

Meetings

Five decades of invasion genetics

Invasion Genetics: The Baker and Stebbins Legacy, Asilomar, California, USA, August 2014

In 1964, some of the most prominent scientists in the history of ecology and evolutionary biology met on the Pacific coast at Asilomar, California to discuss the genetics of colonizing species. Pointed (but polite) exchanges were recorded between Ernst Mayr, G. Ledyard Stebbins, E. O. Wilson, Theodosius Dobzhansky, Richard Lewontin, John Harper, C. H. Waddington, R. W. Allard, Herbert Baker, and 21 others. The resulting symposium volume (Baker & Stebbins, 1965) became an enduring classic, still widely cited today by students of microevolution and invasion biology.

The beach poppies (*Eschscholzia californica*) then flowered 50 times before invasion geneticists once again colonized the Asilomar dunes. At the behest of organizers Spencer Barrett, Rob Colautti, Katrina Dlugosch, and Loren Rieseberg, 74 participants from 12 countries met to celebrate the achievements of the remarkable 1964 group, and to assess the progress made and the challenges remaining in the field of invasion genetics. Participants in the 1964 and 2014 symposia enthusiastically shared a conviction that invasions, range expansions, and colonization events provide unique windows on fundamental evolutionary processes.

'What allows invasive species to outperform natives, when the latter should be well-adapted to their habitats?'

Matching new environments: pre-adaptation, post-invasion adaptation, and plasticity

What allows invasive species to outperform natives, when the latter should be well-adapted to their habitats? The mechanisms favored by the 1964 participants included pre-invasion pre-adaptation, post-invasion adaptation, and phenotypic plasticity. The 2014 symposium provided evidence that each of these mechanisms has facilitated invasion; the jury is out on whether one pathway dominates. In support of pre-adaptation, Johanna Schmitt (University of California, Davis, CA, USA) presented compelling evidence that the performance of translocated *Arabidopsis thaliana* can be predicted by the climatic niches of source populations. Ongoing mapping of the climatic distributions of individual alleles within the native range will help determine if 'climatically matched' alleles enhance fitness in the introduced range.

However, rapid evolution following arrival is clearly a feature in many invasions. Lee Ann Rollins (Deakin University, Burwood, Australia) provided a striking example from invasive cane toads in Australia, which have evolved greater dispersal abilities via longer leg length, greater endurance, more linear dispersal trajectories, and possibly altered immune function. Robert Colautti (University of British Columbia, Vancouver, Canada) provided evidence of rapid evolution of *Lythrum salicaria*'s flowering time and size at reproduction following northward migration in eastern North America. Results from common garden experiments confirmed that clines observed in the invasive range result from local adaptation to growing season length, rather than simple dispersal and founder effects. John Pannell (Universite de Lausanne, Switzerland) showed that extinction and colonization events promote variation in reproductive strategies; in particular he showed the benefits of self-compatible hermaphroditism over unisexuality in plant metapopulations.

The 1964 participants also hypothesized that phenotypic plasticity can increase colonization success, as epitomized by H.G. Baker's famous 'general purpose genotype' concept in which select individuals can succeed in a wide range of environments. Mark van Kleunen (University of Konstanz, Germany) provided support for the importance of plasticity in a comparison of root foraging across 12 invasive and 12 naturalized (but not invasive) plant species. Invasive species showed greater plasticity in allocation to roots, leading to increased efficiency of foraging and (perhaps) to more uniform fitness across heterogeneous habitats. Russell Lande (Imperial College London, UK) provided theoretical evidence that while plasticity may indeed function as a pre-adaptation allowing successful colonization, plasticity itself can evolve – and may be transient during the colonization process. Such a dynamic could help to reconcile contrasting reports in the contemporary literature (e.g. Davidson *et al.*, 2011; Palacio-López & Gianoli, 2011), where the plasticity of invasive species does not consistently trump that of natives or ancestors.

Hybridization and admixture as evolutionary stimuli

Given that waiting times for beneficial mutations can be long, what enables the rapid evolution seen in so many invasions? The 1964 participants proposed that interspecific hybridization and intra-specific admixture may supply novel genetic combinations that could trigger increased performance and invasiveness. Elaborating on this hypothesis, Mark Kirkpatrick provided evidence for a new example in which massive range expansion in the mosquito (and malaria vector) *Anopheles gambiae* may have been triggered by capture of a cassette of adaptive alleles from the dry-climate adapted *A. arabensis*. Mixing of genetic material from divergent (but not too divergent) populations within a species can also improve performance, as was shown by Katrina Dlugosch (University of Arizona,

Tucson, AZ, USA) in the highly invasive yellow star thistle *Centaurea solstitialis*.

These patterns match recent trends in the literature: both intraspecific and interspecific admixture are commonly associated with performance increases in invasive plants, animals, and fungi (see syntheses in Rius & Darling, 2014; Hovick & Whitney, 2014). However, a fundamental question is still up for grabs: how critical is such admixture for invasive success? As with post-invasion adaptation, does evolutionary change resulting from admixture ever turn a failed colonization event into a successful invasion, or does such change simply fine-tune an already invasive lineage? These questions about whether invaders are 'born' or 'made' are at the heart of invasion biology, but answers have proven elusive. Given that experimental work in nature with highly invasive organisms may carry significant risk, we suggest that cracking this issue may take a combination of mesocosm experiments and modeling approaches.

Constraints on evolution and colonization

While invasive species (and the natives they impact) are justly recognized for providing some of our most spectacular examples of rapid evolutionary change, there are limits. Mark Blows (University of Queensland, Brisbane, Australia) demonstrated that nearly-null genetic subspaces – trait combinations that have little or no genetic variance – may severely constrain evolutionary responses to selection. Even apparently unrelated traits may commonly exhibit pleiotropy. Perhaps unfortunately for practitioners, such constraints are not apparent from simple inspection of pairwise genetic covariances in the G-matrix. Troy Day (Queen's University, Kingston, Canada) presented a new method for quantifying such constraints using information theory, which can predict the number of actual trait dimensions available to selection. His analyses confirmed that this number can be substantially smaller than the nominal number of traits under analysis. To illustrate how spatial structure can also limit performance of invasive species, Stephan Peischl (University of Bern, Switzerland) presented a spatially explicit model of genetic surfing, revealing that (for species that expand in a wave-like fashion) genetic drift can result in high frequencies of deleterious alleles at the invasion front. Such 'expansion load' can slow or even stop invasive spread, but can be ameliorated via the evolution of recombination modifiers such as chromosomal inversions.

These studies highlight an interesting thematic disconnect between the symposium's theoretical studies, which emphasized evolutionary constraint, and the empirical studies, which emphasized the evolutionary flexibility apparent when invasive species interact with new environments. The exception was provided by Jennifer Lau (Michigan State University, East Lansing, MI, USA), who painted a detailed picture of the challenges of predicting evolutionary change in invaded communities. In experimental field studies, the native plant *Lotus wrangelianus* has shown little (or apparently maladaptive) evolutionary response to fluctuating selection imposed by an invasive plant and an introduced enemy, suggesting that complex community-level interactions may limit adaptation within affected species. We find it fascinating that these

two types of constraint – internal genetic vs external environmental – may be simultaneously operating in invasions and look forward to convergence between theoretical and empirical lines of research. Such a synthesis should include outcomes from artificial selection experiments, where rapid phenotypic change can ensue even when quantitative genetic methods predict strong constraint (Conner, 2012).

Effects of propagule pressure, genetic diversity, and gene flow

Propagule pressure (the number of individuals dispersing into a recipient habitat) is a known correlate of invasion success (Lockwood *et al.*, 2005). Focusing on birds as a model group for which much is known about both successful and failed invasions, Tim Blackburn (Zoological Society of London, UK) reviewed the overwhelming evidence that propagule pressure is indeed highly predictive of establishment success. However, because propagule pressure is usually confounded with other population-level properties (e.g. genetic diversity, admixture), we argue that the mechanisms underlying this relationship are not yet clear. Large founder populations might indeed succeed via the classic mechanism: increased numbers reduce risk associated with demographic or environmental stochasticity. However, they may also succeed because high genetic diversity allows higher performance via sampling or complementarity effects (as in species diversity–ecosystem functioning relationships; Forsman, 2014), and/or because high genetic diversity allows more rapid adaptive evolution (Rius & Darling, 2014). In poster sessions, Ruth Hufbauer's group (Colorado State University, Fort Collins, CO, USA) showed that in experimental flour beetle systems, migration of a single distantly related individual increases colonization success as much as migration of many closely related individuals, indicating that genetic effects of propagule pressure can be as important as purely demographic effects (see also Szucs *et al.*, 2014).

Applying new genetic and genomic tools to invasions

Perhaps the biggest change in the 50-year span between the symposia is the development of genetic and genomic tools for studying invasions. Kathryn Hodgins (Monash University, Melbourne, Australia) demonstrated the use of comparative genomics in an attempt to identify candidate loci involved in weediness and invasion in the Compositae. Such approaches provide starting points, but further work is needed to confirm the involvement of particular loci and to elucidate their phenotypic effects. Neil Tsutsui (University of California, Berkeley, CA, USA) outlined current work using RNAi knockdowns to identify the genetic underpinnings of self/nonself recognition, which play a large role in the invasive success of social species such as the ants. Katrina Dlugosch (University of Arizona) demonstrated the use of quantitative trait locus (QTL) mapping to identify loci of large effect differing between native range and invasive range populations of yellow star thistle. Future surveys will determine if these QTL alleles conferring high growth rate have gone to high frequency in the invasive range and are a causal agent behind

invasive spread. Finally, new genetic and historical techniques are also allowing biologists to develop a detailed picture of the origins and historical patterns of spread of invasive species: Melania Cristescu (McGill University, Montréal, Canada) used such techniques to infer that rates of cladoceran invasions from Eurasia into the North American Great Lakes are 5000 times that of historical norms.

Of course, successful applications of genetic and genomic tools require a solid understanding of the natural histories of focal species. Pierre Gladieux (Université Paris Sud, France) suggested that while invasive fungi seem to share many characteristics of other invasive lineages (e.g. adaptive introgression), interpretations are hampered by incomplete understanding of native fungal diversity and natural history. As the use of molecular tools increases, we should ensure that the natural history context keeps pace.

Conclusions: the next 50 years

In closing remarks, Loren Rieseberg (University of British Columbia) highlighted the 'known knowns, the known unknowns, and the unknown unknowns' of invasion genetics. He emphasized that the general outlines of invasion genetics as proposed by the 1964 participants have withstood the test of time, with the major exception that the role of stochastic forces may have been overemphasized; today, for example, genetic drift is generally understood as a negative (rather than positive) force in invasion success. Spencer Barrett (University of Toronto, Canada) developed the case that the 1964 symposium represented an important turning point in invasion biology, from a field focused primarily on ecological mechanisms (Elton, 1958) to one that also recognized the fundamental importance of genetics and evolutionary change. This shift was already firmly established by the time that molecular genetic techniques came into widespread use and provided even stronger evidence for the evolutionary dynamism of invasions.

In our view, it is high time for the Eltonian and Baker/Stebbinsonian schools of invasion biology to converge. Curiously absent from much of the symposium discussion were many of the hypotheses that have driven rafts of recent work by invasion ecologists: tradeoffs between defense and growth/reproduction (e.g. the Evolution of Increased Competitive Ability or EICA hypothesis, Blossey & Notzold, 1995); the role of niche similarity and competition in community assembly and thus invasions (Mayfield & Levine, 2010; Thuiller *et al.*, 2010); the enemy release hypothesis (Keane & Crawley, 2002), and others. These hypotheses emphasize interspecific interactions over intraspecific genetics, yet seem ripe for exploration with molecular genetic techniques. For example, do pleiotropically acting alleles that increase competitive ability but decrease defense exist, as predicted by EICA? Are there genomic signatures associated with release from natural enemies? Clearly, much could be gained via a union of invasion ecology and molecular genetics.

Finally, while it is now clear that most of the mechanisms identified in the Baker and Stebbins volume *can* operate within and/or facilitate invasions, we have made far less progress in understanding *how often* and *when* they matter, and their

importance relative to purely ecological drivers of invasion (e.g. enemy release). Answering these questions will require synthesis across many types of taxa with quite different life histories, genetic systems, and dispersal behaviors. Progress here may be made by simplifying some of the complexity of the field via controlled laboratory-based experiments (e.g. Agashe, 2009; Miller & Inouye, 2013; Szucs *et al.*, 2014). With luck, in 50 years' time, the next generation of invasion geneticists will have answers to these questions as well.

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