

INVASION GENETICS: THE BAKER AND STEBBINS LEGACY

INTRODUCTION

Foundations of invasion genetics: the Baker and Stebbins legacy

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Invasion genetics is a relatively new discipline that investigates patterns of genetic variation in populations of invasive species and their ecological and evolutionary consequences. Evolutionary biologists have a long-standing interest in colonizing species, owing to their short life cycles and widespread distributions, but not until publication of *The Genetics of Colonizing Species* (1965), edited by H.G. Baker and G.L. Stebbins, was a synthesis on the genetics and evolution of colonizers available. Here, I make the case that the Baker and Stebbins volume is the foundational document for invasion genetics, and in conjunction with the increased use of genetic markers and development of invasion biology, resulted in the birth of this new field over the past two decades. I consider the historical origins and legacy of the Baker and Stebbins volume and review some of the key issues that were addressed. I provide biographical sketches of the two editors, emphasizing their contrasting backgrounds and personalities. I review examples from my own work on plant invasions that are relevant to issues discussed by contributors to the volume. These include the following: determinants of invasion success, life history trade-offs, generalist vs. specialist strategies, general-purpose genotypes, adaptive phenotypic plasticity, mating systems and the influence of bottlenecks on genetic variation. I conclude by posing several key questions in invasion genetics and argue that one of the main challenges that the area faces is to integrate experimental field studies of the ecology and demography of populations with the largely descriptive approaches that have tended to dominate most research to date.

Keywords: biological invasions, colonizing species, G.L. Stebbins, general-purpose genotypes, genetic variation, H.G. Baker, phenotypic plasticity, population bottlenecks

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Introduction

Colonization is the establishment of a species at a site that it does not currently occupy and is necessarily a feature of the population biology of all organisms. Territorial expansion occurs at a range of spatial and temporal scales, from intercontinental migration to the local patch, and over geological epochs to the transport of species by humans in more recent times. The ecological and evolutionary consequences of colonization are

therefore highly scale dependent and species vary in the extent to which recurrent colonizing episodes have shaped their ecology, life histories and genetic systems. The scale of colonization also has important genetic consequences as the amounts and kinds of genetic variation transferred from one place to another can influence the likelihood of successful establishment, future spread and evolutionary potential.

Long-distance dispersal can expose colonizing populations to novel selective forces because of different abiotic and biotic conditions in the introduced compared to the native range. Most species introductions fail owing to maladaptation or chance, but those that are

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successful represent 'experiments in evolution', particularly when adaptive responses occur over short time-scales. Among introduced species, some are successful at confronting the many challenges presented by novel environments, as a result they can become highly invasive and exhibit rapid range expansion. A key question of importance to biologists interested in biological invasions concerns the extent to which *in situ* evolutionary changes occur during the invasion process. Here, I trace the foundations of the fledgling field of invasion genetics and identify the publication of the edited volume *The Genetics of Colonizing Species* (Baker & Stebbins 1965) as being particularly influential because it considered for the first time in detail the evolutionary processes that occur in species particularly adept at colonization.

Invasion biology is an applied scientific discipline concerned with the introduction and spread of introduced (non-native) species throughout the world, along with their environmental, health and economic impacts. Although invasion biology is multidisciplinary, addressing diverse basic and applied questions, a dominant paradigm focuses on determining the factors that cause species to become invasive and trying to predict which features of organisms and their new environments promote invasion success. Although several early naturalists reported on species introductions (e.g. Darwin discussed the invasiveness of thistles and cardoon in Argentina during his voyage on the *Beagle*, reviewed in Chew 2011), it was not until Charles Elton (1958) published *The Ecology of Invasions by Plant and Animals* that a synthetic treatment of numerous case studies was attempted. Elton's monograph is often considered the foundation for the scientific study of biological invasions (Richardson & Pyšek 2008), but significantly, it was not associated with a surge of interest on the topic. Simberloff (2011) has persuasively argued that the real impetus for the birth of invasion biology came later in the 1980s, from the volumes published on the ecology of invasions by the Scientific Committee on Problems of the Environment (SCOPE) beginning in 1982 (e.g. Mooney & Drake 1986). Subsequently, the field of invasion biology experienced exponential growth, and by the end of the 1990s, the journal *Biological Invasions* appeared, devoted to publications on species introductions.

For most of its short history, invasive biology has focused primarily on ecological questions, and until recently, there has been a striking disassociation between studies on the ecology of invasions from those concerned with their genetics and evolution. Although Elton (1958) briefly mentioned the possible role of genetics in the decline of Canadian Pondweed (*Elodea canadensis*) in the United Kingdom, the evolution of resistance in insect pests and fungi and the occurrence of hybridization and polyploidy in *Spartina* invasions,

he did not consider in any detail the possibility that many invasive populations may have the capacity to respond adaptively to novel ecological conditions. Elton was an ecologist not an evolutionist, and because of this, his perspective was mainly on species interactions and community ecology. It is noteworthy that his book was barely cited in the Baker & Stebbins (1965) volume, despite the fact that both works are concerned with species invasions (Simberloff 2011). Similarly, with few exceptions (e.g. Baker 1986; Barrett & Richardson 1986), the SCOPE volumes, following the mandate of the committee, were largely restricted to ecological studies of invasive species, with little consideration of whether the genetic characteristics of invasive populations might have relevance to their spread and management.

During the 1970–80s, evolutionary biologists, following the lead provided by the Baker & Stebbins (1965) volume, began to investigate a variety of questions in ecological and evolutionary genetics using invasive species as study systems (e.g. Allard *et al.* 1972; Selander & Kaufman 1973; Richardson *et al.* 1980). Significantly, this work had little influence on the early development of invasion biology (Callaway & Maron 2006), but over time several volumes (Parsons 1983; Williamson 1996; Cox 2004; Sax *et al.* 2005) dealt with genetic issues in invasion biology, and this helped to integrate ecological and evolutionary approaches to the study of species introductions. In concert with advances in molecular techniques for assaying genetic variation and the development of a growing body of evolutionary theory relevant to evolutionary processes in colonizing populations, this led to the birth of invasion genetics.

In this introductory chapter to the special issue of *Molecular Ecology* on invasion genetics, I provide a historical background to the *The Genetics of Colonizing Species* and consider its scientific legacy. My treatment does not attempt to be comprehensive and instead involves selected examples, particularly on plant invasions as I know these best. It is written from a personal perspective. I was a former PhD student of H.G. Baker who went to California in the early 1970s after being 'turned on' by reading the Baker and Stebbins volume at Reading University, U.K., where I was taking a degree in the Department of Agricultural Botany. The book had an enormous influence on my thinking and initiated a lifelong interest in the ecology and genetics of plant invasions.

I begin this article by considering the goals of the 1964 Asilomar symposium that gave rise to the volume edited by Baker and Stebbins the following year. I provide short biographical sketches of the two editors based in part on my own interactions with them. I consider how their backgrounds and research interests may have influenced the choice of contributors and the main

themes of the meeting. I make the case that the Baker and Stebbins volume helped to initiate research on a range of fundamental problems concerned with the ecological and evolutionary genetics of colonization, which now form the conceptual foundations of invasion genetics. I briefly review selected topics in invasion genetics, evaluating progress made since Asilomar, and conclude by considering key questions and challenges for the fledgling field. *The Genetics of Colonizing Species* can lay claim to being the foundational document for invasion genetics and its historical legacy was celebrated by a 50th anniversary symposium held at Asilomar in August 2014, which forms the basis of this special issue.

Historical background

The Genetics of Colonizing Species is a collection of studies and discussions that arose from a symposium held from 12 to 16 February 1964 at Asilomar, a charming seaside retreat on the Pacific coast of California, near Monterey. The initial idea for the symposium came from the influential British geneticist Cyril H. Waddington, who at the time was the President of the International Union of Biological Sciences (IUBS), a nongovernmental organization for advancing knowledge of biology in the service of human improvement. Waddington, Baker and Stebbins selected the speakers for the meeting and their contributions resulted in 27 articles, including the introduction to the symposium by Waddington and a summary chapter by Ernst Mayr.

The objective of the Asilomar meeting was to bring together geneticists, ecologists, taxonomists and applied scientists (e.g. workers in weed control, biological control of insects pests and wildlife biologists) to exchange ideas about the types of evolutionary change that would be likely to occur when organisms are introduced to regions of the world to which they are not native. The meeting lasted 5 days and was attended by approximately 30 participants, a relatively small gathering by today's standards. The contributors represented an international selection coming from USA (12), UK (4), Australia (3), New Zealand (2), Israel (2), Austria (1), Canada (1), Japan (1) and the West Indies (1), and all were male, an unfortunate sign of the times.

Several features of the 1965 volume are particularly noteworthy and have made it a classic and an attractive read for those interested in the history of evolutionary biology. First, the contributors included many individuals who were either leaders in their field or were to become so in later years. These included the following: R.W. Allard, L.C. Birch, Hampton L. Carson, Theodosius Dobzhansky, Friedrich Ehrendorfer, John L. Harper, Charles B. Heiser Jr., R. C. Lewontin, Ernst Mayr, Edward O. Wilson and Daniel Zohary, among others.

The contributors also included less well-known scientists whose careers were given an important boost from being invited to speak (e.g. Gerald Mulligan; see Mulligan 2014). Second, the organizers decided to publish after each contribution the verbal exchanges among the participants over questions that arose. Conducted with grace and wit, and reflecting the personalities of the participants, some of these exchanges provide valuable insights into the thinking at the time, sometimes prescient, in other instances flawed. A fine example is the exchange between Lewontin and Mayr (p. 481) on the influence of founder events on genetic variation. Lewontin gives a lesson in population genetics to Mayr concerning the founder principle that Mayr had earlier made famous.

An unusual feature of *The Genetics of Colonizing Species* is the significant number of botanists among the authors; a striking contrast to today where they are often sparsely represented in symposium volumes on general topics, in part, owing to the slow attrition of plant organismal biology faculty positions at many academic institutions. Twelve of the 27 contributions involved plants, and they featured prominently in the published exchanges. The significant number of plant scientists represented in the volume was undoubtedly a reflection of the fact that the two editors—Baker and Stebbins—were both established botanists and therefore well informed about leading researchers and work being conducted on colonizing plants. Weed biology was a thriving discipline during the 1960s, and many plant ecologists and biosystematists were investigating weedy taxa because of their experimental tractability and interesting variation patterns. Another reason for the significant botanical representation at Asilomar may have been because plants display a greater diversity of genetic and reproductive systems than occurs in most animal groups, a point emphasized by Lewontin (p. 77) in the volume. This diversity lends itself to comparative studies, and such approaches were a prominent feature of many of the botanical contributions including those by Baker and Stebbins. Finally, it is probably not an accident that many of the botanists invited to the meeting had worked in California, which was and still is today a centre for evolutionary research, particularly on plants because of the amazing diversity of the California Floristic Province.

The Editors

Herbert G. Baker—Renaissance botanist and incurable holist

Baker was an outstanding natural historian and field botanist with a broad knowledge of plant diversity, especially crops and weeds. He can probably be consid-

ered one of the first genuine plant evolutionary ecologists and was insistent that ecology and evolution were inseparable disciplines. He published extensively on the breeding systems and pollination biology of flowering plants but is perhaps best known for 'Baker's Law', coined by Stebbins (1957), which refers to the benefits of self-compatible hermaphroditism in establishment following long-distance dispersal, especially to islands where mates or pollinators may be in short supply or absent (Baker 1955, 1967). This topic, which generally concerns the constraints imposed by low-density conditions on colonization and reproduction (e.g. 'allee effects'), continues to stimulate new work (Pannell & Barrett 1998; Dornier *et al.* 2008; Cheptou 2012). Further details of Baker's scientific contributions, which included around 175 publications and a book on plant domestication, can be found in Barrett (2001).

Born in Brighton, England in 1920, Baker received his PhD in 1945 from the University of London. His thesis topic on the consequences of invasion for hybridization and species replacement in *Silene* initiated a lifelong interest in plant invasions. Significantly, Baker explicitly used the term 'invasion' in the title of his classic thesis study (Baker 1948) published in the *Journal of Ecology*. Using this military metaphor may have been associated with the times, Baker had experienced living and working through the Second World War. By sampling variation in populations of *Silene dioica* (then *Melandrium dioicum*) and *Silene latifolia* (*M. album*) from selected regions of the United Kingdom, Baker recognized different stages in the invasion process leading to the replacement of one species by another. He documented extensive hybridization between the two *Silene* species, especially in populations occurring in disturbed habitats.

Baker's first university position was as Lecturer at the University of Leeds (1945–54), where he came under the influence of the distinguished cytologist Irene Manton and through her developed cytological skills and a strong appreciation for chromosomal variation and the evolution of genetic systems. After a short spell as Professor of Botany at the University of Ghana (1954–57), where his long-term interest in the reproductive biology of tropical plants first began, he moved permanently to the USA to take up a position at the University of California (U.C.) until his retirement, where he was Director of the U.C. Botanical Garden and later Professor of Botany. His wife Irene Baker provided both technical and emotional support throughout his career and the two published numerous studies together. The 'Baker laboratory' at Berkeley was always a welcoming place for students, and Baker rarely turned anyone away who wanted to talk about plants. He supervised 49 PhD students during his career, although many of the theses remained on his shelf unpublished because he was

uncomfortable putting pressure on his students and was always occupied by numerous projects of his own.

It was in California that Baker developed his long friendship with G. Ledyard Stebbins. Their shared interest in the Californian flora resulted in many field trips together (Fig. 1) and an appreciation of each other's expertise. In temperament, the two were polar opposites and perhaps this enabled them to get along with one another so well. Baker was gentle, sweet, retiring and hated confrontation. He had few interests outside of research (except track and field sports) and routinely worked on campus during weekends when he was not in the field. Despite his diffident manner, Baker was competitive, ambitious and quite capable of subtle criticism when it was merited. But this was always delivered politely with a minimum of histrionics. This made Baker the perfect foil for the mercurial Stebbins.

G. Ledyard Stebbins—Botanical architect of the evolutionary synthesis

Stebbins is generally considered the botanical architect of the evolutionary synthesis and his monumental work *Plant Variation and Evolution* (Stebbins 1950), in which he synthesized existing knowledge of the genetics and evolution of plants, provided the foundation for the emerging field of plant evolutionary biology. Stebbins was the only botanist included in the group of scientists responsible for the modern evolutionary synthesis—



Fig. 1 Herbert G. Baker and G. Ledyard Stebbins in the field, Napa County, California 1973, on an excursion organized by the Bay Area Biosystematists.

Theodosius Dobzhansky, Ernst Mayr, George Gaylord Simpson and Julian Huxley—and was a dominant intellectual figure in mid-20th century evolutionary biology. He authored several other books and monographs, which covered a remarkable range of topics including local floras, chromosome evolution, macroevolution and developmental biology, as well as several general texts on evolution. Stebbins was especially adept at synthesis and among the ~260 articles that he wrote, his reviews were especially notable. His biographer Vassiliki Betty Smocovitis has written extensively on Stebbins' life and scientific accomplishments (Smocovitis 2001, 2006; Crawford & Vassiliki 2004), and I therefore provide only a brief summary, primarily on aspects of his career relevant to the Asilomar meeting and his relationship with Baker.

Born in 1906 in Lawrence, New York, USA, Stebbins obtained his PhD in 1931 from Harvard University where he worked on geographical variation and evolution in *Antennaria*, focusing in particular on chromosomal variation, hybridization and apomixis. At Harvard, he was strongly influenced by the geneticist Karl Sax, much to the chagrin of his supervisor, morphologist E.C. Jeffrey, who was not a fan of the 'new genetics' being promoted by Thomas Hunt Morgan and Sax (Smocovitis 2001). In 1935, Stebbins moved to U.C. Berkeley to work with E.B. Babcock on an ambitious project to understand the genetic mechanisms governing variation and evolution in *Crepis*, an herbaceous genus composed of polyploid and apomictic forms, and in which there were several introduced weedy taxa. Their monograph on *Crepis* (Babcock & Stebbins 1938) foreshadowed many of the themes that were later to become major components of his 1950 book—geographical variation, hybridization, polyploidy, speciation and variation in reproductive systems, all themes that also appear in *The Genetic of Colonizing Species*. In 1936, Stebbins met Dobzhansky for the first time. 'Dobie' became the single most important influence on Stebbins and was largely responsible for Stebbins' transformation from a plant geneticist to an evolutionary biologist (Smocovitis 2006).

It is unclear when Stebbins and Baker first met. By the time Baker arrived at Berkeley in 1957, Stebbins had left to help organize a new genetics department at U.C. Davis, where he widened his interests to include studies of crop plants and developmental genetics. However, Stebbins continued to make regular visits to the Berkeley campus where he continued to teach well into the 1960s. Therefore, it seems quite likely that the two developed their friendship through these visits and during field excursions and regular meetings of the 'Bay Area Biosystematists', a group of like-minded evolutionists and systematists who met regularly at

various locations in the San Francisco Bay area to hear invited lectures and discuss the latest efforts to integrate ecology and genetics into systematics. This was a select group to which graduate students were not generally invited and nor were woman until the 1970s (V.B. Smocovitis, personal communication).

Stebbins had boundless energy, was full of ideas and had a deep passion for plants and conservation. He was an engaging and charismatic undergraduate lecturer and could be warm, generous and funny, especially when he broke into songs from Gilbert and Sullivan, which he often did. He had an eccentric streak and in class would occasionally step into waste paper baskets by accident and appeared to be completely oblivious about combing his hair and zipping up his fly in front of the class. Those who had the experience of driving with Stebbins never forgot the experience, as he talked constantly at the same time as scanning the passing countryside for interesting plants. Stebbins also had a reputation for being a difficult person, and he was prone to losing his temper and being overly domineering. In conversation, it was often nearly impossible to be on an equal footing because of his impatient, quick mind and his tendency to constantly interrupt. Stebbins was also not especially open to having his ideas questioned, as occurred when the late David G. Lloyd (University of Canterbury) pointed out to him publically in Christchurch that some of his interpretations on the evolution of genetic systems involved group selection. Stebbins blew up and had a temper tantrum!

In contrast to Baker, Stebbins was the primary supervisor to very few graduate students and while at Davis, he fell out with several prominent faculty members including Robert Allard and Leslie Gottlieb, who were often not on speaking terms with him. Yet, Stebbins also played important mentorship roles in the careers of Verne Grant, Charles Heiser Jr. and Peter Raven, and he could be gracious and generous with his ideas. Baker was fully aware of Stebbins' volatile personality, and perhaps because Baker was deferential and full of admiration for Stebbins, he was happy to live in his colleague's shadow, chirping up politely when Stebbins monologues had ended. Others were less tolerant. Nevertheless, Stebbins was admired by many senior figures in evolutionary biology, and the inclusion of so many of them in *The Genetics of Colonizing Species* was undoubtedly a result of his influence.

Several topics identified in *The Genetics of Colonizing Species*

The 27 contributions that make up *The Genetics of Colonizing Species* can be grouped into three loosely connected themes—concepts related to colonization,

case histories of particular taxonomic groups and the management of invasive species, especially through biological control. Here, I highlight several topics that emerged in the volume that have subsequently been the focus of increased attention, and some of which stimulated work in my own laboratory.

Conceptual beginnings

The book begins with a series of contributions on general concepts relevant to colonizers, including species interactions, island colonization, mating systems, selection, population differentiation and genetic drift. Among these contributions was the only theoretical chapter in the volume, by Lewontin on selection for colonizing ability (p. 77), including the influences of inter-demic selection and changing environments. His analysis highlights the classic trade-off between development rate and fecundity. Our recent work indicates the importance of life history trade-offs in colonizing species. Local adaptation to growing season length with northern migration in eastern N. American populations of the wetland invader *Lythrum salicaria* involves a trade-off between flowering time and size (which determines reproductive output) and suggests a genetic constraint to further northward migration for populations at the current range margin (Colautti *et al.* 2010a; Colautti & Barrett 2013). Lewontin's chapter represents one of the earliest efforts to use theory to predict optimal strategies for colonizing species and presaged the subsequent development of a rich theoretical literature concerned with many different aspects of biological invasions (e.g. Andow *et al.* 1990; Shigesada & Kawasaka 1997; Higgins & Richardson 1999; García-Ramos & Rodríguez 2002). As is evident from this special issue, theory is now an integral component of invasion genetics.

Determinants of invasion success—the comparative approach

The second series of contributions in *The Genetics of Colonizing Species* largely focused on case histories and analyses of successful colonizers in particular geographical regions. A recurrent theme was the effort to predict which traits characterize successful colonizers. Baker's chapter (p. 147) on the mode of origin of weeds exemplifies this approach and spurred much subsequent work and some controversy. Through comparative experimental studies of several taxa, he identified a suite of traits that distinguished closely related weeds and nonweeds. These included self-compatibility, high phenotypic plasticity, short life cycles and rapid flowering. Based on these comparisons and his wide

knowledge of common weeds, Baker drew up a list of 14 characteristics that might be expected in the 'ideal weed' (p. 166). This was obviously a heuristic exercise, and Baker was clear that it was unlikely that any species possessed all of the features he listed. Nevertheless, subsequent studies (Perrins *et al.* 1992; Williamson & Fitter 1996; Moles *et al.* 2008) questioned the value of Baker's ideal weed list and argued that environmental conditions in the introduced range, particularly biotic challenges, will play a crucial role in whether an introduced species becomes invasive. They also argued that invasive plants as a group were simply too heterogeneous to draw the kinds of generalizations implied by Baker's list.

Despite these valid concerns, efforts to identify the determinants of invasiveness have burgeoned over the past few decades. Considerable progress has been made in identifying traits of invaders using phylogenetic and experimental approaches and taking into account a variety of other influences including historical, biogeographical and habitat factors (e.g. Rejmánek & Richardson 1996; Gravuer *et al.* 2008; Ahern *et al.* 2010; van Kleunen *et al.* 2010a,b; Kuester *et al.* 2014). By today's standards, Baker's pairwise congeneric comparisons of weeds and nonweeds seem rudimentary. The comparisons were limited to a few taxa and did not appear to involve sister taxa. Congeneric species pairs were not grown in experimental mixtures, as suggested by Harper in his chapter as the most appropriate way to detect differences in ecology (p. 262). However, despite these shortcomings, Baker's work on weeds did identify an important question and pointed the way forward to the use of more robust comparative approaches.

Both generalists and specialists

One tension that emerged in *The Genetics of Colonizing Species* concerned the extent to which invaders are commonly generalists or specialists. In his chapter, Harper repeatedly stressed the specialized character of many plant invaders (p. 244), whereas by contrast, Baker viewed weeds as commonly exhibiting a 'jack-of-all-trades-master-of-none' strategy arising from 'general-purpose genotypes' (p. 158). He suggested that such genotypes provide colonizers with wide environmental tolerance and an ability to grow in a multitude of climates and edaphic conditions through phenotypic plasticity. Today, we recognize that both Harper and Baker were partially right. Because of the wide range of strategies that are evident among invasive species, both generalists and specialists occur. Comparative studies of members of the barnyard grass complex (*Echinochloa crus-galli* and relatives) illustrate the diversity of strate-

gies in invasive plants (Fig. 2; reviewed in Barrett 1983, 1988, 1992). *Echinochloa crus-galli* is cosmopolitan in distribution and considered one of the world's worst weeds (Holm *et al.* 1977). Native to the Old World, it ranges in distribution from 50°N to 40°S, occurring in a wide range of disturbed environments, and is recorded from 36 crops in 61 countries. It is a generalist par excellence. In contrast, *Echinochloa phyllopogon* and *Echinochloa oryzoides* (*E. crus-galli* var. *oryzicola*) are specialized mimics of rice restricted in distribution to cultivated rice fields. The generalist and specialist species differ in a suite of life history traits reflecting contrasting ecological preferences: the generalist flowers faster and produces larger numbers of smaller, dormant seeds. In contrast, flowering in the mimics is delayed, coinciding with that of rice, and plants produce fewer, larger seeds that lack dormancy. In addition, the generalist is more plastic in its growth and development and maintains more genetic variation in populations than the two rice weed specialists. Thus, even among this closely related complex of annual selfing weeds, both generalist and specialist strategies have evolved.

General-purpose genotypes and adaptive plasticity

In his chapter, Baker used a variety of examples to illustrate his 'general-purpose genotype' concept, but in all cases, the species he identified possess uniparental reproduction. These included species with prolific clonal reproduction, such as the sterile pentaploid *Oxa-*

lis pes-caprae and the floating aquatic *Eichhornia crassipes* (Fig. 3A,B), as well as apomictic *Poa pratensis* and autogamous *Eupatorium microstemon*. He proposed that outbreeders of undisturbed natural communities would be unlikely to possess general-purpose genotypes and instead would evolve finely adapted ecotypes specialized to local conditions, and at least in their own habitats, they would be superior to generalist weeds. Following Baker, the concept of general-purpose genotypes has been extended to several animal groups, particularly obligately asexual polyploid species that exhibit geographical parthenogenesis (reviewed in Lynch 1984). In principle, there is no reason why generalist genotypes could not develop in outbreeding populations, depending on the 'grain of the environment' (see Levins 1968), but as yet most cases where the general-purpose genotype concept has been applied involve species with uniparental reproduction.

Baker's embryonic ideas on general-purpose genotypes are directly relevant to the evolution of reaction norms and adaptive phenotypic plasticity (Sultan 1987; Pigliucci 2001). A recent meta-analysis reported that invasive species possess higher phenotypic plasticity than native species (Davidson *et al.* 2011), a finding that supports Baker's ideas on the benefits of plasticity in generalist weeds. However, other studies comparing related invasive and noninvasive native species have failed to show any consistent pattern (Palacio-López & Gianoli 2011), perhaps because plasticity evolves and changes during the invasion process. Although many

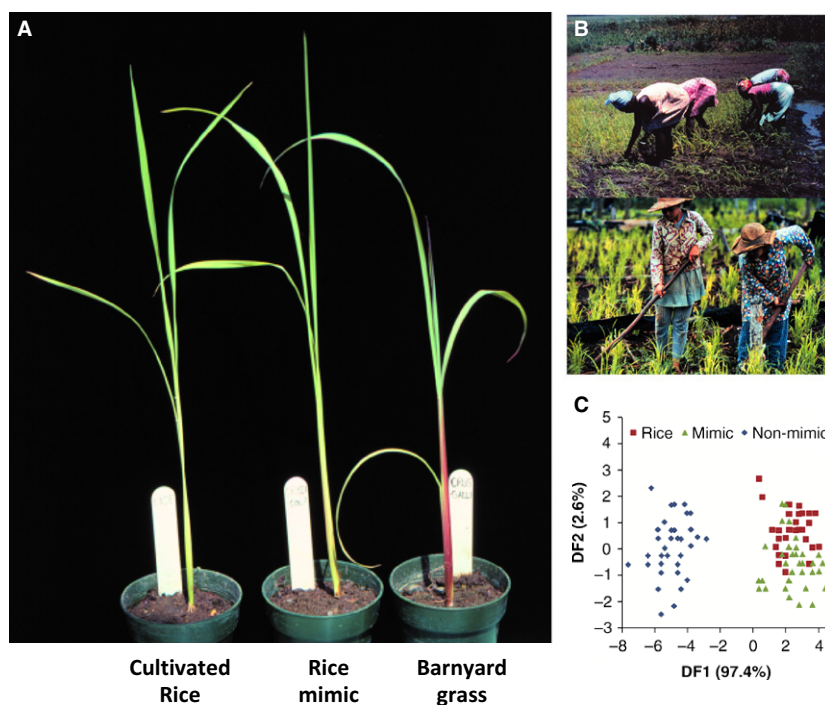


Fig. 2 Generalist and specialist weeds in the barnyard grass complex; (A) from left to right—cultivated rice, the specialist rice mimic *Echinochloa phyllopogon*, and the generalist *Echinochloa crus-galli*; (B) weeding practices in rice exert selection pressures on the morphology of weed populations favouring variants of barnyard grass that resemble rice; (C) phenotypic resemblance between the generalist, the rice mimic and rice based on a discriminant functions analysis of nine quantitative characters. For further details, see Barrett (1983).



Fig. 3 Two invasive weeds identified by Baker (1965) as possessing general-purpose genotypes. (A) The sterile pentaploid short-styled morph of tristylous *Oxalis pes-caprae*, Tel Aviv, Israel (2013); (B) The clonal aquatic *Eichhornia crassipes* at Bacon Island Slough near Stockton, California (2014). The population of *E. crassipes* is composed of a single clone of the mid-styled morph and has persisted at this site for 40 years and during this time has dramatically increased in size as a result of clonal growth. Sexual reproduction is prevented at the site despite seed production because of unsuitable conditions for seed germination and seedling establishment (see Barrett 1980).

successful weeds do indeed display extraordinarily high phenotypic plasticity, many nonweeds of heterogeneous environments show similar behaviour, leaving open the relative importance of plasticity and local adaptation for invasion success. Addressing this issue and finding support for the general-purpose genotype concept are now a focus of current research (e.g. Parker *et al.* 2003; Dybdahl & Kane 2005; Richards *et al.* 2006; Hulme 2008). Experimental studies of the annual selfing herb *Polygonum cespitosum*, introduced to North America from eastern Asia, have revealed individuals that resemble the kind of general-purpose genotype envisioned by Baker (Matesanz & Sultan 2013). Eight of 14 invasive populations investigated by these authors contained varying (3–21%) proportions of ‘high-performance genotypes’ that maintained high reproductive output across a range of moisture and light levels. Additional evidence from a ‘resurrection study’ over an 11-year period demonstrated rapid postintroduction

evolutionary change in adaptive plasticity (Sultan *et al.* 2012). In this species, it will be interesting to determine the extent to which plasticity might be gradually replaced by local adaptation as the invasion matures or whether ongoing population turnover and colonizing episodes maintain a high degree of plasticity among most genotypes. Of course, both plasticity and local adaptation are likely to play important roles in most sexual invaders; the main future challenge will be to determine their relative contribution to fitness and invasive spread, as well as the role of pre-adaptation.

Mating systems in invasive populations

Several contributors to *The Genetics of Colonizing Species* considered the extent to which the mating system was important for colonizing success. Allard (p. 49) pointed out that among the world’s most successful plant colonizers, the vast majority were predominantly selfing, and Baker (p. 147) and Mulligan (p. 127) emphasized the importance of self-compatibility in the evolution of weediness. However, Stebbins found no evidence for an overrepresentation of selfing species in his survey of native weeds, and Heiser (p. 391) pointed out that among annual sunflowers (*Helianthus*), the majority are self-incompatible, including the widespread and weedy *Helianthus annuus*. This raises two questions for workers today: Is there an optimal mating system for an invasive species, and is there evidence for the selection of selfing during the invasion process?

Currently, there are no definitive answers to either of these questions. Some progress has been made in clarifying why reproductive systems are of importance for invasion success (reviewed in Barrett 2011), and several phylogenetically controlled analyses show that the facility for autonomous self-pollination is overrepresented among invasive species (van Kleunen & Johnson 2007; van Kleunen *et al.* 2008; Burns *et al.* 2011), a pattern consistent with Baker’s Law. However, many perennials and even some annual colonizers are self-incompatible, and there is still scant empirical evidence that selection for reproductive assurance during the invasion process drives evolutionary transitions from outcrossing to selfing. Support for Baker’s Law comes largely from comparative evidence or case studies of island colonization by weedy species (e.g. Barrett & Shore 1987; Barrett *et al.* 1989), but at more restricted spatial scales, it has proven more difficult to find evidence for predictable patterns of mating-system variation, such as the breakdown of self-incompatibility to self-compatibility along gradients of colonization or succession (Colautti *et al.* 2010b; but see Cheptou *et al.* 2002). Selection for selfing in colonizing populations depends on several factors including the spatial scale of colonization, gene flow,

inbreeding depression and the availability of standing genetic variation in mating-system modifiers.

Models investigating the benefits of reproductive assurance in a metapopulation suggest that an optimal mating system for an invader should include the ability to modify selfing rates according to the patch density (Pannell & Barrett 1998). During colonizing episodes when populations are small or are at low density, plants should self to maximize fecundity. However, when populations become larger and mates or pollinators are less likely to be limiting, outcrossing should become more beneficial, promoting recombination and adaptive evolution. Future work on invasive populations might usefully investigate the extent to which the mating systems of self-compatible colonizers are indeed flexible and that patterns of mating are context dependent. In addition, experimental field studies demonstrating selection for traits providing reproductive assurance in small populations, similar to those recently conducted on noninvasive *Clarkia* by Moeller & Geber (2005), would be most valuable.

Evolutionary history, bottlenecks and genetic diversity

Many of the contributors to *The Genetics of Colonizing Species* discussed the importance of understanding the evolutionary history of colonization and the extent to which demography may influence the amount of genetic variation in populations. Whereas some authors (e.g. Mayr, Carson) placed considerable emphasis on the role of small population size in reducing diversity, others (e.g. Lewontin, Fraser) were less convinced that bottlenecks were likely to be important in limiting evolutionary potential (see for example, pp. 123–125, 481). Several of the exchanges were in essence versions of the classic Fisher–Wright debate on the significance of stochastic forces in evolution.

At the time of the Asilomar meeting, most inferences about the evolutionary history of colonizing species were based on guesswork, or less often, records from herbaria and museum collections. Today, through the use of genetic markers, we are in a much better position to reconstruct the migratory history of invasions and assess the magnitude of genetic bottlenecks and founder events. There is now evidence from neutral loci that many populations of introduced species have less genetic variation than populations in the native range. However, a survey of 80 species of plants, animals and fungi revealed that the overall average loss in allelic richness was only 15.5% (Dlugosch & Parker 2008), much less than might have been predicted by several of the participants at Asilomar. It is now recognized that assessing the genetic and evolutionary consequences of bottlenecks depends on a variety of biological and his-

torical factors including the types of genes examined (e.g. Mendelian loci vs. quantitative variation; Lewontin 1984), the reproductive systems of species (biparental vs. uniparental; Novak & Mack 2005), the frequency of bottlenecks (single vs. repeated; Nei *et al.* 1975), the occurrence of multiple introductions and admixture (Keller *et al.* 2014), and the extent of interspecific hybridization (Ellstrand & Schierenbeck 2000). These influences, in addition to knowledge of the ecology and demography of populations, should be taken into account when interpreting patterns of genetic diversity in invasive species.

Founder events and bottlenecks are not unexpected in introduced species with uniparental reproduction. In selfers, inbreeding preserves multilocus associations established through founder events and genetic drift (Golding & Strobeck 1980; Brown 1983), and the lack of sexual reproduction in many asexual populations freezes standing variation following a bottleneck and prevents opportunities to regain diversity through recombination, although somatic mutations may play some role in increasing diversity as reported in some clonal plants (Ally *et al.* 2008; Bobiwash *et al.* 2013). Bottlenecks of varying severity have been commonly detected in selfing and clonal species using neutral genetic markers (e.g. Husband & Barrett 1991; Kliber & Eckert 2005; Zhang *et al.* 2010). However, even highly selfing populations are able to maintain considerable amounts of quantitative genetic variation because of the high mutability of polygenic characters and the fact that many genes contribute to the expression of these traits. Theoretical studies by Lande (1976, 1977) suggest that if populations expand after a bottleneck, as occurs during many invasions, sufficient genetic variability at quantitative trait loci can be generated for rapid adaptive evolution. Unfortunately few, if any, studies of invasive species have compared additive genetic variation and evolvability of ecologically relevant traits in native and introduced populations using appropriate breeding designs. So, it is too early to say if introduced populations generally have less quantitative genetic variation than native populations. However, based on the spate of recent examples of rapid evolutionary change in invasive species over the past decade (reviewed in Cox 2004; Whitney & Gabler 2008; Suarez & Tsutsui 2008), it seems probable that most invasive populations of both outbreeding and inbreeding species have sufficient standing genetic variation to respond adaptively to local ecological conditions. In contrast, clonal species with limited or no sexual reproduction occurring in invasive populations (Fig. 3) meet the challenges of novel environments through a different strategy—phenotypic plasticity.

Native or alien invasions?

Occasionally, in the study of invasive species, it is unclear whether populations in a particular region are native or alien. For example, this occurred with the originally described Californian endemic *Bacopa nobisiana*, which on further study turned out to be the introduced *B. rotundifolia* (Barrett & Strother 1978). Although most biological invasions involve introduced species, this is not necessarily the case if human disturbance opens up novel environments and native species are provided an opportunity to multiply and spread (e.g. many weeds of Californian rice fields; Barrett & Seaman 1980). Indeed, in his contribution to *The Genetics of Colonizing Species*, Stebbins (p. 173) reviewed many other examples of colonizing species of the native Californian flora that, following European settlement, spread rapidly to become successful weeds. Harper (p. 244) also discussed native species that have invaded agricultural land from native plant communities in Britain. As is often the case for plant invasions, anthropogenic disturbance is usually the key ecological factor promoting spread.

Our molecular studies of the annual aquatic *Eichhornia paniculata* illustrate how information on demographic history can be used to determine whether a species is native or introduced to a particular region. Populations of *E. paniculata* are native to N.E. Brazil where they are largely outcrossing, inhabit temporary pools and ditches and are pollinated by specialist long-tongued bees (Fig. 4). However, populations also occur in Cuba and Jamaica where they are predominantly

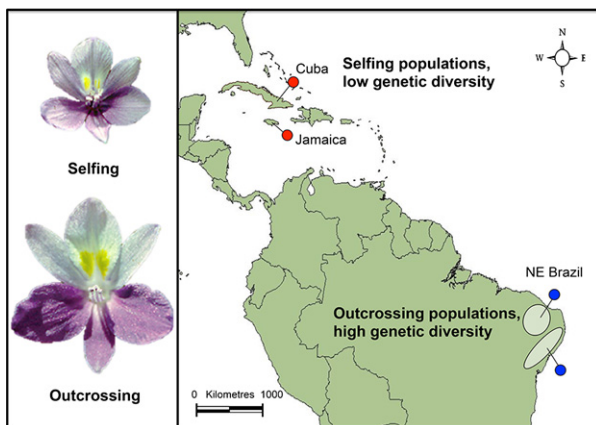


Fig. 4 The geographical distribution of *Eichhornia paniculata* illustrating part of its disjunct distribution; populations in N.E. Brazil are large flowered, outcrossing, genetically diverse and noninvasive, in Cuba and Jamaica, the species has smaller flowers, is highly selfing, has much less genetic diversity and has invaded rice fields on both islands. The establishment of selfing populations in the Caribbean is an example of Baker's Law.

selfing and infest cultivated rice fields and other disturbed habitats associated with agricultural land. Phylogeographical studies and comparisons of nucleotide diversity indicate a moderate bottleneck associated with long-distance dispersal from Brazil to the Caribbean (Husband & Barrett 1991; Ness *et al.* 2010). Caribbean populations are considered native to the islands but an alternative possibility is that they were introduced in historic times, perhaps associated with agriculture. We investigated these alternative hypotheses using coalescent simulations of the demographic history of populations. The results clearly indicate that *E. paniculata* was not introduced to the Caribbean in historic times. Rather, natural colonization probably mediated by long-distance dispersal by migratory birds, occurred ~125 000 years before present, well before the origins of agriculture (Ness *et al.* 2010). Here, a species with a markedly disjunct neotropical distribution has become invasive through colonization of a novel niche (rice fields) not available at the centre of its range in N.E. Brazil.

What is invasion genetics?*History and definition*

In contrast to the limited influence that Elton's book had on the early development of invasion ecology in the first few decades after it appeared (Simberloff 2011), *The Genetics of Colonizing Species* stimulated considerable research activity soon after its publication, leading to a steady increase in citations to the book (Fig. 5). The growing interest in the genetics of colonizing species was undoubtedly also associated with the 'electrophoresis revolution', following landmark studies by Lewontin & Hubby (1966) and Harris (1966) reporting the utility of electrophoretic techniques for measuring genetic diversity in populations. Within a short period, many laboratories adopted these approaches, resulting in a flood of data on allozyme variation in plant and animal populations, including many colonizers (reviewed in Nevo 1978; Brown 1979; Hamrick *et al.* 1979; Barrett & Shore 1989).

In his contribution to *The Genetics of Colonizing Species* on the genetic systems of selfing plants, Allard (p. 49) reported estimates of outcrossing and the amounts of quantitative genetic variation in populations using morphological markers and phenotypic traits, respectively. But shortly after, it became possible using enzyme polymorphisms to obtain more precise estimates of mating-system parameters and to survey numerous natural populations to measure heterozygosity, allelic richness and population genetic structure. Anthony Brown (Fig. 6), then a new graduate student with Allard from

Australia, was dispatched to Lewontin's laboratory at Chicago in the late 1960s to learn electrophoretic techniques. Soon, the Allard laboratory was leading the way in studies of the population genetics of plant populations and attracting many trainees, several of whom (e.g. S.K. Jain, A.H.D. Brown, M.T. Clegg, J.L. Hamrick) would go on to make valuable contributions to our understanding of the genetics of plant colonization. In particular, Brown returned to CSIRO in Australia where his laboratory pioneered investigations of the mating systems and population genetic structure of diverse colonizing species (e.g. Brown & Burdon 1983) and co-

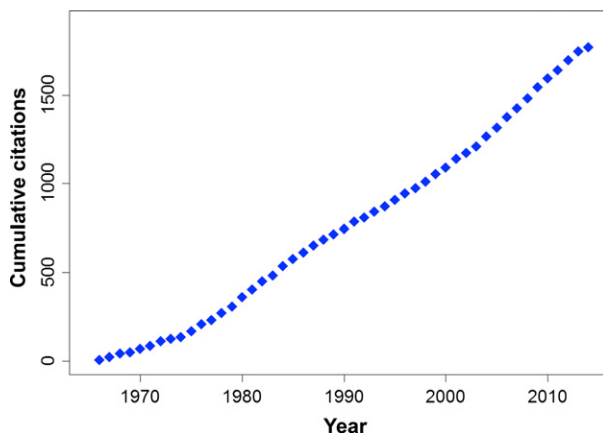


Fig. 5 Cumulative citations of the Baker and Stebbins volume *The Genetics of Colonizing Species* and chapters therein from its publication to the present; data obtained from Web of Science July 2014.



Fig. 6 Anthony H.D. Brown an early pioneer in the electrophoretic study of enzyme polymorphisms in plant populations, including many colonizing species. Brown is seen here scoring starch gels at CSIRO, Canberra, Australia, 1984.

authored an influential review on evolutionary change during invasion (Brown & Marshall 1981). Significantly, the extensive data that accumulated in the 1970s and 80s from allozyme studies of genetic variation in colonizing species while enriching evolutionary biology had relatively little influence on the early development of invasion biology.

The range of genetic markers diversified during the 1980s and 90s to include RAPDs, AFLPs, cpDNA, microsatellites and finally DNA sequences, giving rise to the birth of molecular ecology, in which questions in ecology and evolution were addressed using a diversity of molecular genetic techniques. In 1991, the journal *Molecular Ecology* appeared for the first time and was to provide an important forum for studies concerned with genetic variation in invasive species. The awakening of public awareness of the 'invasive species problem' in the 1990s, and the increasing availability of funding sources to investigate nuisance species, resulted in a greater number of workers from the long-standing sub-disciplines of ecology and evolution becoming interested in invasion biology. Because of the threat posed by invasive species to biodiversity and ecosystem function, invasion biology became incorporated into the broader field of conservation biology, and *Molecular Ecology* widened its scope to include articles relevant to conservation, some of which dealt with genetic aspects of biological invasions. The first study explicitly using 'invasion genetics' in the title appeared at the end of the decade in a study of the Mediterranean fruit fly (Villablanca *et al.* 1998), and the term has subsequently been used frequently in the titles of articles reporting work on a wide range of organisms (e.g. spiny water flea—Colautti *et al.* 2005; freshwater mussel—Therriault *et al.* 2005; Eurasian round goby—Brown & Stepien 2009; vase tunicate *Ciona*—Zhan *et al.* 2010; black rat—Konečný *et al.* 2013). A Web of Science search conducted during the preparation of this article using the key words 'invasion genetics' revealed numerous articles, and, although the field is relatively young, it is developing rapidly.

The first definition of invasion genetics in the literature appears to be by Colautti *et al.* (2005), who described the field as 'the application of genetic techniques to investigate biological invasions'. While this is straightforward and sufficient, I offer an alternative definition that attempts to place more emphasis on the biological questions commonly addressed. In my view invasion genetics is *the study of the historical, ecological and demographic processes responsible for the patterns of genetic diversity in populations and their influence on invasion success and contemporary evolution during biological invasion*'. As this definition makes clear, invasion genetics is not only an integral part of invasion biology,

serving as an equal partner to invasion ecology, it is also very much a contributor to the broader area of contemporary evolution (Stockwell *et al.* 2003; Carroll *et al.* 2007; Westley 2011), in which evolutionary change over timescales of a few hundred years is the focus of attention.

Future challenges and key questions

What are the challenges and opportunities ahead for invasion genetics? I conclude by providing a series of questions that collectively form a solid foundation for the field and consider how invasion ecology and invasion genetics could become more fully integrated. The genesis of many of these questions was the Baker & Stebbins (1965) chapters, including the published dialogue between authors. At the time, the toolbox of techniques available to researchers was much more limited and thus opportunities to definitively answer these questions were difficult. Additional questions have arisen more recently as a result of new theory in evolutionary genetics and techniques in molecular genetics.

- 1 What are the source populations for biological invasions and how many times, when and where have immigrants been introduced to the alien range?
- 2 How important is pre-adaptation vs. postinvasion adaptation to invasive spread?
- 3 How important is genetic variation to colony establishment and as a contributory factor to the lag-phase that characterizes many biological invasions?
- 4 Is population genetic structure different between native and introduced populations and is diversity reduced compared to the native range as a result of bottlenecks, or increased because of gene flow and hybridization?
- 5 What is the relative importance of new mutations vs. standing genetic variation to evolution in invasive populations?
- 6 What are the agents of natural selection resulting in the evolution of local adaptation in introduced populations? How quickly does adaptation occur and what types of constraints limit selection response?
- 7 Does the evolution of local adaptation increase invasion success resulting in further range expansion?
- 8 Are particular reproductive and genetic systems favoured in invasive species and does the invasion process itself promote evolutionary changes in them?
- 9 What are the relative roles of phenotypic plasticity and local adaptation to fitness during invasion and how might this be quantified?
- 10 Do some species possess general-purpose genotypes and how do they originate and spread?

Perhaps the biggest future challenge that invasion genetics faces is to fully integrate existing approaches with ecological and demographic studies of invasive species. Much work in invasion genetics to date can be characterized as an extension of the 'find them and grind them' approach that characterized the early stages of the electrophoresis revolution but using more powerful markers and sophisticated population genetics software programs. In future, it will be important to complement such descriptive work with manipulative field experiments that go beyond the common garden studies that are commonly employed today (reviewed in Colautti *et al.* 2009). Early pioneering work by Martins & Jain (1979) tracked artificially established colonies of *Trifolium hirtum* with known genetic inputs to investigate the adaptive role of genetic variation to colonizing ability. Surprisingly, there has been little subsequent work of this type on invasive species despite the diversity of markers that are now available and the popularity of large-scale field experiments in ecology. Colonizing species generally possess short life cycles and offer tractable systems for field studies of experimental evolution, so long as quarantine regulations and management concerns can be thoroughly satisfied. When combined with genomic analysis and field manipulations of environmental and demographic variables, they offer exciting opportunities to provide new insights into the genetics of biological invasions and on contemporary evolution.

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