



Adaptive Dynamics and Technological Change

**Dercole, F., Dieckmann, U., Obersteiner, M. and
Rinaldi, S.**

**IIASA Interim Report
December 2006**



Dercole, F., Dieckmann, U., Obersteiner, M. and Rinaldi, S. (2006) Adaptive Dynamics and Technological Change. IIASA Interim Report. Copyright © 2006 by the author(s). <http://pure.iiasa.ac.at/8029/>

Interim Report on work of the International Institute for Applied Systems Analysis receive only limited review. Views or opinions expressed herein do not necessarily represent those of the Institute, its National Member Organizations, or other organizations supporting the work. All rights reserved. Permission to make digital or hard copies of all or part of this work for personal or classroom use is granted without fee provided that copies are not made or distributed for profit or commercial advantage. All copies must bear this notice and the full citation on the first page. For other purposes, to republish, to post on servers or to redistribute to lists, permission must be sought by contacting repository@iiasa.ac.at

Interim Report

IR-06-070

Adaptive dynamics and technological change

Fabio Dercole (dercole@elet.polimi.it)
Ulf Dieckmann (dieckmann@iiasa.ac.at)
Michael Obersteiner (oberstei@iiasa.ac.at)
Sergio Rinaldi (sergio.rinaldi@polimi.it)

Approved by

Leen Hordijk
Director, IIASA

January 2006



The Evolution and Ecology Program 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 Evolution and Ecology Program 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 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: *Evolution Management: Taking Stock - 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-03-077 (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* 17:613-628 (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* 68:041-903 (2003).
- No. 87 de Mazancourt C, Dieckmann U: *Trade-off Geometries and Frequency-dependent Selection*. IIASA Interim Report IR-04-039 (2004). *American Naturalist* 164:765-778 (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). *Journal of Ecology* 93:305-314 (2005).
- No. 91 Dieckmann U, Doebeli M: *Pluralism in Evolutionary Theory*. IIASA Interim Report IR-05-017 (2005). *Journal of Evolutionary Biology* 18:1209-1213 (2005).
- No. 92 Doebeli M, Dieckmann U, Metz JAJ, Tautz D: *What We Have Also Learned: Adaptive Speciation is Theoretically Plausible*. IIASA Interim Report IR-05-018 (2005). *Evolution* 59:691-695 (2005).
- No. 93 Egas M, Sabelis MW, Dieckmann U: *Evolution of Specialization and Ecological Character Displacement of Herbivores Along a Gradient of Plant Quality*. IIASA Interim Report IR-05-019 (2005). *Evolution* 59:507-520 (2005).
- No. 94 Le Galliard J, Ferrière R, Dieckmann U: *Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility*. IIASA Interim Report IR-05-020 (2005). *American Naturalist* 165:206-224 (2005).
- No. 95 Doebeli M, Dieckmann U: *Adaptive Dynamics as a Mathematical Tool for Studying the Ecology of Speciation Processes*. IIASA Interim Report IR-05-022 (2005). *Journal of Evolutionary Biology* 18:1194-1200 (2005).
- No. 96 Brandt H, Sigmund K: *The Logic of Reprobation: Assessment and Action Rules for Indirect Reciprocity*. IIASA Interim Report IR-04-085 (2004). *Journal of Theoretical Biology* 231:475-486 (2004).
- No. 97 Hauert C, Haiden N, Sigmund K: *The Dynamics of Public Goods*. IIASA Interim Report IR-04-086 (2004). *Discrete and Continuous Dynamical Systems - Series B* 4:575-587 (2004).
- No. 98 Meszéna G, Gyllenberg M, Jacobs FJA, Metz JAJ: *Link Between Population Dynamics and Dynamics of Darwinian Evolution*. IIASA Interim Report IR-05-026 (2005). *Physical Review Letters* 95:Article 078105 (2005).
- No. 99 Meszéna G: *Adaptive Dynamics: The Continuity Argument*. IIASA Interim Report IR-05-032 (2005).
- No. 100 Brännström NA, Dieckmann U: *Evolutionary Dynamics of Altruism and Cheating Among Social Amoebas*. IIASA Interim Report IR-05-039 (2005). *Proceedings of the Royal Society London Series B* 272:1609-1616 (2005).
- No. 101 Meszéna G, Gyllenberg M, Pasztor L, Metz JAJ: *Competitive Exclusion and Limiting Similarity: A Unified Theory*. IIASA Interim Report IR-05-040 (2005).
- No. 102 Szabo P, Meszéna G: *Limiting Similarity Revisited*. IIASA Interim Report IR-05-050 (2005).
- No. 103 Krakauer DC, Sasaki A: *The Greater than Two-Fold Cost of Integration for Retroviruses*. IIASA Interim Report IR-05-069 (2005).
- No. 104 Metz JAJ: *Eight Personal Rules for Doing Science*. IIASA Interim Report IR-05-073 (2005). *Journal of Evolutionary Biology* 18:1178-1181 (2005).
- No. 105 Beltman JB, Metz JAJ: *Speciation: More Likely Through a Genetic or Through a Learned Habitat Preference?* IIASA Interim Report IR-05-072 (2005). *Proceedings of the Royal Society of London Series B* 272:1455-1463 (2005).
- No. 106 Durinx M, Metz JAJ: *Multi-type Branching Processes and Adaptive Dynamics of Structured Populations*. IIASA Interim Report IR-05-074 (2005). Haccou P, Jager P, Vatutin V (eds): *Branching Processes: Variation, Growth and Extinction of Populations*, Cambridge University Press, Cambridge, UK, pp. 266-278 (2005).
- No. 107 Brandt H, Sigmund K: *The Good, the Bad and the Discriminator - Errors in Direct and Indirect Reciprocity*. IIASA Interim Report IR-05-070 (2005). *Journal of Theoretical Biology* 239:183-194 (2006).
- No. 108 Brandt H, Hauert C, Sigmund K: *Punishing and Abstaining for Public Goods*. IIASA Interim Report IR-05-071 (2005). *Proceedings of the National Academy of Sciences of the United States of America* 103:495-497 (2006).
- No. 109 Ohtsuki A, Sasaki A: *Epidemiology and Disease-Control Under Gene-for-Gene Plant-Pathogen Interaction*. IIASA Interim Report IR-05-068 (2005).
- No. 110 Brandt H, Sigmund K: *Indirect Reciprocity, Image-Scoring, and Moral Hazard*. IIASA Interim Report IR-05-078 (2005). *Proceedings of the National Academy of Sciences of the United States of America* 102:2666-2670 (2005).
- No. 111 Nowak MA, Sigmund K: *Evolution of Indirect Reciprocity*. IIASA Interim Report IR-05-079 (2005). *Nature* 437:1292-1298 (2005).
- No. 112 Kamo M, Sasaki A: *Evolution Towards Multi-Year Periodicity in Epidemics*. IIASA Interim Report IR-05-080 (2005). *Ecology Letters* 8:378-385 (2005).

- No. 113 Dercole F, Ferrière R, Gragnani A, Rinaldi S: *Co-evolution of Slow-fast Populations: Evolutionary Sliding, Evolutionary Pseudo-equilibria, and Complex Red Queen Dynamics*. IIASA Interim Report IR-06-006 (2006). *Proceedings of the Royal Society B-Biological Sciences* 273:983-990 (2006).
- No. 114 Dercole F: *Border Collision Bifurcations in the Evolution of Mutualistic Interactions*. IIASA Interim Report IR-05-083 (2005). *International Journal of Bifurcation and Chaos* 15:2179-2190 (2005).
- No. 115 Dieckmann U, Heino M, Parvinen K: *The Adaptive Dynamics of Function-Valued Traits*. IIASA Interim Report IR-06-036 (2006). *Journal of Theoretical Biology* 241:370-389 (2006).
- No. 116 Dieckmann U, Metz JAJ: *Surprising Evolutionary Predictions from Enhanced Ecological Realism*. IIASA Interim Report IR-06-037 (2006). *Theoretical Population Biology* 69:263-281 (2006).
- No. 117 Dieckmann U, Brännström NA, HilleRisLambers R, Ito H: *The Adaptive Dynamics of Community Structure*. IIASA Interim Report IR-06-038 (2006). Takeuchi Y, Iwasa Y, Sato K (eds): *Mathematics for Ecology and Environmental Sciences*, Springer, Berlin Heidelberg, pp. 145-177 (2007).
- No. 118 Gardmark A, Dieckmann U: *Disparate Maturation Adaptations to Size-dependent Mortality*. IIASA Interim Report IR-06-039 (2006). *Proceedings of the Royal Society London Series B* 273:2185-2192 (2006).
- No. 119 van Doorn G, Dieckmann U: *The Long-term Evolution of Multi-locus Traits Under Frequency-dependent Disruptive Selection*. IIASA Interim Report IR-06-041 (2006). *Evolution* 60:2226-2238 (2006).
- No. 120 Doebeli M, Blok HJ, Leimar O, Dieckmann U: *Multimodal Pattern Formation in Phenotype Distributions of Sexual Populations*. IIASA Interim Report IR-06-046 (2006). *Proceedings of the Royal Society London Series B* 274:347-357 (2007).
- No. 121 Dunlop ES, Shuter BJ, Dieckmann U: *The Demographic and Evolutionary Consequences of Selective Mortality: Predictions from an Eco-genetic Model of the Smallmouth Bass*. IIASA Interim Report IR-06-060 (2006).
- No. 122 Metz JAJ: *Fitness*. IIASA Interim Report IR-06-061 (2006).
- No. 123 Brandt H, Ohtsuki H, Iwasa Y, Sigmund K: *A survey on indirect reciprocity*. IIASA Interim Report IR-06-065 (2006). Takeuchi Y, Iwasa Y, Sato K (eds): *Mathematics for Ecology and Environmental Sciences*, Springer, Berlin Heidelberg, pp. 21-51 (2007).
- No. 124 Dercole F, Loiacono D, Rinaldi S: *Synchronization in ecological networks: A byproduct of Darwinian evolution?* IIASA Interim Report IR-06-068 (2006).
- No. 125 Dercole F, Dieckmann U, Obersteiner M, Rinaldi S: *Adaptive dynamics and technological change*. IIASA Interim Report IR-06-070 (2006).

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

Contents

Abstract.....	2
1 Introduction	3
2 Adaptive Dynamics: An overview	5
3 A simple example of technological branching	14
4 Concluding remarks.....	20
Acknowledgements	23
References	24
Figure captions	30
Figures	31

Adaptive dynamics and technological change

Fabio Dercole¹, Ulf Dieckmann², Michael Obersteiner^{2,3,4}, Sergio Rinaldi^{1,2}

¹DEI, Department of Electronics and Information
Politecnico di Milano
Via Ponzio 34/5, 20133 Milano, Italy
Ph: +39 02 2399 3555[3563]; Fax: +39 02 2399 3412
dercole[rinaldi]@elet.polimi.it

²IIASA, International Institute for Applied Systems Analysis
Schlossplatz 1, 2361 Laxenburg, Austria
Ph: +43 2236 8070; Fax: +43 2236 71313
oberstei[dieckmann]@iiasa.ac.at

³Department of Economics and Finance
IHS, Institute for Advanced Studies
A-1060 Vienna, Austria

⁴To whom correspondence should be addressed

Abstract

This paper is about the emergence of technological variety arising from market interaction and technological innovation. Existing products in the market compete with innovative ones resulting in a slow and continuous evolution of the underlying technological characteristics of successful products. When technological evolution reaches an equilibrium, it can either be an ESS (Evolutionary Stable Strategy), where marginally innovative products do not penetrate the market, or a branching point, where new products coexist along with established ones. Thus, technological branching can give rise to product variety. In the paper we first introduce Adaptive Dynamics (AD), a recently proposed theory of evolutionary processes, aiming at modelling various features of technological change. Then, a first application of AD in economics is presented and discussed in detail. The limitations of the AD approach, as well as some promising further applications in economics and social sciences, are briefly discussed at the concluding section.

Key words: adaptive dynamics, market dynamics, innovation dynamics, characteristic trait, technological branching, technological variety

1 Introduction

Technological change is a major driver of economic development (Burda & Wyplosz, 1997; Harberger, 1998). New growth theory has claimed the understanding of the implications of technological advancement for economic policy making mainly focusing on efficiency gains (see, for instance, Romer, 1990; Grossman & Helpman, 1991; Aghion & Howitt, 1992; Kortum, 1997; Peretto, 1998; Segerstrom, 1998; Young, 1998). One of the fundamental empirical trends in economic development is the trend toward growing variety. Although some, like Schumpeter (1912), realised early on that variety in consumer goods is “one of the fundamental impulses that set and keep the capitalist engine in motion”, relatively little attention has traditionally been devoted to the systematic exploration of the nature of diversity in economics.

Diversity is variously argued to be a major factor in the fostering of innovation and growth, an important strategy for hedging against intractable uncertainty and ignorance, the principal means to mitigate the effects of “lock-in” under increasing returns and a potentially effective response to some fundamental problems of social choice. Grübler (1998) argues that technological diversity is both a means and a result of economic development. Saviotti (1996), a crucial contribution on the subject, establishes two explicit hypotheses linking variety to economic development: (1) The growth in variety is a necessary requirement for long-term economic development; (2) variety growth, leading to new sectors, and productivity growth in pre-existing sectors, are complementary and not independent aspects of economic development. Stirling (1998), who provides an excellent literature review on diversity in the economy, concludes that the concept of diversity (and especially technological diversity) is of considerable general significance in economics.

It is the purpose of this paper to propose a rigorous modelling framework describing the interaction of technology with its social and physical environment leading to technological diversity. In our opinion *Adaptive Dynamics* (AD), a general theory of evolutionary processes (Dieckmann & Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998), offers tools to explicitly study the process of technological change and its interaction with the market process. Viewed through the lenses of AD technological change is mainly based on a large number of small intentional or spontaneous innovations, recombinations and rearrangements of technological and economic characteristic traits. Firms compete in terms of the efficiency with which they produce or by changing products and processes. Efficiency gains as well as changes in products or processes are measured by “characteristic traits”. When a new technological variant enters the market, it is subjected to severe selection by customers and other agents such as banks, courts of appeal, democratic votes, and

so on. Under these circumstances and a few other technical assumptions discussed in the next section, AD predicts the following series of facts that one can often observe in real economies, at least at a stylised level.

1. Technological innovations are either rejected or win the competition with established products, thus becoming the new predominant type. A small variation of the technological characteristic traits is associated to each invasion and substitution event. The result is a slow and smooth evolution of the traits.
2. Evolution can slow down and approach an equilibrium, but it can also tend toward a cyclic or chaotic regime (Khibnik & Kondrashov, 1997). Moreover, it is not said that all evolutionary paths tend toward the same attractor: in other words, the long term implications of the innovation process can strongly depend upon the innovation paths followed in the past. Finally, technological change can also transform particular products which in the past were predominant types into obsolete products which are swept out from the market.
3. Evolutionary equilibria can be terminal points of technological change where, typically, no marginal innovation can penetrate the market (Hamilton, 1967; Maynard Smith & Price, 1973; Maynard Smith, 1974, 1982; Nash). However, they can also be branching points, where the new variant can penetrate without substituting the old products. This technological branching explains the emergence of technological variety. Repeated branchings can give rise to rich clusters of products coexisting in the market.
4. The above processes of disappearance and emergence of specific technologies are largely influenced, if not dominated, by consumer behaviour and other market conditions which act as the economic filter for innovations and either pull or suppress the diffusion of new technologies (see e.g. Kelm, 1997; Hodgson, 1997; Brooks, 1980)

The paper is organised as follows. In the next section we present the general framework of AD by adapting it to the problem of technological change. In particular, we show why the separation between market and technological innovation timescales is needed to technically derive from AD principles a formal mathematical machinery, the so-called AD canonical equation. Then, we present the first original application of AD to a specific problem of technological change. The problem we discuss is intentionally very simple, in order to obtain the AD equation in closed form and point out from it the properties mentioned above.

Finally, in the conclusion we discuss the limitation and the advantages of the AD approach and give a short overview of the wide scope of evolutionary phenomena that AD could potentially explain in economics and social sciences.

2 Adaptive Dynamics: An overview

In this section we present the general framework of AD by focusing our attention on a specific market with N coexisting products (namely entities, artefact's or services), hereafter called *established products*. The starting point of AD is the description of the dynamics of the product densities in the market (e.g. the number of items owned by 1000 persons) through a system of ordinary differential equations (ODEs).

AD is based on four technical assumptions:

- a. Each product is identified by a *characteristic trait* (simply *trait* in the following) quantifying its features by a positive real number. We assume that products with a higher trait are technologically more advanced. However, this does not imply that more advanced products are necessarily preferred by consumers, since elasticities of the products as well as budgetary constraints are also important. Simple examples of characteristic traits are the waterproof characteristic for watches, the internet capabilities for mobile phones or the graphical user interface features of a software.
- b. In the absence of innovations, product densities tend to a market equilibrium. The timescale on which product densities vary is called *market timescale*.
- c. Innovation events are rare on the market timescale, i.e. they occur on a longer timescale that we call *innovation timescale*. In other words, we assume that market clearing occurs instantaneously on the innovation timescale. The separation between the market and innovation timescales allows one to assume that when an innovative product appears the established products are at market equilibrium, and the market is challenged by one innovation at a time.
- d. Innovations are small, i.e. the trait of the innovative product differs only slightly from the trait of one of the established products. In other words, we consider the case of “marginal” innovation, where innovations are new but similar versions of the existing products.

The principles and methods of AD are presented in the founding papers of Metz *et al.* (1996) and Geritz

et al. (1997, 1998), and in Dieckmann & Law (1996), Champagnat *et al.* (2001), Geritz *et al.* (2002). We now discuss the core of the theory by adapting it to the context of technological change.

Denote by n_1, \dots, n_N and x_1, \dots, x_N the densities and traits of the N established products. For notational convenience, we often indicate these densities and traits as vectors n and x . On the market timescale (fast *market dynamics*), the traits are constant while the densities vary in accordance with N ODEs of the form:

$$\dot{n}_j = n_j F_j(n_1, \dots, n_N, x_1, \dots, x_N), \quad j = 1, \dots, N \quad (1)$$

where F_j is the relative diffusion rate of the j -th product. For example, if $N = 1$, there is a single product in the market and its diffusion can be modelled through the classical logistic growth equation (see e.g. Fisher & Pry, 1971):

$$\dot{n}_1 = r(x_1)n_1 \left[1 - \frac{n_1}{K(x_1)} \right]$$

where $r(x_1)$ is the maximum diffusion rate and $K(x_1)$ is the market equilibrium density.

In the following, model (1) is assumed to have a stable and strictly positive equilibrium $\bar{n}(x)$, called *market equilibrium*, for each x belonging to a region of the trait space called *stationary coexistence region*. We also assume that $\bar{n}(x)$ is globally stable in the positive orthant. This condition is not necessary, but it simplifies the discussion (see Dercole *et al.* (2002) and Dercole & Rinaldi (2002) for relevant exceptions and Dercole *et al.* (2003) for a case of cyclic coexistence).

We now show why the four stylised facts mentioned in the Introduction can be derived from AD theory.

1. Canonical equation

The dynamics of the traits, hereafter called *innovation dynamics*, should reflect the characteristics of the innovation and the market selection processes, which, however, are not included in model (1). In order to describe the competition between the established products and an innovative product, we split the i -th product into two sub-products (established and innovative) with densities n_i and n'_i and traits x_i and x'_i , so that the model reads:

$$\begin{aligned} \dot{n}_j &= n_j f_j(n, n'_i, x, x'_i), \quad j = 1, \dots, N \\ \dot{n}'_i &= n'_i f'_i(n, n'_i, x, x'_i) \end{aligned} \quad (2)$$

Obviously, model (2) contains more information than model (1). Indeed, model (1) can be immediately derived from model (2) by disregarding the equation of the innovative product and letting $n'_i = 0$, thus

obtaining:

$$F_j(n, x) = f_j(n, 0, x, x'_i), \quad j = 1, \dots, N$$

where the function $f_j(n, 0, x, x'_i)$ does not depend on x'_i . The functions f_j and f'_i , at the right-hand sides of model (2) enjoy the following structural properties:

$$f_j(n, n'_i, x, x_i) = F_j(n_1, \dots, n_{i-1}, n_i + n'_i, n_{i+1}, \dots, n_N, x), \quad j = 1, \dots, N \quad (3)$$

$$f'_i(n, n'_i, x, x_i) = f_i(n, n'_i, x, x_i) = F_i(n_1, \dots, n_{i-1}, n_i + n'_i, n_{i+1}, \dots, n_N, x) \quad (4)$$

because, if $x'_i = x_i$, the established and innovative products do not differ, so that only the total density ($n_i + n'_i$) matters. Moreover

$$f'_i(n, n'_i, x, x'_i) = f_i(n', n_i, x', x_i) \quad (5)$$

where

$$n' = (n_1, \dots, n_{i-1}, n'_i, n_{i+1}, \dots, n_N)$$

and

$$x' = (x_1, \dots, x_{i-1}, x'_i, x_{i+1}, \dots, x_N) \quad (6)$$

because any one of the two sub-products can be considered as innovative, provided the other is considered as established. Notice that property (4) is implied by properties (3) and (5).

We can now derive how the traits vary in time. Since model (1) is, by assumption, at its equilibrium $\bar{n}(x)$ when an innovation occurs, the initial conditions in model (2) are $(\bar{n}(x), n'_i)$. Thus, $\dot{n}'_i > 0$, i.e. the innovative product penetrates the market, if $f'_i(\bar{n}(x), n'_i, x, x'_i) > 0$, which is guaranteed if $f'_i(\bar{n}(x), 0, x, x'_i) > 0$ since n'_i is small (the innovative product is initially present in a few items). The function $f'_i(\bar{n}(x), 0, x, x'_i)$, called *invasion fitness*, is strategically important and is abbreviated, in the following, as $\bar{f}'_i(x, x'_i)$, i.e.

$$\bar{f}'_i(x, x'_i) = f'_i(\bar{n}(x), 0, x, x'_i) \quad (7)$$

Notice that property (4) implies that the invasion fitness vanishes for $x'_i = x_i$, i.e.

$$\bar{f}'_i(x, x_i) = 0$$

because the established products are at equilibrium.

The invasion fitness \bar{f}'_i represents the relative diffusion rate of a few innovative items in the market set by the established products. Innovations originate by chance but their fate depend on their competitiveness, i.e. on their capacity to penetrate into the market. Competitiveness is, therefore, a concept relevant on the market timescale, that necessarily depends on the innovative trait x'_i , as well as on the current market conditions, which are defined by the established product traits x . In other words, the invasion fitness of the novel product provides a summary of the underlying market selection process. As we shall see in the rest of the section, such a summary and a proper stochastic description of the innovation process are necessary and sufficient to make the step to macro-evolutionary considerations on the innovation timescale.

If $\bar{f}'_i(x, x'_i) < 0$, it follows from model (2) that just after the innovation $\dot{n}'_i < 0$, i.e. the innovative product does not penetrate and actually exits the market. Thus, the final result is still a set of N established products with traits x and densities $\bar{n}(x)$. By contrast, if $\bar{f}'_i(x, x'_i) > 0$, the innovative product initially penetrates and, under very general conditions, the i -th established product exits the market, being replaced by its new version. Thus, in this case, the trajectory of model (2) originating at $(\bar{n}(x), n'_i)$ ends at

$$\bar{n}^{(i)}(x') = (\bar{n}_1(x'), \dots, \bar{n}_{i-1}(x'), 0, \bar{n}_{i+1}(x'), \dots, \bar{n}_N(x'), \bar{n}_i(x')) \quad (8)$$

i.e. the final result is a new set of N established products with traits x' and densities $\bar{n}(x')$ (see (6)). In other words, each innovation brings a new trait into the market, but competition between established and innovative products selects the winner, namely the trait that remains in the market.

The conditions under which the innovative product replaces the established one are known as the *invasion implies substitution principle* (see Dercole, 2002, for a proof) and require that $\bar{n}(x)$ is continuous with respect to x_i at x and

$$\left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{x'_i=x_i} (x'_i - x_i) > 0 \quad (9)$$

Notice that the equilibrium $\bar{n}^{(i)}(x')$ (see (8)) exists because, by assumption, $\bar{n}(x)$ is continuous with respect to x_i at x . By developing \bar{f}'_i in Taylor series with respect to x'_i , and recalling that innovations are small (i.e. x'_i differs only slightly from x_i and $n'_i(0)$ is very small), one obtains:

$$\dot{n}'_i(0) \simeq n'_i(0) \left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{x'_i=x_i} (x'_i - x_i) \quad (10)$$

where $t = 0$ is the time at which the innovation occurs. Thus, condition (9) implies $\dot{n}'_i(0) > 0$, i.e. initial penetration of the innovative product.

The quantity

$$\left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{x'_i=x_i} \quad (11)$$

is called *selection derivative*, and the vector with components (11), $i = 1, \dots, N$, is called *selection gradient*. Thus, as long as the selection gradient does not vanish, the dynamics of the traits are characterised by

$$\dot{x}_i \begin{cases} > 0 & \text{if } \left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{x'_i=x_i} > 0 \\ < 0 & \text{if } \left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{x'_i=x_i} < 0 \end{cases} \quad i = 1, \dots, N$$

The selection gradient gives the direction of technological change and describes a continuous feedback between the innovation and the market selection processes. In fact, technological change, i.e. \dot{x}_i , depends on consumption patterns which develop on the market timescale in accordance with model (2) and are summarised by the invasion fitness (7) (through the selection gradient). In turn, consumption patterns are affected by the current market conditions condensed by x .

The process of innovation and selection can be further specified by making suitable assumptions on the frequency and distribution of innovations. The speed of innovation is influenced by three primary factors: how often an innovation occurs; how large a trait change an innovation causes; and how likely it is that an initially scarce set of new products penetrates. By suitably modelling these three factors, one can prove that if innovations are sufficiently small, the innovation process proceeds by a large number of subsequent penetrations and substitutions and can be approximated by the following system of ordinary differential equations (Dieckmann & Law, 1996; Champagnat *et al.*, 2001):

$$\dot{x}_i = \frac{1}{2} \mu_i(x) \bar{n}_i(x) \sigma_i^2(x) \left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{x'_i=x_i}, \quad i = 1, \dots, N \quad (12)$$

called the *canonical equation* of AD. With reference to the i -th product, μ_i is the probability of an innovation per event of production of a new item, $\mu_i \bar{n}_i$ is thus proportional to the number of innovations that are put on the market per unit of time (on the innovation timescale), and σ_i^2 is the variance of the trait change of an innovation (with expected change equal to zero). The probability of penetration consists of two factors. First, if the selection derivative (11) does not vanish, only innovations with trait value either larger or smaller

than that of the established product can penetrate; in other words, half of the innovations are at selective disadvantage. This leads to the factor $1/2$ in the canonical equation. Second, innovations at selective advantage may be accidentally lost in the initial phase of invasion when they are present only in a few items. The probability of not being lost is proportional to the selective advantage of the innovation as measured by the selection derivative (11).

In conclusion, we have obtained the following model

$$\dot{x}_i = G_i(x_1, \dots, x_N), \quad i = 1, \dots, N \quad (13)$$

where

$$G_i(x) = \frac{1}{2} \mu_i(x) \bar{n}_i(x) \sigma_i^2(x) \left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{x'_i=x_i}$$

Such a model describes the technological coevolution of N products coexisting at market equilibrium under the assumption of rare innovations of small effect.

2. Long term scenarios

In contrast to prevailing economic theories that focus on the properties of the equilibrium, the AD approach is based on a dynamical framework which accounts for the full dynamics of technological change and its concomitant changes in the market, including, for instance, the description of the evolutionary transient. Notice that the evolutionary model (13) is an autonomous system of ODEs. Thus, economic systems perpetually reshape themselves, thereby changing their own basis in terms of technologies in use and market environment, which are both condensed in the trait vector x .

It is important to remark that the AD canonical equation models a coevolutionary context where innovation in one product leads to coevolutionary changes in all other related products in the market under consideration. The importance of this mutual interactions is best described by Ziman (2000) who says “... material artefact’s cannot be considered in isolation from their cognitive and social correlates... as the artifact changes, so does the cloud of ideas and social activities that surround it”.

Moreover, model (13) is in general nonlinear, which means that the interactions between technology and its market are capable to give rise to a rich set of scenarios. In the simplest evolutionary scenario one can imagine (Fig. 1A), technological change converges to a particular combination of the traits, no matter

what the initial conditions are. A wilder scenario is that of never ending ups and downs of the traits like those recorded in the skirt length of women's formal evening dresses reconstructed from the analysis of fashion magazines over two centuries (Lowe & Lowe, 1990). In these cases the traits evolve either toward a limit cycle (Fig. 1B) or toward a strange attractor as discussed in Khibnik & Kondrashov (1997). Another case of interest (Fig. 1C) is that of alternative equilibria (or attractors). This means that the long term implications of the innovation process can depend upon the innovation paths followed in the past. Such path dependency could for example explain divergence phenomena discussed in development economics, where some developing countries seem to fall into a technological and economic underdevelopment trap, while, industrialised countries converge to a high technological level. Finally, it can also happen (Fig. 1D) that some evolutionary trajectories reach the boundary of the coexistence region where one of the products cannot be sustained in the market. This is, for example, what happened to the telex technology and what is expected to happen in the near future to the fax technology.

3. Emergence of diversity

We call *evolutionary equilibrium* a constant solution of the canonical equation (12), i.e. a set of traits \bar{x} at which all selection derivatives (11) vanish

$$\left. \frac{\partial \bar{f}'_i}{\partial x'_i} \right|_{\substack{x'_i = \bar{x}_i \\ x = \bar{x}}} = 0, \quad i = 1, \dots, N$$

Of course, evolutionary equilibria can be either stable or unstable equilibria of the canonical equation (12). If innovation dynamics have found a halt at a stable evolutionary equilibrium \bar{x} , where the first order term of $\dot{n}'_i(0)$ vanishes (see eq. (10)), in order to establish if an innovation is initially successful or not one can develop \bar{f}'_i in Taylor series up to the second order term, thus obtaining:

$$\dot{n}'_i(0) \simeq n'_i(0) \left. \frac{\partial^2 \bar{f}'_i}{\partial x'^2_i} \right|_{\substack{x'_i = \bar{x}_i \\ x = \bar{x}}} (x'_i - x_i)^2$$

The result is that the innovation initially penetrates if

$$\left. \frac{\partial^2 \bar{f}'_i}{\partial x'^2_i} \right|_{\substack{x'_i = \bar{x}_i \\ x = \bar{x}}} > 0 \tag{14}$$

no matter if the trait value x'_i is larger or smaller than the established trait \bar{x}_i . If condition (14) holds with the opposite inequality sign for all $i = 1, \dots, N$, then \bar{x} is protected against invasion and is, therefore, a so-called *evolutionarily stable strategy* (ESS) as defined in evolutionary game theory (Hamilton, 1967; Maynard Smith & Price, 1973; Maynard Smith, 1974, 1982; Nash). In other words, technological evolution by means of small innovations can drive an economic system to a terminal point of the evolutionary process, a trap from which the system can possibly escape only by exogenously injecting radically different products into the market.

Understanding the long term consequences of an invasion at \bar{x} is not an easy problem since we cannot rely on the invasion implies substitution principle, which indeed does not hold at an evolutionary equilibrium. However, Geritz *et al.* (2002) have shown that it is not possible that an initially penetrating innovative product is ruled out from the market in the long term. Thus, only two possibilities remain: either the innovative product substitutes the established product or it coexists with it at a stable and strictly positive market equilibrium. In accordance with the verbal definition given at point 3 of Section 1, \bar{x} is a branching point if

- it is a stable evolutionary equilibrium;
- the innovative product coexists with the established product, thus becoming an established product itself with density n_{N+1} and trait x_{N+1} ;
- the traits x_i and x_{N+1} are initially very close but, then, differentiate in accordance with the new $(N+1)$ -dimensional canonical equation.

Geritz *et al.* (1997, 1998) have shown that if $\bar{n}(x)$ is continuous at a stable evolutionary equilibrium \bar{x} , then \bar{x} is a branching point if, for some i , condition (14) holds and

$$\left. \frac{\partial^2 \bar{f}'_i}{\partial x_i \partial x'_i} \right|_{\substack{x'_i = \bar{x}_i \\ x = \bar{x}}} < 0 \quad (15)$$

If the branching conditions (14) and (15) hold for more than one product, it is a matter of chance which product will branch first.

Technological branching occurs when the selective forces acting on the market first allow the coexistence of two slightly different types of products and then become repulsive, therefore favouring the diversification of two technologies originating from the same trait. Think, for example, to mobile and fixed phones: the

first mobile phones were heavy car phones, different from fixed phones only for the presence of an antenna instead of a wire.

Notice that there are evolutionary equilibria which are neither ESSs nor branching points. Indeed, it can be shown (see Dercole, 2002) that an innovative product can penetrate the market and substitute the corresponding established product, thus leading to a new trait assembly x close to \bar{x} ; but at this new trait composition the canonical equation (12) holds and, if \bar{x} is stable, then x converges back to \bar{x} , which is, then, a terminal point of the evolutionary process, even if it is not protected against penetration. For this reason we refer to stable ESSs and to this subset of stable evolutionary equilibria as evolutionarily terminal strategies.

After a branching has occurred in the i -th product, the market is composed of $(N + 1)$ diversified products. Thus, one can derive the new $(N + 1)$ -dimensional canonical equation and repeat the analysis for the new market. If, again, technological change will evolve toward a branching point, the result will be a market with $(N + 2)$ diversified products, and so on. Since no limit exists on the number of possible repeated branchings there is room for the formation of rich clusters of products. Long sequences of technological branchings are empirically evident in almost every market segment. Consumers worldwide can witness that an increasing number of products that match their expectations are available on the market (see e.g. Grübler, 1998; Saviotti, 2001). For example, (Ausubel, 1990) showed that the average number of items on sale in a typical large US supermarket has increased from 2000 in 1950 to 18000 items in the 1990s.

4. Exogenous factors

The market competition model (2) and the frequency and distribution of mutations depend upon exogenous factors like consumer preferences, social and political structures, international relationships, availability of natural resources, and many others. In order to simplify the analysis, these factors can be left out from the model, but they can also be explicitly included in the model and measured through some strategic parameter, in which case the canonical equation (12) will depend explicitly upon a set of parameters. The role played by exogenous factors on the dynamics of technological change can then be identified by studying the canonical equation for all possible values of the exogenous parameters. This naturally calls for numerical bifurcation analysis (Kuznetsov, 1998), which is the most powerful technique for identifying the long term consequences of parameter perturbations in ODEs models.

Before presenting an explicit application of AD in economics, it is worth stressing that the analysis

described until now applies only to marginal innovations. In the case of a radical innovation (e.g. an invention, the establishment of a new import/export protocol, . . .), namely when the innovative product trait is remarkably different from all other traits established in the market, the outcome of the competition must be established by means of model (2). Once the new market equilibrium has been determined, the method of analysis discussed in this section can be used again to detect the consequences of new marginal innovations. Thus, the process of technological change, described by AD as a continuous process due to marginal innovations, is punctuated from time to time by major breakthroughs. Moreover, radically innovative products can penetrate the market without substituting the previous established products. Thus, the AD approach interestingly shows that the emergence of new products can be attributed to both marginal and radical innovation events. While it is rather obvious, as noted already by Schumpeter (1912), that radical innovations can generate product diversity, it is less obvious that product diversification can emerge through technological branching of incremental innovation steps. Thus, technological branching helps explaining increasing product diversity in a world that is dominated by incremental innovations.

3 A simple example of technological branching

We now present the first application of AD in economics. The problem we consider is intentionally simple in order to obtain the AD canonical equation in closed form and clearly identify the stylised properties mentioned in the first section. Although the model is far from being empirically testable, it provides some insights on the market conditions which favour technological branching and the emergence of product clusters.

We assume that different products $j = 1, \dots, N$ characterised by a single technological trait x_j compete in the market according to the following model:

$$\dot{n}_j = r(x_j)n_j \left[1 - \frac{1}{K(x_j)} \sum_{l=1}^N \alpha(x_j, x_l)n_l \right], \quad j = 1, \dots, N \quad (16)$$

where the functions $r(x_j)$, $K(x_j)$ and $\alpha(x_j, x_l)$ describe the market environment and have the following economic interpretation. The function $r(x_j)$ is the maximum diffusion rate of the j -th product, which is realised only when the product is present in the market in small quantities (n_j very small) and there are no competitors ($n_l = 0$ for all $l \neq j$). The function $r(x_j)$ is therefore a theoretical measure of the penetration

power of the product in an empty market. Similarly, $K(x_j)$ is the equilibrium density reached by the j -th product penetrating an empty market, under the normalisation property $\alpha(x_j, x_j) = 1$. Thus, $K(x_j)$ gives a theoretical measure of the product density absorbable by the market and will be hereafter called *absorptive capacity* of the market. Finally, the *competition function* $\alpha(x_j, x_l)$ measures the reduction of the rate of diffusion of the j -th product due to the presence in the market of the competitor l -th product.

Model (16) is a special type of bilinear competition model, which has, generically, a unique strictly positive equilibrium satisfying the following system of N linear algebraic equations:

$$\sum_{l=1}^N \alpha(x_j, x_l) \bar{n}_l(x) = K(x_j), \quad j = 1, \dots, N \quad (17)$$

Model (16) is quite special because it describes a purely competitive market. However, the analysis performed in the following can certainly be extended to a wide spectrum of behavioural interactions, ranging from competition to cooperation. Various notions of *Homo reciprocans* and *Homo economicus* could be modelled, reflecting certain social mechanisms and institutions that punish anti-social behaviour (Boyd & Richerson, 1992; Fehr & Gächter, 1998) but also reward image scoring (Nowak & Sigmund, 1998).

Let us assume that r is independent upon the trait and that the competition and absorptive capacity functions are given by:

$$\alpha(x_j, x_l) = \exp\left(\frac{\ln^2 \beta}{2\sigma_\alpha^2}\right) \exp\left[-\frac{1}{2\sigma_\alpha^2} \left(\ln \frac{x_l}{\beta x_j}\right)^2\right] \quad (18)$$

$$K(x_j) = K_0 \exp\left[-\frac{1}{2\sigma_K^2} \left(\ln \frac{x_j}{x_0}\right)^2\right] \quad (19)$$

where β , σ_α , K_0 , x_0 , σ_K are constant positive parameters. The competition function (18) satisfies the normalisation property $\alpha(x_j, x_j) = 1$, depends only upon the ratio x_j/x_l of its arguments and tends to zero when such a ratio tends either to zero or to infinity, reflecting the fact that very diversified products compete only weakly (e.g. Ferrari and Fiat in the car market). Two parameters, namely β and σ_α , control the shape of the competition function. For $\beta = 1$, competition is symmetric, i.e. $\alpha(x_j, x_l) = \alpha(x_l, x_j)$ and $\alpha(x_j, x_l)$ is maximum (and equal to one) for $x_j = x_l$. For $\beta \neq 1$, competition is asymmetric and $\alpha(x_j, x_l)$ is maximum for $x_l = \beta x_j$ (see eq. (18) and Fig. 2A). This implies that for $\beta > 1$ products with higher technological content tend to have a competitive advantage. Analogously, for $\beta < 1$ products with less technological

content are better competitor. The parameter σ_α controls the sensitivity of the strength of competition with respect to the ratio of the technological traits of competing products. High sensitivity (i.e. small σ_α) means that only very similar products compete, while if σ_α is large competition is high even between quite different products. Graphically (see Fig. 2A) σ_α is a measure of the wideness of the bell shaped graph representing the competition function with respect to the technological trait x_l . Three parameters, namely K_0 , x_0 and σ_K , characterise the absorptive capacity function (19), which is bell shaped and peaks at some intermediate trait, given by x_0 . The economic interpretation is that in a single product market x_0 is the technology which is most absorbable by the market, while the equilibrium density of a technologically very poor or very sophisticated product vanishes with a sensitivity controlled by σ_K . High or low sensitivity (small and large values of σ_K) respectively represent market structures where products concentrate around the technological characteristic trait x_0 or where consumers are to a large degree indifferent to different products satisfying a specific need. Graphically (see Fig. 2B) σ_K is a measure of the wideness of the bell shaped graph of the absorptive capacity function.

Consider now the case of a market with a single established product and denote by n'_1 and x'_1 the density and trait of the innovative product. From eqs. (16) and (17), it follows that the market equilibrium $\bar{n}_1(x_1)$, the invasion fitness $\bar{f}'_1(x_1, x'_1)$ and the selection derivative (see eqs. (7) and (11)) are given by:

$$\begin{aligned}\bar{n}_1(x_1) &= K(x_1) \\ \bar{f}'_1(x_1, x'_1) &= r \left[1 - \frac{\alpha(x'_1, x_1)K(x_1)}{K(x'_1)} \right] \\ \left. \frac{\partial \bar{f}'_1}{\partial x'_1} \right|_{x'_1=x_1} &= \frac{r}{x_1} \left(\frac{1}{\sigma_\alpha^2} \ln \beta - \frac{1}{\sigma_K^2} \ln \frac{x_1}{x_0} \right)\end{aligned}$$

Therefore, the AD canonical equation (see eq. (12)) is

$$\dot{x}_1 = \frac{1}{2} \mu_1 \bar{n}_1(x_1) \sigma_1^2 \left. \frac{\partial \bar{f}'_1}{\partial x'_1} \right|_{x'_1=x_1} \quad (20)$$

where μ_1 and σ_1 are assumed to be independent upon the trait. Eq. (20) admits a unique evolutionary equilibrium

$$\bar{x}_1 = x_0 \beta \left(\frac{\sigma_K}{\sigma_\alpha} \right)^2 \quad (21)$$

which is always an attractor, since its associated eigenvalue is negative, because it has the same sign than

$$\frac{d}{dx_1} \left(\frac{\partial \bar{f}'_1}{\partial x'_1} \Big|_{x'_1=x_1} \right) \Big|_{x_1=\bar{x}_1} = -\frac{r}{(\bar{x}_1 \sigma_K)^2} < 0 \quad (22)$$

Thus, in a market with a single product, repeated innovations and replacements of old variants with new ones drive the technological trait x_1 toward the equilibrium value \bar{x}_1 . At \bar{x}_1 two selective forces acting on the market balance: the desire of a producer to be a better competitor by being distinct in technological content (under asymmetric competition) and the tendency to harvest on the median consumer in order to maximise the number of product items absorbable by the market (battle for market share). If, for example, higher technological traits are favoured ($\beta > 1$), the economic intuition for reaching an equilibrium of zero technological change would be that there are cognitive, informational or physical limitations of consumers to absorb high technology, or simple budget constraints. Such limitations are modelled by the ratio σ_α/σ_K (see eq. (21)). Notice that when x_1 is slightly larger [smaller] than x_0 and $\beta > 1$ [$\beta < 1$], a penetrating innovative product conquers the market, even if this implies a loss in product density.

In order to assess if the evolutionary equilibrium \bar{x}_1 marks the end of technological change or is a branching point, we can use the branching conditions (14) and (15), which in the present case are

$$\frac{\partial^2 \bar{f}'_1}{\partial x'^2_1} \Big|_{\substack{x'_1=\bar{x}_1 \\ x_1=\bar{x}_1}} = \frac{r}{\bar{x}_1^2} \left(\frac{1}{\sigma_\alpha^2} - \frac{1}{\sigma_K^2} \right) > 0 \quad (23)$$

$$\frac{\partial^2 \bar{f}'_1}{\partial x_1 \partial x'_1} \Big|_{\substack{x'_1=\bar{x}_1 \\ x_1=\bar{x}_1}} = \frac{d}{dx_1} \left(\frac{\partial \bar{f}'_1}{\partial x'_1} \Big|_{x'_1=x_1} \right) \Big|_{x_1=\bar{x}_1} - \frac{\partial^2 \bar{f}'_1}{\partial x'^2_1} \Big|_{\substack{x'_1=\bar{x}_1 \\ x_1=\bar{x}_1}} < 0 \quad (24)$$

Notice that, condition (24) is implied by the stability of \bar{x}_1 (see eq. (22)) and by condition (23). Thus, the equilibrium \bar{x}_1 is a branching point if the sensitivity of the competition function σ_α is smaller than the sensitivity σ_K of the absorptive capacity function; of course, in the opposite case the evolutionary equilibrium is an ESS. Although the two sensitivities govern the dynamics of product densities on the market timescale (see eq. (16)), they ultimately manifest themselves on the innovation timescale. Then, the difference $\sigma_K - \sigma_\alpha$ is a measure of the strength of diversification through technological change. Taking into account the geometric characteristics of the competition and absorptive capacity functions, we can say that our simple model suggests that technological branching occurs when the absorptive capacity is more flat than the competition function (see Fig. 2).

A relatively flat absorptive capacity would arise in situations when consumers are to a large extent indifferent to products satisfying a specific need. A typical example in a market for meat would be when consumers are indifferent to various sources of protein be it red meat, white meat, or meat imitations like soya products. The absorptive capacity function could also be interpreted as an aggregated utility function. In this case, the curvature, i.e. the second derivative of the utility function, is a measure for risk aversion. Hence a relatively flat absorptive capacity could be interpreted as a more risk taking representative agent (in this case consumer). Given such an interpretation less risk aversion would, according to our model, lead to product diversification.

On the other hand, competition functions are narrow when despite of a relatively small difference in the characteristic traits, the respective products weakly suffer from each other by competition. For example, the competition between “Breitling” and “Swatch” watches, or between stocks within the NASDAQ index, could be modelled by narrow competition functions.

A specific example of innovation dynamics under asymmetric competition ($\beta > 1$) is shown in Fig. 3 for the particular parameter setting (specified in the caption) for which the equilibrium \bar{x}_1 is a branching point. Starting with a single product with trait x_1 smaller than \bar{x}_1 , the trait first increases toward \bar{x}_1 , as shown in Fig. 3A for $0 < t < t_2$. On the innovation timescale the equilibrium density $\bar{n}_1(x_1)$ declines when $x_1 > x_0$ (see eq. (21)), i.e. for $0 < t < t_2$ except for the very first part of the time interval where $x_1 < x_0$, as shown in the lower panel of Fig. 3A. In Fig. 3B the transients of the densities due to two particular successful innovations are shown on the market timescale. The first one (upper panel) corresponds to the market conditions holding at time t_1 in Fig. 3A: the density n_2 of the innovative product is initially very small, but then grows toward an equilibrium, while the density n_1 of the established product declines to zero, thus revealing that the innovative product has substituted the established product. In the lower panel of Fig. 3B, corresponding to the branching occurring at time t_2 , the innovative product penetrates the market but does not substitute the established product, as shown by the graph of n_1 , which declines but does not vanish.

After the branching has occurred, the innovation dynamics is given by the competition between a challenging innovative product and two distinct established products. The analysis of the two-products market can be performed by analysing the corresponding second order canonical equation. Denoting by n'_i and x'_i the density and trait of the innovative product and recalling eqs. (16) and (17), then the two-products market equilibrium $\bar{n}(x_1, x_2)$, the invasion fitness $f'_i(x, x'_i)$ and the selection gradient (see eqs. (7) and (11)) are

given by:

$$\begin{aligned}\bar{n}(x) &= \frac{1}{1 - \alpha(x_1, x_2)\alpha(x_2, x_1)} \begin{bmatrix} K(x_1) - \alpha(x_1, x_2)K(x_2) \\ -\alpha(x_2, x_1)K(x_1) + K(x_2) \end{bmatrix} \\ \bar{f}'_i(x, x'_i) &= r \left[1 - \frac{\alpha(x'_i, x_1)\bar{n}_1(x_1, x_2) + \alpha(x'_i, x_2)\bar{n}_2(x_1, x_2)}{K(x'_i)} \right] \\ \frac{\partial \bar{f}'_i}{\partial x'_i} \Big|_{x'_i=x_i} &= -\frac{r}{K(x_i)} \left[\frac{\partial \alpha(x'_i, x_1)}{\partial x'_i} \Big|_{x'_i=x_i} \bar{n}_1(x_1, x_2) + \frac{\partial \alpha(x'_i, x_2)}{\partial x'_i} \Big|_{x'_i=x_i} \bar{n}_2(x_1, x_2) \right] + \\ &\quad + \frac{r}{k^2(x_i)} \frac{dK(x_i)}{dx_i} [\alpha(x_i, x_1)\bar{n}_1(x_1, x_2) + \alpha(x_i, x_2)\bar{n}_2(x_1, x_2)]\end{aligned}$$

$i = 1, 2$, provided that $x_1 \neq x_2$. Therefore, the second order AD canonical equation (see eq. (12)) is

$$\begin{aligned}\dot{x}_1 &= \frac{1}{2} \mu_1 \bar{n}_1(x_1, x_2) \sigma_1^2 \frac{\partial \bar{f}'_1}{\partial x'_i} \Big|_{x'_i=x_1} \\ \dot{x}_2 &= \frac{1}{2} \mu_2 \bar{n}_2(x_1, x_2) \sigma_2^2 \frac{\partial \bar{f}'_2}{\partial x'_i} \Big|_{x'_i=x_2}\end{aligned} \tag{25}$$

where μ_i and σ_i , $i = 1, 2$, are assumed to be independent upon the traits.

The relevant trajectory of model (25) is that originating from point $(\bar{x}_1, \bar{x}_1 + \epsilon)$ (ϵ very small), corresponding to the market condition holding at time t_2 in Fig. 3A just after the transient depicted in the lower panel of Fig. 3B, i.e. just after the branching has occurred. The evolution of the traits x_1 and x_2 and that of the corresponding product densities $\bar{n}_1(x_1, x_2)$ and $\bar{n}_2(x_1, x_2)$ along such a trajectory are shown in Figs. 3A and B, respectively ($t > t_2$). Figure 3A shows that the trait in one branch permanently increases, while in the other it initially decreases. This was expected because at a branching point the old and the new version of the product coexist under opposite selection pressures. Notice that the product associated with the upper branch (away from x_0) has a lower density, i.e. it is present in the market with fewer items, which, however, have a competitive advantage with respect to those in the lower branch, which resist competition being close to the trait (x_0) that matches the median consumer. Finally, Fig. 3A shows that the innovation dynamics drive the traits x_1 and x_2 of the two coexisting products toward a stable evolutionary equilibrium (\bar{x}_1, \bar{x}_2) . At this equilibrium the branching conditions (14) and (15) have been numerically tested by varying all the parameters of the model and the result is that again conditions (14) and (15) hold for both products if $\sigma_K > \sigma_\alpha$.

Of course, to understand the evolution of the system after the second branching, the analysis can be

repeated, starting from the new (third order) canonical equation. By means of a systematic bifurcation analysis of the third and higher order canonical equations, we checked that the traits of N coexisting products always converge toward a unique stable evolutionary equilibrium at which the branching conditions (14) and (15) hold for all products if $\sigma_K > \sigma_\alpha$ (more weakly as N increases). This numerical analysis has been performed for wide ranges of all the parameters of the model (and various N) and has always brought to the same conclusion, namely that $\sigma_K > \sigma_\alpha$ implies the formation of rich clusters of products through a long sequence of technological branchings.

4 Concluding remarks

The purpose of this paper was to show how a recently proposed theory of evolutionary processes called Adaptive Dynamics (AD), could be used to explain the emergence of technological variety in economic systems. For this, we have first presented AD by adapting it to fit the properties of economic systems. Then, we have used AD for studying the evolution of the technological traits of the products present in a market. Our analysis is based on an abstract model which is intentionally very simple in order to obtain an analytically tractable problem. It is clear, however, that the analysis can be extended to much more realistic and complex situations, provided analytical tractability is not required.

Since some of the assumptions underneath AD are rather extreme, one must be careful in applying it to real situations. For example, technological change is an economic phenomenon taking place at different levels of temporal aggregation of the economy, involving individual consumers, businesses, markets, science, technology, formal and informal institutions and culture at wider levels (Nelson, 1995; North, 1997; Hayek, 1967). In real economic systems the market and innovation timescales are sometimes comparable, while AD requires that they are fully separated. However, quite frequently competition and technological change occur on contrasting timescales. Technological change slowly proceeds by means of continual replacement of established entities by novel ones on the micro-level, i.e. as a result of the fast interaction between economic actors on the market timescale. In consequence, AD provides a reasonable approximation of the process of technological change with the major promise of elucidating the long-term effects of the interplay between the single entities on a micro-level and the system's evolutionary fate on a macro-level.

Perhaps, the most relevant advantage of AD with respect to other theories is the possibility of clearly explaining the emergence of technological diversity and the formation of rich clusters of products. In-

deed, it is empirically evident that technological diversity is a natural characteristic of industries undergoing technological change (see e.g. Bernard *et al.*, 1994; Metcalfe, 1988). However, there is little room for technological diversity in classical economic models: when the best practise is common knowledge it is instantly adopted and diversity has no theoretical justification (Jonard & Yildizoglu, 1999). Yet diversity is the basis for consumer choice and a prerequisite for competition. With the advent of evolutionary approaches and institutional approaches the role of variety, as called by Schumpeter, became a renascent topic. Stirling (1998) and various papers by Saviotti provide excellent reviews of the literature on the economics of diversity and shall not be repeated here. There is detailed empirical and theoretical work in areas like consumer characteristics, production processes and organisational forms, research strategies, competences and learning processes, technologies and modes of innovation, investor expectations and customer choice and competition.

Some of the evolutionary approaches to industrial dynamics explain the emergence of diversity by including uncertainty in the diffusion process, bounded rationality, imperfect information, demand slacks and endogenously determined market structures (Nelson & Winter, 1982; Dalle, 1998; Saviotti, 2001; Witt, 2001). However, at least in the limit case, in all models the selective pressures and the mechanical nature of diffusion lead to just one dominant technology. De Palma *et al.* (1998) show that in the presence of network externalities, diversity prevails as long as the effect of consumer heterogeneity overrules the effect of network externalities. These models, however, have to assume differentiated markets from the beginning and are not explicit on the emergence of diversity. Another popular hypothesis in economic theory is that local interaction (e.g. localisation of imitation and localisation of network externalities) is a condition for aggregate diversity (see e.g. Jonard & Yildizoglu, 1998a,b; Nelson & Winter, 1982). In these models diversity is explained through geographically disjoint technological path dependencies leading to localised positive feedback economies such as agglomeration economies (Matsuyama, 1995; Arthur, 1990; Porter, 1990; Engländer, 1926; Ritschl, 1927; Palander, 1935). Earlier models in spatial economics that can be associated with the names of von Thünen (1826), Weber (1909), Christaller (1933), Loesch (1941) see locational patterns as independent of history, inevitable, and thus lead to a unique equilibrium determined by, among others, geographical endowments, infrastructures and firms' needs. Geographically disjoint technological development is, however, in conflict with the empirical observations of spatial clusters, which consist of a complex of competing and complementary firms (or even branches within firms) involved in producing similar goods and services (see e.g. Marshall, 1920; Dunning, 2000). By contrast, AD allows for the

evolution of technological diversity emerging in the same geographic area due to technological branching.

As this paper represents a first attempt to develop a dynamic model of technological change consistent with AD and compatible with several results from existing economic models, we have also shown that AD carries the potential to lead to new insights in the analysis of the metabolism and development of traits of economic systems. Many are, in fact, the evolutionary phenomena one can think to tackle by means of the AD approach. For example, apart from the increase in numbers of products through technological branching, we also see increase in product complexity. Illustrative for increasing complexity is the fact that the 1885 Rover safety bicycle consisted of about 500 parts, a modern car involves as many as 30,000 components and a Boeing 747 roughly 3.5 million (Ayres, 1988). Thus, product complexity could be modelled as trait of a suitable AD model, in order to investigate the economic conditions that lead to increasing complexity and their consequence on technological change and economic development.

Another scenario that can be interpreted by the AD approach is the convergence toward an underdevelopment trap, an ESS that can only be broken by a radical innovation. Modelling aggregate traits such as the level of technological development, one could use AD to show that developing countries are often destined to reach an ESS at a low level of technological development, from which they can hardly escape. In fact, for many developing countries, the relevant technological traits are defined more by epigenetic codes such as formal institutions and tacit social norms, which are more difficult to change radically as they acquire more and longer-lasting information than individual agents. On these lines Greif (1994) argues that “the capacity of societal organisation to change is a function of history, since institutions are combined of organisations and cultural beliefs, . . . and past organisations and beliefs influence historically subsequent games, organisations and equilibria”. The work of Hayek (1967) is more inspired by the idea of spontaneous evolution of conventions and institutions (Vromen, 1995) explaining radical changes of epigenetic codes.

Finally, outside the economic field, AD can be of great help for understanding various problems in social sciences. Even if many human behaviours are culturally transmitted, learned, or imitated (Boyd & Richerson, 1985), they can be treated as heritable traits: if differences in possible behaviours affect some measure of success, i.e. fitness, then behaviours can evolve through an innovation-selection process, where innovation simply means a behavioural change. Two relevant examples of behavioural evolution are fashion and cooperation.

The role of fashion is “identity display”. The tendency to imitate certain stereotypes with desirable characteristics and the opposite tendency to diverge from them in order to proclaim an identity are contrasting

selective forces. The trade-off between imitation and personalisation might induce complex evolutionary dynamics of fashion traits, as shortly mentioned in Section 2 in the discussion of long term evolutionary scenarios.

The evolution of cooperation among non-related individuals is one of the fundamental problems in social sciences. Experimental economists investigate this issue by public goods games, confronting individuals with the temptation to defect, i.e. to exploit the reward obtained from the public good without contributing to it. This is known as “The Tragedy of the Commons” (Hardin, 1968). Experimental results (Boyd & Richerson, 1992; Fehr & Gächter, 2000; Fischbacher *et al.*, 2001; Fehr & Gächter, 2002) show that, without a mechanism for punishing defectors, groups of cooperators do better than groups of defectors, but defectors always outperform the cooperators in their group. In a recent theoretical study Hauert *et al.* (2002) describe the dynamics of the densities of cooperators, defectors and loners in the population, but do not allow their characteristic behaviour to evolve. Thus, AD could be used to study the evolution of the propensity to cooperate, measured through a trait which is positive in the case of cooperation and negative in the case of defection.

In conclusion, beyond the intentionally simplified example presented in this paper, we believe that the AD approach is particularly suited to analyse technology-society interactions.

Acknowledgements

The authors are grateful to two anonymous reviewers for useful suggestions and comments on a first draft of this manuscript of. F.D. and S.R. acknowledge the support of MIUR (under project FIRB-RBNE01CW3M).

References

- Aghion, P. & Howitt, P. (1992) A model of growth through creative destruction. *Econometrica* **60**, 323–351.
- Arthur, W. B. (1990) Silicon valley's locational clusters: When increasing returns imply monopoly. *Mathematical Social Sciences* **19**, 235–251.
- Ausubel, J. H. (1990) Hydrogen and the green wave. *The Bridge* **20**, 17–22.
- Ayres, R. U. (1988) Complexity, reliability, and design: Manufacturing implications. *Manufacturing Review* **1**, 26–35.
- Bernard, J., Canter, U., Hnusch, H., & Westerman, G. (1994) Detecting technological performance and variety. EUNETIC Conference, October 6-7, Strasbourg.
- Boyd, R. & Richerson, P. J., eds. (1985) *Culture and the Evolutionary Process*. The University of Chicago Press.
- Boyd, R. & Richerson, P. J. (1992) Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* **13**, 171–195.
- Brooks, H. (1980) Technology, evolution, and purpose. *Daedalus* **109**, 65–81.
- Burda, M. & Wyplosz, Ch. (1997) *Macroeconomics: A European Text*. Oxford University Press.
- Champagnat, N., Ferrière, R., & Ben Arous, G. (2001) The canonical equation of adaptive dynamics: A mathematical view. *Selection* **2**, 73–83.
- Christaller, W. (1933) *Central Places in Southern Germany*. Prentice-Hall.
- Dalle, J. M. (1998) Local interaction structures, heterogeneity and diffusion of technological innovations. In *Advances in Self-Organization and Evolutionary Economics*, eds. Lesourne, J. & Orléan, A., Economica, London, pp. 240–264.
- De Palma, A., Kilani, K., & Lesourne, J. (1998) How network externalities affect product variety. In *Advances in Self-Organization and Evolutionary Economics*, eds. Lesourne, J. & Orléan, A., Economica, London, pp. 57–76.

- Dercole, F. (2002) *Evolutionary Dynamics through Bifurcation Analysis: Methods and Applications*. Ph.d. thesis, Department of Electronics and Information, Politecnico di Milano, Milano, Italy.
- Dercole, F., Ferrière, R., & Rinaldi, S. (2002) Ecological bistability and evolutionary reversals under asymmetrical competition. *Evolution* **56**, 1081–1090.
- Dercole, F., Gragnani, A., Ferrière, R., & Rinaldi, S. (2003) Coevolution of slow-fast populations: An application to prey-predator systems. *The American Naturalist* (submitted).
- Dercole, F. & Rinaldi, S. (2002) Evolution of cannibalism: Scenarios derived from adaptive dynamics. *Theoretical Population Biology* **62**, 365–374.
- Dieckmann, U. & Law, R. (1996) The dynamical theory of coevolution: A derivation from stochastic ecological processes. *Journal of Mathematical Biology* **34**, 579–612.
- Dunning, J. H. (2000) Regions, globalization, and the knowledge economy: The issues stated. In *Regions, Globalization, and the Knowledge Economy*, ed. Dunning, J., Oxford University Press, pp. 1–29.
- Engländer, O. (1926) *Kritisches und Positives zu einer allgemeinen reinen Lehre von Standort*. Zeitschrift für Volkswirtschaft und Sozialpolitik, Neue Folge 5.
- Fehr, E. & Gächter, S. (1998) Reciprocity and economics: The economic implications of homo reciprocans. *European Economic Review* **42**, 845–59.
- Fehr, E. & Gächter, S. (2000) Cooperation and punishment in public goods experiments. *American Economic Review* **90**, 980–994.
- Fehr, E. & Gächter, S. (2002) Altruistic punishment in humans. *Nature* **415**, 137–140.
- Fischbacher, U., Gächter, S., & Fehr, E. (2001) Are people conditionally cooperative? Evidence from a public goods experiment. *Economics Letters* **71**, 397–404.
- Fisher, J. C. & Pry, R. H. (1971) A simple substitution model of technological change. *Technological Forecasting and Social Change* **3**, 75–88.
- Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A., & Parvinen, K. (2002) Invasion dynamics and attractor inheritance. *Journal of Mathematical Biology* **44**, 548–560.

- Geritz, S. A. H., Kisdi, E., Meszéna, G., & Metz, J. A. J. (1998) Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Ecology* **12**, 35–57.
- Geritz, S. A. H., Metz, J. A. J., Kisdi, E., & Meszéna, G. (1997) The dynamics of adaptation and evolutionary branching. *Physical Review Letters* **78**, 2024–2027.
- Greif, A. (1994) Cultural beliefs and the organization of society: A historical and theoretical reflection on collectivist and individualist societies. *Journal of Political Economy* **102**, 912–950.
- Grossman, G. M. & Helpman, E. (1991) *Innovation and Growth in the Global Economy*. MIT Press.
- Grübler, A. (1998) *Technology and Global Change*. The Press Syndicate of the University of Cambridge, Cambridge, UK.
- Hamilton, W. D. (1967) Extraordinary sex ratios. *Science* **156**, 477–488.
- Harberger, A. C. (1998) A vision of the growth process. *American Economic Review* **88**, 1–32.
- Hardin, G. (1968) The tragedy of the commons. *Science* **162**, 1243–1248.
- Hauert, C., De Monte, S., Hofbauer, J., & Sigmund, K. (2002) Volunteering as Red Queen mechanism for cooperation in public goods games. *Science* **296**, 1129–1132.
- Hayek, F. A. (1967) *Studies in Philosophy, Politics, and Economics*. Routledge & Kegan Paul, London.
- Hodgson, G. M. (1997) The evolutionary and non-Darwinian economics of Joseph Schumpeter. *Journal of Evolutionary Economics* **7**, 131–146.
- Jonard, N. & Yildizoglu, M. (1998a) Interaction between local interactions: Localized learning and network externalities. In *The Economics of Networks: Interaction and Behaviours*, eds. Cohendet, P., Llerena, P., Stahn, H., & Umbhauer, G., Springer Verlag, Berlin, pp. 189–204.
- Jonard, N. & Yildizoglu, M. (1998b) Technological diversity in an evolutionary model with localized learning and network externalities. *Structural Change and Economic Dynamics* **9**, 35–55.
- Jonard, N. & Yildizoglu, M. (1999) Sources of technological diversity. Cahiers de l'innovation n. 99030, CNRS, Paris.

- Kelm, M. (1997) Schumpeter's theory of economic evolution: A Darwinian interpretation. *Journal of Evolutionary Economics* **7**, 97–130.
- Khibnik, A. I. & Kondrashov, A. S. (1997) Three mechanisms of Red Queen dynamics. *Proceedings of the Royal Society of London B* **264**, 1049–1056.
- Kortum, S. (1997) Research, patenting, and technological change. *Econometrica* **65**, 1389–1419.
- Kuznetsov, Yu. A. (1998) *Elements of Applied Bifurcation Theory*. Springer Verlag, Berlin, 2nd ed.
- Loesch, A. (1941) *The Economics of Location*. Yale University Press.
- Lowe, E. D. & Lowe, J. W. (1990) Velocity of the fashion process in women's formal evening dress, 1789-1980. *Clothing and Textiles Research Journal* **9**, 50–58.
- Marshall, A. (1920) *Principles of Economics*. MacMillan Publishing, 8th ed.
- Matsuyama, K. (1995) Complementarities and cumulative processes in models of monopolistic competition. *Journal of Economic Literature* **33**, 701–729.
- Maynard Smith, J. (1974) The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology* **47**, 209–221.
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge University Press.
- Maynard Smith, J. & Price, J. (1973) The logic of animal conflicts. *Nature* **246**, 15–18.
- Metcalfe, J. S. (1988) The diffusion of innovation: An interpretative survey. In *Technical Change and Economic Theory*, eds. Dosi, G., Freeman, C., Silverberg, R. N. G., & Soete, L., Francis Pinter, London, pp. 560–589.
- Metz, J. A. J., Geritz, S. A. H., Meszéna, G., Jacobs, F. J. A., & van Heerwaarden, J. S. (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. & Verduyn Lunel, S. M., NHA, pp. 183–231.
- Nash, J. () *Essays on Game Theory*. Edward Elgar, Princeton, NJ.

- Nelson, R. (1995) Recent evolutionary theorizing about economic change. *Journal of Economic Literature* **33**, 48–90.
- Nelson, R. & Winter, S. (1982) *An Evolutionary Theory of Economic Change*. Harvard University Press, Cambridge, MA.
- North, D. C. (1997) The contribution of the new institutional economics to the understanding of the transition problem. WIDER Annual Lectures 1, World Institute for Development Economics Research, Helsinki.
- Nowak, M. A. & Sigmund, K. (1998) Evolution of indirect reciprocity by image scoring. *Nature* **393**, 573–577.
- Palander, T. (1935) *Beiträge zur Standortstheorie*. Uppsala, Almqvist and Wiksells.
- Peretto, P. (1998) Technological change and population growth. *Journal of Economic Growth* **3**, 238–311.
- Porter, M. E. (1990) *The Competitive Advantage of Nations*. The Free Press.
- Ritschl, H. (1927) Reine und historische Dynamik des Standortes der Erzeugungszweige. *Schmollers Jahrbuch* **51**, 813–870.
- Romer, P. M. (1990) Endogenous technological change. *Journal of Political Economy* **98**, 71–102.
- Saviotti, P. P. (1996) *Technological Evolution, Variety and the Economy*. Edward Elgar, Cheltenham.
- Saviotti, P. P. (2001) Variety, growth and demand. *Journal of Evolutionary Economics* **11**, 119–142.
- Schumpeter, J. A. (1912) *Theorie der wirtschaftlichen Entwicklung*. Dunker und Humbolt, Leipzig.
- Segerstrom, P. (1998) Endogenous growth without scale effects. *American Economic Review* **88**, 1290–1310.
- Stirling, A. (1998) On the economics and analysis of diversity. SPRU Electronic Working Paper Series n. 28.
- von Thünen, J. H. (1826) *Der isolierte Staat in Beziehung auf Landwirtschaft und Nationalökonomie*. Hamburg.
- Vromen, J. J. (1995) *Economic Evolution: An Enquiry Into the Foundations of New Institutional Economics*. Routledge, London.
- Weber, A. (1909) *The Theory of Location of Industries*. The University of Chicago Press.

Witt, U. (2001) Learning to consume: A theory of wants and of growth of demand. *Journal of Evolutionary Economics* **11**, 23–36.

Young, A. (1998) Growth without scale effects. *Journal of Political Economy* **106**, 41–63.

Ziman, J. (2000) Evolutionary models for technological change. In *Technological Innovation as an Evolutionary Process*, ed. Ziman, J., Cambridge University Press, pp. 41–52.

Figure captions

Figure 1

Possible evolutionary scenarios: convergence toward an equilibrium (*A*) or a limit cycle (*B*) from any initial conditions; alternative equilibria (*C*); evolutionary extinction of a product (*D*).

Figure 2

(*A*) The strength of competition exerted by the l -th product on the rate of diffusion of the j -th product with trait \bar{x}_j , as a slice of the competition function $\alpha(x_j, x_l)$ along the plane $x_j = \bar{x}_j$; straight lines on the (x_j, x_l) plane: $x_l = x_j$ on which $\alpha(x_j, x_l) = 1$; $x_l = \beta x_j$ on which $\alpha(x_j, x_l)$ is maximum; parameter values $\bar{x}_j = 0.5$, $\beta = 1.2$, $\sigma_\alpha = 0.3$. (*B*) The absorptive capacity function; parameter values $K_0 = 1000$, $x_0 = .5$, $\sigma_K = .3$.

Figure 3

Innovation dynamics. (*A*) Characteristic traits (first row) and equilibrium densities (second row) obtained through simulation of models (20) and (25) with the initial condition $x_1(0) = 0.5$. (*B*) two examples of market dynamics obtained through simulation of model (16): product substitution (first row, $x_1 = 2$, $x_2 = x_1 * 1.01$, $n_1(0) = \bar{n}_1(x_1) = 786.45$, and $n_2(0) = 1$); branching (second row, $x_1 = \bar{x}_1=2.0736$, $x_2 = \bar{x}_1 * 1.01$, $n_1(0) = \bar{n}_1(x_1) = 766.49$, and $n_2(0) = 1$); on the innovation timescale, these examples correspond to the instants denoted by t_1 and t_2 in (*A*). Parameter values: $\mu_1 = \mu_2 = 1$, $\sigma_1 = \sigma_2 = 1$, $r = 1$, $\beta = 1.2$, $\sigma_\alpha = 0.5$, $K_0 = 1000$, $x_0 = 1$, $\sigma_K = 1$.

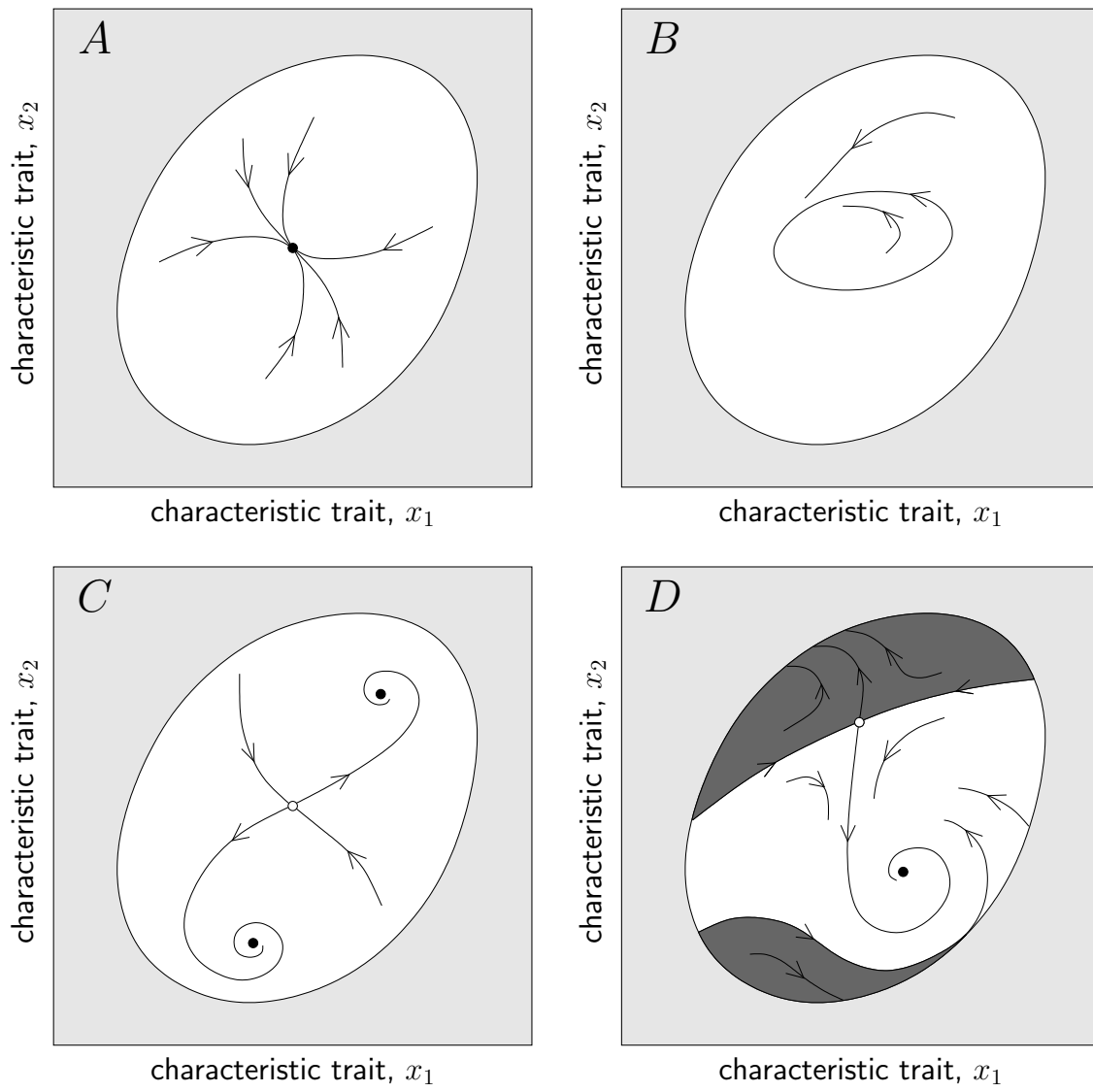


Figure 1

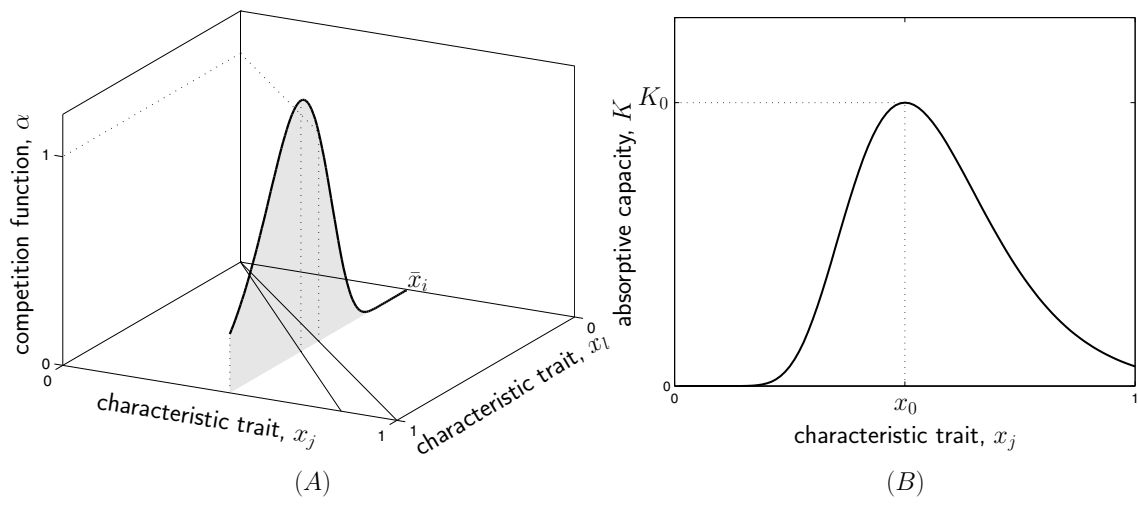


Figure 2

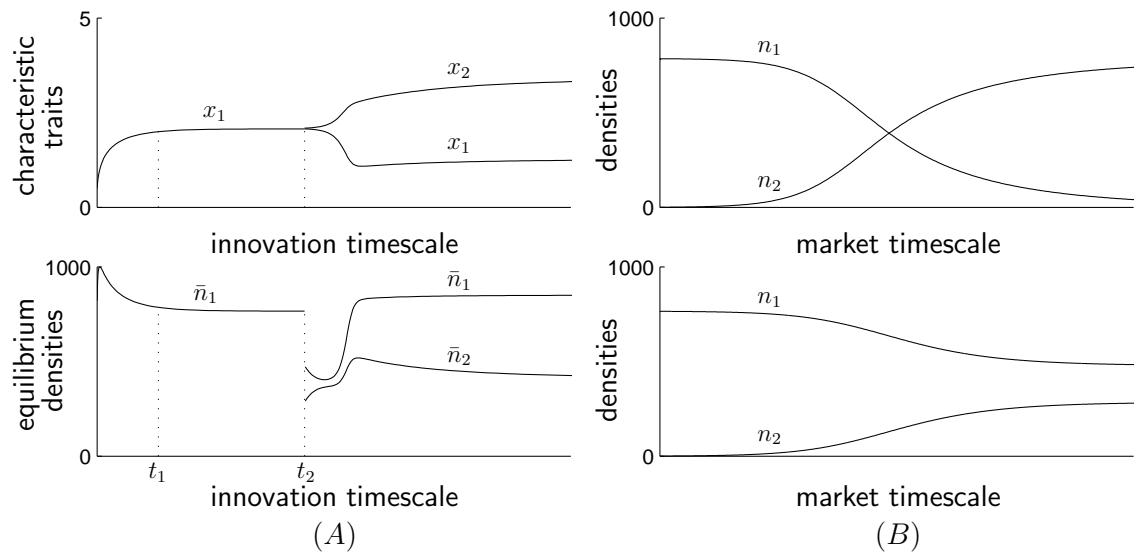


Figure 3