that already produced a factor necessary for wasp oogenesis. The host then lost the capacity to produce this costly factor itself, thus becoming totally dependent on the bacteria for reproduction. Similar losses of function have been reported in other insect-*Wolbachia* interactions. For example, there are several cases in which parthenogenesis induction by *Wolbachia* infection can be reversed by curing the infection (Stouthamer, 1997), but in some cases the host species can no longer function successfully as a sexual taxon due to adverse changes in male and/or female traits (Arakaki et al., 2001; Gottlieb & Zchori-Fein, 2001; Hunter, 1999). Gottlieb and Zchori-Fein (2001) argue that since sexual reproduction has ceased, selection on sexual traits has been removed, leading to the disappearance of or reduction in these traits. They suggest that in symbionts that manipulate their host's reproduction to induce parthenogenesis, the host is being captured by the bacteria for the latter's transmission benefit, leaving no other way of reproduction for the host. These cases are clear examples of obligate proximate mutualisms, where the main benefits for the host come from evolved dependence. We suggest that these interactions are unlikely to be ultimate mutualisms, but this has not yet been tested.

Even for interactions that went through a phase of ultimate mutualism it is plausible that the interaction's ultimate costs escalate over evolutionary time. Such a development is especially likely for species that evolve an extreme dependence on their partner, and therefore cannot get out of an interaction even if its costs escalate (Pellmyr et al., 1997). As ultimate costs grow, the obligate interaction is likely to cease to be an ultimate mutualism. For example, Johnson et al. (1997) argue that plants that are highly dependent on mycorrhizae for nutrient uptake might have a greater risk of mycorrhizal parasitism in highly fertilized systems, because they might not closely control “unnecessary” root growth or rate of colonisation. It is possible that a plant in an obligate mycorrhizal association might be “trapped” in this obligate interaction even when conditions change and the interaction no longer implies any ultimate benefit.

Questions resulting from comparing proximate and ultimate responses in mutualism research

So far, in empirical studies, measured costs and benefits are almost exclusively proximate (i.e., the same group of genotypes was compared with and without the partner; Bronstein, 1994b). New and interesting research directions could thus be opened up by investigating ultimate costs and benefits where possible, and by looking for genetic trade-offs between genotypes differentially adapted to a partner’s absence and presence.

A very important question in mutualism research is the evolution and maintenance of mutualisms in the presence of cheaters (Bronstein, 2001; Denison et al., 2003; Ferriere et al., 2002; Freckleton & Cote, 2003; Hoeksema & Kummel, 2003; Johnstone & Bshary, 2002; Law et al., 2001; Yu, 2001). Measuring the costs induced by the presence of cheaters is essential to tackle this question, and contrasting proximate and ultimate costs might thus be a key element in advancing this line of research. For example, nectar robbers damage floral parts and take resources without effecting pollination (Inouye, 1980). Most removal experiments assess the cost of robbers on the female fitness of the plant by experimentally removing robbers, thus assessing the proximate cost of robbers’ presence. However, robbers also induce an ultimate cost that is likely to be higher than the proximate cost. Roubik et al. (1985) showed that the flowers of a tropical forest understory treelet, *Quassia amara*, had lower corolla length and nectar production on an island where nectar robbers were absent. This suggests that without robbers, there is selection against these traits, so that the performance of plants adapted to robbers is suboptimal. Accordingly, evolved dependence enlarges the ultimate cost of robbers' presence relative to the corresponding proximate cost. Measuring the evolved dependence for this system would involve comparing the performances of different plant genotypes in the presence and absence of robbers, in order to establish whether these plants show variation in their adaptation to the presence of cheaters.

Evolution in a mutualism

We now examine a third dimension according to which mutualisms can be assessed: the concept of *mutualistic evolution* is key to many discussions about mutualism. We define mutualistic evolution as evolution of investment in the partner. Such an adaptation has a direct cost to the bearer, but, other things being equal, increases the performance of both partners. It is important to realize that not all adaptations to a mutualistic partner qualify as mutualistic evolution. This is because traits may also evolve to allow better exploitation of the partner or to prevent better exploitation by the partner; in addition, certain functions may be lost evolutionarily if they are provided more efficiently by the partner (Connor, 1995).

Where does the benefit of an interaction come from?

For defining proximate and ultimate mutualism above, we used criteria based on the net effect of the presence of the partner (an effect-based definition; Abrams, 1987), rather than descriptions of the physiological and ecological processes through which benefits are gained (a process-based definition; Abrams, 1987). For defining mutualistic evolution it is interesting to distinguish between different categories of benefit gained from an interaction. Connor (1995) classifies the benefits derived from an interaction as (a) *by-product benefits*, occurring incidentally at no cost to the donor (as for two plants accidentally growing together with one taking advantage of the other's protective thorns). Connor contrasts this with (b) *purloined benefits*, obtained by exploiting the partner (as a predator would), and (c) *invested benefits*, obtained despite a direct cost because the partner is giving something for a return.

Proximate and ultimate mutualisms can result from benefits of any of these types. Several authors, however, have demanded evidence of evolution of invested benefits as demonstration that an interaction is "truly" mutualistic (Belsky et al., 1993; Agrawal, 2000). Below we argue that such evolution does not necessarily happen either in a proximate or in an ultimate mutualism, and that it can occur even towards an exploitative partner. We describe scenarios that would lead to such counterintuitive results, by considering simple cases of two interacting species coevolving in a constant environment. We note that since coevolution is often diffuse (Agrawal & Van Zandt, 2003; Inouye & Stinchcombe, 2001), theory taking into account this complexity needs to be developed (Loreau et al., 2003; Stanton, 2003) – but this cannot be the purpose of our present study.

Antagonistic strategies can be selected for in mutualistic interactions

A mutualistic strategy might be counter-selected in a proximate or ultimate mutualism. This is because investment in the partner is not selected for if the benefit of the interaction has to be shared with too many conspecifics, illustrating the well-known fact that evolution of investment in the partner requires that "the partner must reciprocate and that the reciprocated benefit must be captured by the initial giver or its offspring" (Yu, 2001). Thus, a trait will not evolve if its beneficial effect is uniformly distributed over all conspecifics. A case in point is the evolution of fruit abortion in senita cacti or yuccas as a means of decreasing seed predation by their respective pollinators: such adaptations will only occur if the pollinator population is localized on the individual plant (Holland & DeAngelis, 2002). If the benefit of an investment in the partner is distributed over conspecifics, there might even be selection for an antagonistic strategy, as we show below in a plant-herbivore example.

Selection can favour investment into an exploiting partner

A possible scenario involves evolution of a trait that benefits the bearer by protecting it against predation. For example, the majority of the estimated 6000 species of Lycaenids have associations with ants that range from mutualism to parasitism (Pierce et al., 2002). A standard interpretation of the mutualistic association is that lycaenid larvae produce secretions in order to attract ants and benefit from their protection from parasitoids. However, another interpretation is possible: Malicky (1970) has suggested that lycaenid larvae might produce secretions in order to prevent predation by ants. These secretions would then be an example of an investment into an exploiting partner.

II. Plant-herbivore interactions

Plant proximate response to herbivore removal

Experimental studies have demonstrated that, under some conditions, herbivory leads to increased plant fitness. Lifetime reproductive output (seed production of monocarpic plant species, controlling for seed weight and germination potential) was increased by grazing or cutting for some populations of *Ipomopsis aggregata* (Gronemeyer et al., 1997; Paige, 1992; Paige & Whitham, 1987) and *Gentianella campestris* (Huhta et al., 2000b; Juenger et al., 2000; Lennartsson et al., 1997, 1998). Other monocarpic species can show increased seed production following moderate cutting under field conditions (Huhta et al., 2003) or artificial conditions such as reduced competitive pressure and/or fertilizer application (Alward & Joern, 1993; Benner, 1988; Huhta et al., 2000a). The results on *Ipomopsis aggregata* and *Gentianella campestris* thus suggest that a proximate mutualism can exist between these plants and their herbivores.

Some authors (Agrawal, 2000; Vail, 1994) accept this evidence as confirmation of a possible benefit of the plant from herbivory, leading to the claim that plant-herbivore mutualism may exist.

Evolved dependence of plants towards their herbivores

Increased seed production in overcompensating plants results from the release of apical dominance and from the production of numerous tillers (Benner, 1988; Huhta et al., 2000b; Juenger et al., 2000; Lennartsson et al., 1997, 1998; Paige, 1999; Paige & Whitham, 1987; Strauss & Agrawal, 1999). If the probability of herbivory is high, a plant that produces multiple shoots from the beginning of the season will lose them all to the herbivore (Crawley, 1987). If, however, herbivory only occurs during a short period, damage by herbivores can serve as a signal for the plant that the risk of herbivory soon will be over, and post-herbivory activation of dormant meristems is selected for (Tuomi et al., 1994b; Vail, 1992). Several models suggest that plants adapted to herbivory should have developed mechanisms for resource mobilization triggered by herbivory (Jaremo et al., 1999; Lehtila, 2000; Mathews, 1994; Nilsson et al., 1996a, 1996b; Simons & Johnston, 1999; Tuomi et al., 1994b; Vail, 1992, 1994). This adaptation leads to low reproduction in the absence of herbivory, *just because this plant genotype is not adapted to a situation without herbivores*, and there is a trade-off between the ability of a plant to perform with and without herbivores. In the presence of herbivores, it is advantageous to wait before allocating resources to growth. In the absence of herbivores, however, this trait is disadvantageous and plants should instead allocate all their resources to growth as soon as possible. Mechanisms like this might explain the proximate benefit that these plants derive from herbivores.

Evolved dependence has likely arisen in many plant-herbivore interactions. In *Gentianella campestris*, the plant's ability to produce more seeds after herbivore damage only occurs in populations adapted to either herbivory or mowing (Lennartsson et al., 1997, 1998). Similarly, the ability to tolerate herbivory was negatively correlated with fitness in the absence of herbivory in *Ipomoea purpurea* (Tiffin & Rausher, 1999).

Because overcompensation is likely to result from evolved dependence rather than any other mechanism of "real" benefit, some authors do not accept the proximate response of overcompensation as sufficient proof that plants might benefit from herbivory (Belsky et al., 1993; Järemo et al., 1999; Mathews, 1994; Tuomi et al., 1994b).

Ultimate mutualism in plant-herbivore interactions

Theoretical arguments for plant-herbivore interactions causing an ultimate cost to plants

Vail (1992) built a model showing that plants benefit from herbivory because plants adapted to herbivores should perform best with herbivores. However, he noted that although removal of herbivores reduces fitness in the short term, "that would simultaneously impart a selective pressure… and thus raise fitness in the long run." Mathews (1994) criticized Vail's interpretation: "although Vail speculates about the benefits of herbivory, his model in fact contradicts him because plant fitness is higher in the absence of herbivory than anywhere else." For Mathews, the proximate criterion is not valid for testing benefits from herbivory: there needs to be an ultimate benefit resulting from the presence of herbivores. Also in other recent studies there seems to be some convergence towards using the ultimate response criterion (Järemo et al., 1999; Nilsson et al., 1996a, 1996b; Simons & Johnston, 1999; Stowe et al., 2000; Tuomi et al., 1994a, 1994b), and rejecting the validity of a proximal response criterion.

No empirical evidence for plant-herbivore interactions causing an ultimate benefit for plants

Järemo et al. (1999) measured the ultimate response of *Gentianella campestris* to herbivore removal. Based on existing data, they compared populations that have evolved with the herbivore to populations that have evolved without it. They found no empirical evidence for an ultimate benefit for the plant, but there was also no evidence for an ultimate cost.

In a different study, the comparison of reaction norms of maternal lines of *Gentianella campestris* from different populations also failed to show any trade-off between fitness in the absence of herbivory and the ability to compensate for herbivory (Juenger et al., 2000). To conclude, this plant seems to show no strong ultimate response to herbivores: herbivores seem ultimately neutral.

Mutualistic evolution in plant-herbivore interactions

Belsky et al. (1993) define a “mutualistic plant” as a plant that “makes some portion of their bodies available to herbivores” (i.e., a plant that invests in the herbivore), whereas an “antagonistic plant” defends itself against herbivores. They argue that if the plant-herbivore interaction was a mutualism, then we should witness the evolution of mutualistic plants, implying mutualistic evolution through which a plant evolves to invest in its herbivore. However, here we argue that this is not necessarily the case.

If herbivores have a positive effect on plant fitness through the efficient recycling of nutrients (de Mazancourt et al., 2001), then plants receive a benefit from the presence of herbivores. The more efficient the herbivore is at recycling nutrients, the more benefit there is to the plant, and at high herbivore recycling efficiencies the interaction can well be a proximate or even an ultimate mutualism. However, when nutrient cycling is redistributed amongst all plants, mutualistic plants experience a direct cost and exert a positive effect on the herbivore. They do not receive a one-on-one benefit, as all plants receive a benefit through the herbivore. It can be shown that the more efficient the herbivore becomes at recycling nutrients, the more selection favours defended plants, because they benefit more from nutrients recycled from less defended plants. Therefore, the more herbivores recycle, the more antagonistic plant strategies are selected for and plant defences thus go up. At the same time, nevertheless, the interaction can become a proximate and even an ultimate mutualism, as long as herbivores conserve nutrients in the system to and extent that enables plants to perform better on the whole.

Although there have been many empirical studies on the effects of herbivores on nutrient cycling (Carpenter & Kitchell, 1984; Chaneton et al., 1996; Detling, 1988; Floate, 1981; Jarvis et al., 1989; Pastor & Cohen, 1997; Ritchie et al., 1998; Ruess et al., 1989; Ruess & McNaughton, 1988; Seagle et al., 1992; Wilson & Jefferies, 1996), none has yet studied the net effect of herbivory on plant fitness and the resultant selection pressure on plants. Therefore there exists no empirical indication to date that would allow us to assess how widely the scenario sketched here occurs in nature.

Conclusions

So, what is a mutualism when there is adaptation to the partner? In this paper we have defined and systematically contrasted three alternative definitions of mutualism. If we need to choose only one of them, it has to be that of proximate mutualism. If we were to discard the criterion of proximate mutualism, we would abandon core evidence for most studied examples of mutualism. However, in choosing this criterion, we must acknowledge the potential importance of evolved dependence as a valid mechanism that creates a benefit resulting from the partner's presence. In the plant-herbivore debate, this means that we have to accept evidence of overcompensation as evidence that plants indeed benefit from herbivory (provided that overcompensation occurs as a result of a realistic herbivory event), however irritating and counterintuitive this might be. More empirical and theoretical studies should take into account evolved dependence as a possibly crucial mechanism generating mutualism.

Ultimate mutualism is similar to what many people would intuitively like to call mutualism, or "true" mutualism (as stated by Agrawal 2000; i.e., a mutualism that does not stem from evolved dependence). Unfortunately, the ultimate response is not even meaningful in many classical examples of mutualism. Also because of major difficulties involved in its measurement, we believe that the ultimate response will remain an abstraction that is not always useful. Moreover, even obligate mutualisms are not guaranteed to be "true" or ultimate mutualisms.

The plant-herbivore controversy seemed resolved by adopting a criterion of ultimate rather than proximate benefit (Järemo et al., 1999), thus rejecting the proximate criterion of overcompensation. We contend that this is not satisfactory, as the proximate criterion cannot be rejected without serious reconsideration of most classical examples of mutualism. Instead, we argue, we ought to recognise the potentially very important role of evolved dependence in all mutualisms.

Finally, the analysis of adaptations that can bring about, maintain, or jeopardize mutualistic interactions needs to be disentangled from the criteria for mutualism itself. As we have shown, traits that favour or harm a partner might evolve in any type of interaction: hence, defining mutualism through mutualistic evolution seems of limited utility.

Differentiating between the three concepts introduced here allows us to focus on new and stimulating research questions. For many interactions that are considered mutualistic it will be illuminating to evaluate empirically (a) whether there is adaptation to the presence of the partner, (b) through which route evolved dependence has been selected for, (c) how evolved dependence contributes to proximate benefits, and (d) how proximate and ultimate benefits affect the mutualistic or antagonistic evolution of traits.

Acknowledgements

We thank Tim Barraclough, Martin Bidartondo, Judie Bronstein, Austin Burt, James Cook, Angela Douglas, Jaboury Ghazoul, David Gibson, Matt Goddard, Edward Allen Herre, Jason Hoeksema, Mark Rees, Mark Schwartz, Juha Tuomi, Stephen Vail, Andrew Wilby, Doug Yu, and several anonymous reviewers for useful discussions and comments on previous versions of this manuscript. 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.

References

Abrams, P.A. (1987) On classifying interactions between populations. Oecologia, 73, 272-281.

Agrawal, A.A. (2000) Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. Trends in Plant Science, 5, 309-313.

Agrawal, A.A. & Van Zandt, P.A. (2003) Ecological play in the coevolutionary theatre: genetic and environmental determinants of attack by a specialist weevil on milkweed. Journal of Ecology, 91, 1049-1059.

Alward, R.D. & Joern, A. (1993) Plasticity and overcompensation in grass responses to herbivory. Oecologia, 95, 358-364.

Arakaki, N., Miyoshi, T., & Noda, H. (2001) *Wolbachia*-mediated parthenogenesis in the predatory thrips *Fanklintothrips vespiformis* (Thysanoptera : Insecta). Proceedings of the Royal Society of London Series B-Biological Sciences, 268, 1011-1016.

Belsky, A.J., Carson, W.P., Jense, C.L., & Fox, G.A. (1993) Overcompensation by plants: herbivore optimization or red herring? Evolutionary Ecology, 7, 109-121.

Bender, E.A., Case, T.J., & Gilpin, M.E. (1984) Perturbation experiments in community ecology: theory and practice. Ecology, 65, 1-13.

Benner, B.L. (1988) Effects of apex removal and nutrient supplementation on branching and seed production in *Thlaspi arvense* (Brassicaceae). American Journal of Botany, 75, 645-651.

Boucher, D.H., James, S., & Keeler, K.H. (1982) The ecology of mutualism. Annual Review of Ecology and Systematics, 13, 315-347.

Bronstein, J.L. (1994a) Conditional outcomes in mutualistic interactions. Trends in Ecology and Evolution, 9, 214-217.

Bronstein, J.L. (1994b) Our current understanding of mutualism. The Quarterly Review of Biology, 69, 31-51.

Bronstein, J.L. (2001) The exploitation of mutualisms. Ecology Letters, 4, 277-287.

Carpenter, S.R. & Kitchell, J.F. (1984) Plankton community structure and limnetic primary production. The American Naturalist, 124, 159-172.

Chaneton, E.J., Lemcoff, J.H., & Lavado, R.S. (1996) Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate subhumid grassland in Argentina. Journal of Applied Ecology, 33, 291-302.

Connor, R.C. (1995) The benefits of mutualism - a conceptual framework. Biological Reviews of the Cambridge Philosophical Society, 70, 427-457.

Crawley, M.J. (1987) Benevolent herbivores? Trends in Ecology and Evolution, 2, 167-168.

de Mazancourt, C., Loreau, M., & Dieckmann, U. (2001) Can the evolution of plant defense lead to plant-herbivore mutualism ? The American Naturalist, 158, 109-123.

Dedeine, F., Vavre, F., Fleury, F., Loppin, B., Hochberg, M.E., & Bouletreau, M. (2001) Removing symbiotic *Wolbachia* bacteria specifically inhibits oogenesis in a parasitic wasp. Proceedings of the National Academy of Sciences of the United States of America, 98, 6247-6252.

Denison, R.F., Bledsoe, C., Kahn, M., O'Gara, F., Simms, E.L., & Thomashow, L.S. (2003) Cooperation in the rhizosphere and the "free rider" problem. Ecology, 84, 838-845.

Detling, J.K. (1988). Grasslands and savannas: regulation of energy flow and nutrient cycling by herbivores. In Concepts of Ecosystem Ecology (eds L.R. Pomeroy & J.J. Alberts), Vol. 67. Springer-Verlag, New York.

Dieckmann, U., Marrow, P., & Law, R. (1995). Evolutionary cycling in predator-prey interactions: Population dynamics and the Red Queen. Journal of Theoretical Biology, 176, 91-102.

Douglas, A.E. & Smith, D.C. (1989) Are endosymbioses mutualistic ? Trends in Ecology and Evolution, 4, 350-352.

Faeth, S.H. & Sullivan, T.J. (2003) Mutualistic asexual endophytes in a native grass are usually parasitic. American Naturalist, 161, 310-325.

Ferriere, R., Bronstein, J.L., Rinaldi, S., Law, R., & Gauduchon, M. (2002) Cheating and the evolutionary stability of mutualisms. Proceedings of the Royal Society of London Series B-Biological Sciences, 269, 773-780.

Floate, M.J.S. (1981). Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. In Terrestrial Nitrogen Cycles (eds F.E. Clark & T. Rosswall), Vol. 33, pp. 585-601, Stockholm.

Freckleton, R.P. & Cote, I.M. (2003) Honesty and cheating in cleaning symbioses: evolutionarily stable strategies defined by variable pay-offs. Proceedings of the Royal Society of London Series B-Biological Sciences, 270, 299-305.

Gomulkiewicz, R., Thompson, J.N., Holt, R.D., Nuismer, S.L., & Hochberg, M.E. (2000) Hot spots, cold spots, and the geographic mosaic theory of coevolution. American Naturalist, 156, 156-174.

Gottlieb, Y. & Zchori-Fein, E. (2001) Irreversible thelytokous reproduction in *Muscidifurax uniraptor*. Entomologia Experimentalis Et Applicata, 100, 271-278.

Gronemeyer, P.A., Dilger, B.J., Bouzat, J.L., & Paige, K.N. (1997) The effects of herbivory on paternal fitness in scarlet gilia: better moms also make better pops. The American Naturalist, 150, 592-602.

Herrera, C.M. (1987) Components of pollinator quality - comparative-analysis of a diverse insect assemblage. Oikos, 50, 79-90.

Hoeksema, J.D. & Kummel, M. (2003) Ecological persistence of the plant-mycorrhizal mutualism: A hypothesis from species coexistence theory. American Naturalist, 162, S40-S50.

Holland, J.N. & DeAngelis, D.L. (2002) Ecological and evolutionary conditions for fruit abortion to regulate pollinating seed-eaters and increase plant reproduction. Theoretical Population Biology, 61, 251-263.

Huhta, A.P., Hellstrom, K., Rautio, P., & Tuomi, J. (2000a) A test of the compensatory continuum: fertilization increases and below-ground competition decreases the grazing tolerance of tall wormseed mustard (*Erysimum strictum*). Evolutionary Ecology, 14, 353-372.

Huhta, A.P., Hellstrom, K., Rautio, P., & Tuomi, J. (2003) Grazing tolerance of *Gentianella amarella* and other monocarpic herbs: why is tolerance highest at low damage levels? Plant Ecology, 166, 49-61.

Huhta, A.P., Lennartsson, T., Tuomi, J., Rautio, P., & Laine, K. (2000b) Tolerance of *Gentianella campestris* in relation to damage intensity: an interplay between apical dominance and herbivory. Evolutionary Ecology, 14, 373-392.

Hunter, M.S. (1999) The influence of parthenogenesis-inducing *Wolbachia* on the oviposition behaviour and sex-specific developmental requirements of autoparasitoid wasps. Journal of Evolutionary Biology, 12, 735-741.

Inouye, B. & Stinchcombe, J.R. (2001) Relationships between ecological interaction modifications and diffuse coevolution: similarities, differences, and causal links. Oikos, 95, 353-360.

Inouye, D.W. (1980) The terminology of floral larceny. Ecology, 61, 1251-1253.

Jaremo, J., Ripa, J., & Nilsson, P. (1999) Flee or fight uncertainty: plant strategies in relation to anticipated damage. Ecology Letters, 2, 361-366.

Järemo, J., Tuomi, J., Nilsson, P., & Lennartsson, T. (1999) Plant adaptations to herbivory: mutualistic versus antagonistic coevolution. Oikos, 84, 313-320.

Jarvis, S.C., Hatch, D.J., & Roberts, D.H. (1989) The effects of grassland management on nitrogen losses from grazed swards through ammonia volatilization; the relationship to excretal N returns from cattle. Journal of Agricultural Science, Cambridge, 112, 205-216.

Jeon, K.W. (1972) Development of cellular dependence on infective organisms: micrurgical studies in amoebas. Science, 176, 1122-1123.

Johnson, N.C., Graham, J.H., & Smith, F.A. (1997) Functioning of mycorrhizal associations along the mutualism- parasitism continuum. New Phytologist, 135, 575-586.

Johnstone, R.A. & Bshary, R. (2002) From parasitism to mutualism: partner control in asymmetric interactions. Ecology Letters, 5, 634-639.

Juenger, T., Lennartsson, T., & Tuomi, J. (2000) The evolution of tolerance to damage in Gentianella campestris: natural selection and the quantitative genetics of tolerance. Evolutionary Ecology, 14, 393-419.

Klironomos, J.N. (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology, 84, 2292-2301.

Koptur, S. & Lawton, J.H. (1988) Interactions among vetches bearing extrafloral nectaries, their biotic protective agents, and herbivores. Ecology, 69, 278-283.

Krebs, C.J. (1985) Ecology. The experimental analysis of distribution and abundance Harper & Row, New York.

Law, R., Bronstein, J.L., & Ferriere, R.G. (2001) On mutualists and exploiters: Plant-insect coevolution in pollinating seed-parasite systems. Journal of Theoretical Biology, 212, 373-389.

Lehtila, K. (2000) Modelling compensatory regrowth with bud dormancy and gradual activation of buds. Evolutionary Ecology, 14, 315-330.

Lennartsson, T., Nilsson, P., & Tuomi, J. (1998) Induction of overcompensation in the field gentian, *Gentianella campestris*. Ecology, 79, 1061-1072.

Lennartsson, T., Tuomi, J., & Nilsson, P. (1997) Evidence for an evolutionary history of overcompensation in the grassland biennal *Gentianella campestris* (Gentianaceae). The American Naturalist, 149, 1147-1155.

Loreau, M., de Mazancourt, C., & Holt, R.D. (2003). Conserving species or ecosystems? Mutual evolutionary constraints of species and ecosystems: the example of plant-herbivore interactions. In Evolutionary Conservation Biology (eds R. Ferrière, U. Dieckmann & D. Couvet).

Malicky, H. (1970) New aspects on the association between Lycaenid larvae (*Lycaenidae*) and ants (*Formicadea*, Hymenoptera). Journal of the Lepidopterists' Society, 24, 190-202.

Mathews, J.N.A. (1994) The benefits of overcompensation and herbivory : the difference between coping with herbivores and linking them. The American Naturalist, 144, 528-533.

Menge, B.A. (2000) Testing the relative importance of positive and negative effects on community structure. Trends in Ecology & Evolution, 15, 46-47.

Nilsson, P., Tuomi, J., & Aström, M. (1996a) Bud dormancy as a bet-hedging strategy. The American Naturalist, 147, 269-281.

Nilsson, P., Tuomi, J., & Åström, M. (1996b) Even repeated grazing may select for overcompensation. Ecology, 77, 1942-1946.

Paige, K.N. (1992) Overcompensation in response to mammalian herbivory: from mutualistic to antagonistic interactions. Ecology, 73, 2076-2085.

Paige, K.N. (1999) Regrowth following ungulate herbivory in Ipomopsis aggregata: geographic evidence for overcompensation. Oecologia, 118, 316-323.

Paige, K.N. & Whitham, T.G. (1987) Overcompensation in response to mammalian herbivory : the advantage of being eaten. The American Naturalist, 129, 407-416.

Pastor, J. & Cohen, Y. (1997) Herbivores, the functional diversity of plant species, and the cycling of nutrients in boreal ecosystems. Theoretical Population Biology, 51, 165-179.

Pellmyr, O., Massey, L.K., Hamrick, J.L., & Feist, M.A. (1997) Genetic consequences of specialization: Yucca moth behavior and self pollination in yuccas. Oecologia, 109, 273-278.

Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B., & Travassos, M.A. (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology, 47, 733-771.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J., & Rejmanek, M. (2000) Plant invasions - the role of mutualisms. Biological Reviews of the Cambridge Philosophical Society, 75, 65-93.

Ritchie, M.E., Tilman, D., & Knops, J.M.H. (1998) Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology, 79, 165-177.

Roubik, D.W., Holbrook, N.M., & Parra, G. (1985) Roles of nectar robbers in reproduction of the tropical treelet *Quassia-amara* (Simaroubaceae). Oecologia, 66, 161-167.

Roughgarden, J. (1975) Evolution of a marine symbiosis - a simple cost-benefit model. Ecology, 56, 1201-1208.

Ruess, R.W., Hik, D.S., & Jefferies, R.L. (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh. Oecologia, 79, 23-29.

Ruess, R.W. & McNaughton, S.J. (1988) Ammonia volatilization and the effects of large grazing mammals on nutrient loss from East African grasslands. Oecologia, 77, 382-386.

Schoener, T.W. (1983) Field experiments on interspecific competition. The American Naturalist, 122, 240-285.

Seagle, S.W., McNaughton, S.J., & Ruess, R.W. (1992) Simulated effects of grazing on soil nitrogen an mineralization in contrasting Serengeti grasslands. Ecology, 73, 1105-1123.

Simons, A.M. & Johnston, M.O. (1999) The cost of compensation. American Naturalist, 153, 683-687.

Smiley, J. (1986) Ant constancy at passiflora extrafloral nectaries - effects on caterpillar survival. Ecology, 67, 516-521.

Stachowicz, J.J. (2001) Mutualism, facilitation, and the structure of ecological communities. Bioscience, 51, 235-246.

Stanton, M.L. (2003) Interacting guilds: Moving beyond the pairwise perspective on mutualisms. American Naturalist, 162, S10-S23.

Stouthamer, R. (1997). *Wolbachia*-induced parthenogenesis. In Influential passengers, inherited microorganisms and arthropod reproduction (eds S.L. O'Neill, A.A. Hoffmann & J.H. Werren), pp. 102-124. Oxford University Press, Oxford.

Stowe, K.A., Marquis, R.J., Hochwender, C.G., & Simms, E.L. (2000) The evolutionary ecology of tolerance to consumer damage. Annual Review of Ecology and Systematics, 31, 565-595.

Strauss, S.Y. & Agrawal, A.A. (1999) The ecology and evolution of plant tolerance to herbivory. Trends in Ecology and Evolution, 14, 179-185.

Thompson, J.N. & Cunningham, B.M. (2002) Geographic structure and dynamics of coevolutionary selection. Nature, 417, 735-738.

Tiffin, P. & Rausher, M.D. (1999) Genetic constraints and selection acting on tolerance to herbivory in the common morning glory Ipomoea purpurea. American Naturalist, 154, 700-716.

Tuomi, J., Haukioja, E., Honkanen, T., & Augner, M. (1994a) Potential benefits of herbivore behaviour inducing amelioration of food-plant quality. Oikos, 70, 161-166.

Tuomi, J., Nilsson, P., & Aström, M. (1994b) Plant compensatory responses: bud dormancy as an adaptation to herbivory. Ecology, 75, 1429-1436.

Vail, S.G. (1992) Selection for overcompensatory plant responses to herbivory: a mechanism for the evolution of plant-herbivore mutualism. The American Naturalist, 139, 1-8.

Vail, S.G. (1994) Overcompensation, plant-herbivore mutualism, and mutualistic coevolution: a reply to Mathews. The American Naturalist, 144, 534-536.

van Baalen, M. & Jansen, V.A.A. (2001) Dangerous liaisons: the ecology of private interest and common good. Oikos, 95, 211-224.

Wilson, D.J. & Jefferies, R.L. (1996) Nitrogen mineralization, plant growth and goose herbivory in an Arctic coastal ecosystem. Journal of Ecology, 84, 841-851.

Yu, D.W. (2001) Parasites of mutualisms. Biological Journal of the Linnean Society, 72, 529-546.

Box 1: Definition of key terms

Performance: To compare the performance of organisms under different conditions (with or without partners), an absolute measure of performance is required, rather than a relative one. What measure to use is not a trivial question. Possible performance measures include the following. (1) *Absolute fitness* of an individual, i.e., its lifetime reproductive success, always equals 1 when populations are at steady state, so that care must be taken in setting the conditions under which lifetime reproductive success is measured (as described below). Proxies of absolute fitness can sometime be used. (2) *Short-term population growth rate* is a good proxy of lifetime reproductive success under conditions of repeated disturbance, through which a population mostly remains in an exponential growth phase. (3) *Long-term population size* may be a proxy of absolute fitness for populations close to steady state. Discrepancies between the different measures are discussed in Abrams (1987) and van Baalen and Jansen (2001).

Proximate response: Difference in performance of a genotype (or group thereof) before and after short-term removal (or addition) of the partner species. Note that the performance of the same genotype (or group thereof) is thus compared under two conditions, one of which it might not be adapted to. *Measurement* – If performance is measured as lifetime reproductive success, the focal species' density after removal must be kept at its value before removal. We can then consider the focal population with its partner, with LRS = 1, remove the partner, and measure the new lifetime reproductive success, LRSP. The proximate response to removal is LRSP – 1.

Proximate mutualism: Interspecific interaction in which removal of each partner results in a decreased performance of the other. It is characterised by negative proximate responses of each species to the removal of the other species. Such negative proximate responses can be due to “real” or ultimate benefits, but alternatively may merely reflect evolved dependence resulting from adaptation to partner.

Evolved dependence: Through adaptation to the presence of an interacting partner species, a population might lose its ability to perform well in the absence of such a partner. Evolved dependence measures the loss of performance of a focal population in the absence of a partner due to its adaptation to the presence of the partner.

Measurement – If performance is measured as lifetime reproductive success, we can consider the focal population with its partner, remove the partner, and measure the new lifetime reproductive success, LRSP. We can then replace every individual in the focal population with a genotype adapted to the absence of the partner, and measure the new lifetime reproductive success, LRSU. The evolved dependence is LRSU – LRSP.

Ultimate response: Difference in performance before and after “long-term” removal (or addition) of a partner species, allowing for adaptation to take place. Performance of a genotype (or group thereof) adapted to the presence of the partner is measured in the presence of the partner, and compared to the performance of a genotype (or group thereof) adapted to the absence of the partner measured in the absence of the partner.

Measurement – If performance is measured as lifetime reproductive success, the focal species’ density in the presence and absence of its partner must be kept the same. We can then consider the focal population with its partner, with LRS = 1; remove the partner and replace every individual in the focal population with a genotype adapted to the absence of the partner, and measure the new lifetime reproductive success, LRSU. The ultimate response to removal is LRSU – 1.

Ultimate mutualism: Interspecific interaction in which each partner species could never have performed as well without the other, even if it was adapted to the absence of the partner. In other words, an ultimate mutulaism is characterised by negative ultimate responses of each species to the removal of the other species.

Mutualistic evolution: Evolution of a trait that is costly to the bearer but beneficial to its partner in a proximate mutualism (investment in a partner sensu Connor, 1995). Note that adaptation to the partner does not necessarily imply mutualistic evolution; for example, there can be evolution of traits that allow to better exploit the partner.

Obligate mutualism: Interaction in which the removal of the partner results in death or complete loss of reproduction in the focal species. The focal species has therefore a proximate benefit from the interaction, as its proximate response to partner removal is maximally negative. In many cases, the ultimate response to partner removal cannot be measured in obligate mutualisms. (Antonym: ***facultative mutualism***).

Conditional mutualism: Interspecific interaction that is mutualistic (proximately or ultimately) only under specific environmental conditions (Bronstein, 1994a).

Figure 1. Performance of a genotype adapted to the absence of its partner (left column), a genotype adapted to the presence of its partner (right column), both in the presence of the partner (upper row), and in the absence of its partner (lower row). Differences between these four performances measure the responses discussed in the text. The proximate response of the organism to partner removal is measured for individual genotypes, as $F_{Ga/p} - F_{Ga/a}$ for the genotype adapted to the partner, and as $F_{Gp/p} - F_{Gp/a}$ for the genotype adapted to the absence of the partner. The ultimate response of the organism to partner removal is measured as $F_{Gp/p} - F_{Ga/a}$, i.e., as the difference between the performance in the presence of the partner of a genotype that evolved with the partner and the performance in the absence of the partner of a genotype that evolved without the partner. Evolved dependence is measured as the difference between the performance without the partner of a genotype that evolved without the partner and the performance without the partner of a genotype that evolved with the partner, $F_{Ga/a} - F_{Gp/a}$. Note that the ultimate response of a genotype adapted to the partner equals its proximate response minus the evolved dependence.

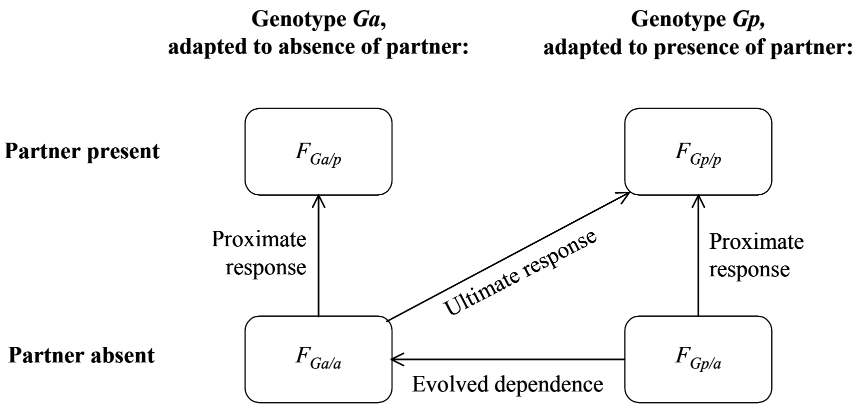

Figure 1
de Mazancourt, Loreau and Dieckmann