

What, then, is $N\mu$ likely to be in natural populations? The mutation rate at microsatellite loci is thought to vary between 10^{-4} and 10^{-3} [3]. Therefore, the size of each of the two subpopulations before admixture occurs needs to be $>10\,000$ individuals for $N\mu$ to be >1 . Such subpopulation sizes are likely to be relatively uncommon, especially for large vertebrates. Moreover, populations of such a size are unlikely to fix many deleterious alleles, because those alleles should spread to fixation by genetic drift only in relatively small populations [4]. Therefore, under admixture of large subpopulations (i.e. the restrictive conditions where d^2 might perform well), the fitness differences among individuals whose parents came from the same or different subpopulations should be small, hence restricting the probability of detecting a correlation between fitness and any measure of inbreeding.

There is an additional problem for d^2 in providing a useful method to determine the level of inbreeding, when there is admixture among different populations: differences in the level of inbreeding among individuals are expected to quickly decay once the populations start interbreeding. This is because every individual will rapidly have a mixed ancestry. After five generations of admixture, for instance, less than one individual in a billion will remain of pure parental origin. Therefore, unless the two subpopulations just came into contact, differences in inbreeding among individuals should vanish very swiftly, which will lower the probability of detecting a correlation between fitness and inbreeding.

Is the correlation between d^2 and fitness real?
Overall, it seems that the conditions where fitness should be more closely correlated

with d^2 than with heterozygosity are very limited. So why has fitness been found to be more closely correlated with d^2 in so many studies (reviewed in [1,2])? One possible explanation is that important factors other than those considered in Tsitroni *et al.*'s [1] model are involved, although it is unclear what these factors could be. Alternatively, it might be that too much enthusiasm has accompanied the development of d^2 and that a more careful examination of the data will lead to a different conclusion. For example, only one or a few components of fitness were correlated with d^2 in most studies where fitness was better correlated with d^2 than was heterozygosity. Perhaps these few significant results correspond to the 5% false positive expected in statistical testing. Indeed, the significant correlation between d^2 and both birth weight and juvenile survival reported previously in the deer population on the isle of Rhum [5] disappeared when a larger number of loci was used (71 instead of nine; [2]). Conversely, heterozygosity, which was not significantly correlated with birth weight in the original study, became significantly correlated in the new study. Moreover, Slate and Pemberton [2] show that individual heterozygosity correlates, albeit weakly, across loci, whereas d^2 does not, leading them to conclude that heterozygosity is a more robust measure of inbreeding than is d^2 .

The work of Tsitroni *et al.* [1] is therefore important for several reasons. First, it indicates that one should not use heterozygosity and d^2 indiscriminately as measures of inbreeding. If inbreeding is expected to have occurred only recently, then heterozygosity should always be preferred to d^2 . Second, it shows that

the conditions under which d^2 performs better than does heterozygosity are quite restricted. Third, their work provides hope that it will soon be possible to determine whether inbreeding occurred deep in the pedigree or more recently (close inbreeding). This will probably require developing new measures of inbreeding and modelling the effect of long- and short-term inbreeding on these measures, but the prospect that this will be done is good. Indeed, new measures of inbreeding accounting for the level of variability at each marker locus have been developed recently [6,7] and Tsitroni and colleagues are currently generalizing their modelling approach to multiple loci.

References

- 1 Tsitroni, A. *et al.* (2001) Heterosis, marker mutational processes and population inbreeding history. *Genetics* 159, 1845–1859
- 2 Slate, J. and Pemberton, J.M. (2002) Comparing molecular measures for detecting inbreeding depression. *J. Evol. Biol.* 15, 20–31
- 3 Weber, J.L. and Wong, J.C. (1993) Mutation of human short tandem repeats. *Hum. Mol. Genet.* 2, 1123–1128
- 4 Lynch, M. *et al.* (1995) Mutation accumulation and the extinction of small populations. *Am. Nat.* 146, 489–518
- 5 Coulson, T.N. *et al.* (1998) Microsatellites measure inbreeding depression and heterosis in red deer. *Proc. R. Soc. London B Biol. Sci.* 265, 489–495
- 6 Coltman, D.W. *et al.* (1999) Parasite-mediated selection against inbred Soay sheep in a free-living, island population. *Evolution* 53, 1259–1267
- 7 Amos, W. *et al.* (2001) The influence of parental relatedness on reproductive success. *Proc. R. Soc. London B Biol. Sci.* 268, 2021–2027

Jérôme Goudet*

Laurent Keller

Institute of Ecology, Biology Building,
Lausanne University, CH-1015 Lausanne,
Switzerland.

*e-mail: jerome.goudet@ie-zea.unil.ch

Meeting Report

Impacts and extent of biotic invasions in terrestrial ecosystems

Carla M. D'Antonio and Salit Kark

The workshop on Impacts and Extent of Biotic Invasions in Terrestrial Ecosystems was held in Barcelona, Spain, from 19 to 22 September 2001.

Published online: 18 February 2002

Invasive species have become a priority concern for conservation biologists and land managers. For basic research scientists, they are a tool with which to examine controls over community structure and ecosystem processes.

However, the field of 'invasion biology' has been almost as resistant to generalization as the broader field of ecology. As a step toward greater synthesis, the Impacts and Extent of Biotic Invasions in Terrestrial

Ecosystems workshop was held with a goal to amass and evaluate the current state of data on three topics central to invasion biology.

Rates of establishment in different regions

A key challenge in invasion biology is to understand the interaction of species traits and ecosystem properties in determining which species will become invasive and where. In this framework, Mark Lonsdale (CSIRO, Canberra, Australia) discussed the intrinsic susceptibility of an ecosystem to invasion (invasibility). Referring to $E = I \times S$ (where E is the number of established exotics in an area, I is the number introduced and S is the survival of I) [1], he pointed out that most information currently available is about E . Yet, because S is what ecologists are most interested in, they try to infer something about S using E .

Mark Williamson (University of York, UK), Lonsdale and others evaluated the controversial Ten's Rule [2] (i.e. 10% of species introduced to an area will become established and 10% of these cause ecological change). This often-cited hypothesis can be partially tested using $I:E$. Peter Pyšek (Academy of Sciences, Pruhonice, Czech Republic) and Williamson added complexity to the simple comparison of $I:E$ by introducing a third category – Casuals (population persistence of these species is dependent upon repeated introductions). Although the utility of this category will undoubtedly be debated, the data sets provided by the participants soundly refuted the 'Ten's Rule'.

The search for species traits that explain invasion potential and for data sets on I and E was further explored by Daniel Sol (McGill University, Montreal, QUE, Canada), who re-examined bird introduction data. Using information from Long [3], he determined that traits correlated with behavior, such as brain size and migratory status, explain the success of bird introductions. Brain was higher in successful than unsuccessful species and migratory species were less successful than were non-migratory ones. A detailed subanalysis of 158 bird species, introduced worldwide over 1500 times, provided valuable insight into the interactions of invader traits with size of founder populations and ecosystem characteristics to explain invasion patterns. His approach

provides a model for the types of data and analysis needed for other taxa.

Salit Kark (Stanford University, CA, USA) brought new insights to questions about invasibility across convergent ecosystems using a bird introduction data set generated using Long [3] and Lever [4], plus verifications with experts, and published reports. She evaluated the success ($I:E$) of bird introductions into the Mediterranean basin, versus other Mediterranean-climate regions (California, the South African Cape, Australia and Chile). Preliminary results suggest that most introductions into the Mediterranean Basin were successful and invasions were just as likely to succeed there as elsewhere, contrary to published contentions [5]. Her data set also allowed evaluation of invasion potential by species and among regions, and forthcoming results are tantalizing.

Williamson raised the unresolved issue of when and why species show lag phases in their rate and pattern of spread after introduction. With data sets obtained from herbarium records, Pyšek found that lag phases were characteristic of species that dominated human-made habitats, whereas nonlag species were more common among invaders of seminatural habitat. Such patterns suggest testable hypotheses about species traits that might predict patterns and rates of spread.

Spatial extent and abundance of invaders

Participants discussed the potential advances that detailed mapping could lead to, and also the needs that future studies of invasion patterns could focus on. These included: identification of invasion hotspots and examination of global patterns across taxa, further study on origins of invaders and how these relate to patterns of success and failure, and comparison of historical versus current spatial patterns of invasion. A decision as to what variables should be mapped will depend on goals of the mapping effort. Mapping should help identify gaps in our knowledge, reveal new patterns, and could be useful in predicting invasions.

Generation of global invasion maps will depend largely on the degree to which data become available and are shared. Thus, focus was on defining the requirements for a user-friendly databank that describes currently available data sets to enhance collaboration, comparative research and data sharing whilst reducing

duplication of scientific efforts. A sample data entry form was produced that will become available in due course. Collaboration with other groups [e.g. The World Conservation Union Invasive Species Specialist Group (IUCN-ISSG), Global Invasive Species Program (GISP), ICE (Information Center for the Environment–UC Davis)] seems essential.

Species impacts

The goals of this session, which was entirely plant focused, were to evaluate how impacts vary depending on the type of effect, the way in which it has been studied or the type of ecosystem that the invader has entered. Sandra Lavorel (CEFE Montpellier, France), and Montserrat Vila (CREAF, Universitat Autònoma de Barcelona, Spain) discussed the relationship between invasibility and impact, citing Parker *et al.*'s [6] equation, $I = R \times A \times E$ (where I is impact, R is range, A is abundance and E is per capita effects of the invader), as a framework for approaching factors influencing impact. They concluded that studies of E are scarce: much of what we know is based on R and A . They also stressed that most studies of E are conducted at small scales and that there is a great need for landscape approaches. Lastly, Lavorel stressed the key role of plant traits in understanding impacts.

As an example of an approach towards greater synthesis, Vila conducted meta-analyses of competitive effects of exotic plants. She divided studies into those that used invader removal experiments versus those that used addition experiments. Interestingly, regardless of research approach, invaders caused a 50% reduction in growth of native species. Further results are forthcoming.

Other participants reviewed evidence relating to various types of effect, such as invader effects on species richness, disturbance regime, nutrient dynamics and hydrological cycles. Common themes were the lack of consistency in metrics of effect, large variation in spatial scale among studies and the lack of research in sites where effects were not already apparent. For example, Carla D'Antonio (University of California, Berkeley, CA, USA) stressed that it is impossible to evaluate the causes of context specificity of invader impacts on disturbance regime, because most studies are conducted in

places where strong impacts are already apparent. Karl Grigulis (CEFE) and Lavorel reported that there is no consistency among studies in metrics used to measure impacts on nutrient cycling and so few studies on any one effect (e.g. carbon accumulation), that it is impossible to draw conclusions about controls over the direction or intensity of impacts. They also reported a strong bias in the types of species and location under study.

Current data sets on invader impacts are generally too fragmentary to conduct analyses that would lead to greater synthesis and generality. Hence, focus was on creating an overarching framework to describe the conditions under which impacts might arise from plant invasions and how the varied examples of invader impacts could then be fitted into the framework. Attempts were made to link community and ecosystem-level impacts by distinguishing circumstances where invaders affect ecosystem processes directly [e.g. nitrogen (N) fixers] and those in which invaders first affect composition with or without subsequent ecosystem impacts.

A call for more data

The workshop was characterized by a sense of a developing and dynamic research area, in which discussion on basic questions often mixes with much more specific and detailed questions, and from which answers are finally beginning to emerge. Many ways were identified in which future research can help to address unresolved questions, particularly by the expansion of the regions and type of species being studied. In addition, recent efforts to build large-scale databanks, and international collaborations on exotic species encompassing different regions, species and sources will lead to promising insights as to the patterns and processes that shape the success and impact of non-native species.

Acknowledgements

The workshop was organized by the Global Change in Terrestrial Ecosystems–International Geosphere–Biosphere Program, the GISP of the Scientific Council on Problems in the Environment, and the Associated European Laboratories between CEFE,

CREAF, UB and UAB. Funding was provided by the European Science Foundation.

References

- 1 Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80, 1522–1536
- 2 Williamson, M. and Fitter, A. (1996) The varying success of invaders. *Ecology* 77, 1661–1666
- 3 Long, J.L. (1981) *Introduced Birds of the World*, Universe Books
- 4 Lever, C. (1987) *Naturalized Birds of the World*, Longman
- 5 Blondel, J. and Aronson, J. (1999) *Biology and Wildlife of the Mediterranean Region*, Oxford University Press
- 6 Parker, I.M. *et al.* (1999) Impact: towards a framework for understanding the ecological effects of invaders. *Biol. Inv.* 1, 3–19

Carla M. D'Antonio*

Dept of Integrative Biology,
University of California, Berkeley,
CA 94720-3140, USA.

*e-mail: Dantonio@socrates.berkeley.edu

Salit Kark

Dept of Biological Sciences,
Stanford University, Stanford,
CA 93405-5020, USA.

Ecological immunity of arthropods – a thread of Ariadne?

Joachim Kurtz, Ineke T. van der Veen and Jonathan J. Ryder

The workshop on Ecological Immunity of Arthropods was held at Losehill Hall, Sheffield, UK, from 6 to 9 December 2001.

Published online: 12 February 2002

Finding one's way through the labyrinth of the immune system is not easy. This is particularly true for evolutionary ecologists interested in the relationship between fitness and immunity to parasites. Recent research on insects and other invertebrates, which have relatively simple immune systems, is currently offering crucial new perspectives, as discussed at a recent European Science Foundation-funded workshop.

How different are bugs and birds?

Insects and other invertebrates differ from vertebrates when it comes to resisting parasitic infection. Whereas vertebrates rely on both adaptive (specific) and innate (unspecific) immunity, insects have only innate immune mechanisms [1]. Our

knowledge of this immunity has increased over the past ten years, offering a deeper understanding of how immunity to parasites relates to fitness in this taxon. Nevertheless, important parallels exist among vertebrates and invertebrates. For example, the sexual hormone testosterone might suppress immune function in vertebrates [2], and Jens Rolff (University of Sheffield, UK) has shown that juvenile hormone probably plays a similar role in mealworm beetles *Tenebrio molitor*, causing a reduction in immune function after mating. Similarly, Michael Siva-Jothy (University of Sheffield) demonstrated that, in insects, tyrosine can be a crucial limiting resource, which can either be invested in sexually selected ornaments (e.g. damselfly wing spots) or used in phenoloxidase-dependent immune defence – a striking parallel to the hypothesized role of carotenoids in vertebrates [3]. Importantly, closer inspection of the underlying physiology of insect immune responses

has also emphasized the fundamental importance of establishing the basic parameters of an immune response (e.g. its time course) before tradeoffs involving immunity are looked for (Siva-Jothy; Tina Trenczek, University of Giessen, Germany).

What about specificity?

The immune system does not usually work perfectly, and one explanation might be that a perfect immune response is too 'expensive'. Several speakers provided examples of costly immunity (Alex Kraaijeveld, Imperial College at Silwood Park, UK; Yannick Moret, ETH-Zürich, Switzerland) and Christine Chevillon (University of Montpellier II, France) highlighted the remarkable parallels to costs of insecticide resistance. An alternative explanation for limited immunity could be host–parasite coevolution. Some of the classic examples include insect hosts, such as *Drosophila* (Yves Carton, Laboratoire Populations,