

this might be a new idea for macroevolutionary developmental biologists, it is an important concept in quantitative genetic analyses of phenotypic evolution [1,2].

This symposium was both timely and topical, and will have far-reaching consequences for how the Evo–Devo field progresses. It is exciting that there are

tools available for merging population and developmental genetics to change potentially our understanding of evolutionary processes by filling in the black hole that exists between the genotype and phenotype in evolution.

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# An evolutionary perspective of biological invasions

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The workshop on the Evolutionary Perspective of Biological Invasions in Terrestrial Ecosystems was held in Halle, Germany from 30 September to 3 October 2002.

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In recent decades, the frequency of biological invasions has increased to an unprecedented level, stimulating a multitude of research projects in population biology and community ecology. Evolutionary processes, however, have long been marginalized in the study of biological invasions, a trend that has been changing only recently [1,2]. Ideally timed to coincide with this increasing evolutionary awareness was a workshop focusing on such aspects, sponsored by the European Science Foundation and organized by Daniel Prati, Oliver Boßdorf and Harald Auge (Centre for Environmental Research, Halle, Germany). As the workshop progressed, it became clear that research efforts so far have focused on aspects of evolutionary changes of the invader, rather than of the recipient communities.

An invasive species must respond quickly and efficiently to new environmental conditions. Changes in the selective regime acting on the invader include both increased selection for adapted genotypes and relaxed selection for defence, because of the absence of coevolved natural enemies. Within this framework, rapid phenotypic response is expected. Indeed, an overwhelming number of studies reported phenotypic divergence between native and invaded populations.

Among the more specific hypotheses considered was the evolution of increased

competitive ability (EICA) of plants in the absence of specific herbivores [3]. In enemy-free space, resources previously used for herbivore defence become dispensable and can be reallocated to growth and reproduction. Such changes can result in the evolution of highly competitive, but less well defended genotypes. Several experimental approaches that used common garden designs clearly showed that such a pattern exists in invasive species. For example, in the perennial *Lythrum salicaria*, introduced individuals exhibited greater biomass than did their ancestral genotypes and were less resistant to, or tolerant of herbivores (Bernd Blossey, Cornell University, Ithaca, USA). William Rogers (Rice University, Houston, TX, USA) demonstrated increased competitive ability of invasive populations of the tree *Sapinum sebiferum* and elimination of this advantage when herbivores from the native range are abundant. Klaas Vrieling (University of Leiden, the Netherlands) presented a special twist of the EICA concept, showing that invasive populations of Asteraceae *Senecio jacobaea* had reduced adaptation to a specialist herbivore, but greater defence against generalist insect herbivores.

Increased competitive ability can emerge not only from the growth and defence tradeoff, but also from weak co-adaptation between native and invasive species. Ray Callaway (University of Montana, Missoula, MT, USA) showed that allelopathic root interaction creates a competitive advantage for *Centaurea maculosa* in invaded North American communities, but not among species of its native range.

Changes in life-history traits are also observed in invasive animals. For

example, invasive ant species, such as the Argentine ant *Linepithema humile*, share an extraordinary social structure called 'unicoloniality', where individuals from physically separated nests mix freely, and form supercolonies (Jes Pedersen, University of Copenhagen, Denmark). Such a structure facilitates the success of an invader but represents an evolutionary paradox. According to kin selection theory, selective processes cannot act upon such systems, because relatedness among altruistic workers is virtually zero. The causes of this major transition in social organization are assumed to depend on the loss of nest-mate recognition cues during invasion owing to genetic bottlenecks or 'genetic cleansing' [4]. Not always, however, are the same life-history traits a guarantee for continued invasion success. Benoit Facon (CNRS Montpellier, France) investigated life-history traits in eight closely related lineages of freshwater molluscs within the thiarid family that invaded Martinique. He showed that lineages that produce numerous small offspring were successful during early invasions, whereas later invaders were more successful if they produce fewer but large offspring.

Because invaders often have low initial genetic diversity, a high degree of plasticity might be an alternative way of dealing with new environments. If plasticity itself were subject to selection, one would expect genotypes from the introduced range to be more plastic than those from the native range. Oliver Boßdorf (UFZ Halle) tested this hypothesis with the use of *Alliaria petiolata*, a European biennial currently invading North American deciduous forests. In this study, however, American plants were no more plastic than were their European counterparts.

Possible genetic mechanisms that facilitate rapid adaptation were also discussed. Benjamin Genton (Université Paris-Sud, France) introduced the concept of 'genetic systems' (i.e. genes that govern the way that other genes are transmitted and associated, and thus determine mutation and recombination rates). Using a modelling approach, he showed that such genes are subject to second-order selection and facilitate rapid evolution in invasive species.

Hybridization and changes in ploidy level might also be a strong determinant of fitness in invasive species. Molecular markers can be used to detect interspecific gene flow (Herbert Hurka, University of Osnabrück, Germany), and it becomes increasingly obvious that horizontal gene flow in higher plants is much more widespread than was previously assumed [5]. Evidence for hybridization as a driver for biological invasions was shown for *Rhododendron ponticum*, where the invasive biotypes seem to be hybrids with 2–3 North American species (Alexandra Erfmeier, University of Göttingen, Germany).

Further research must not only address evolutionary processes in the

invaded communities, but should also concentrate on new conceptual approaches. For example, metapopulation theory can assist in studying the evolution of dispersal (Isabelle Olivieri, Université Montpellier, France), and selection mosaics and variation between populations must be considered when coevolution between invader and native communities is studied (John Thompson, University of California, Santa Cruz, CA, USA). Strong support for the use of model systems, such as *Arabidopsis thaliana*, to study specific genetic mechanisms involved in the invasion process came from research by Thomas Mitchell-Olds (MPI Chemical Ecology, Jena, Germany) and Joy Bergelson (University of Chicago, IL, USA). Although this species might differ from classic biological invasions, the application of a genomic approach reveals the role of gene regulation in modifying the tradeoff between growth and defence. Advances in ecological and evolutionary techniques and theory, and their effective integration, now enables the rigorous testing of hypotheses within a meaningful environmental context.

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Gro Harlem Brundtland, director-general for WHO, said that this initiative was 'perhaps the biggest step ever taken towards reducing the health information gap between rich and poor countries'.

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