Tansley review

Genes to ecosystems: exploring the frontiers of ecology with one of the smallest biological units

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Received: *9 December 2010*
Accepted: *3 March 2011*

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New Phytologist (2011) **191**: 19–36
doi: 10.1111/j.1469-8137.2011.03730.x

Key words: climate change, community genetics postulates, ecosystem services, foundation species, genes-to-ecosystems, invasive species, pollution.

Summary

Genes and their expression levels in individual species can structure whole communities and affect ecosystem processes. Although much has been written about community and ecosystem phenotypes with a few model systems, such as poplar and goldenrod, here we explore the potential application of a community genetics approach with systems involving invasive species, climate change and pollution. We argue that community genetics can reveal patterns and processes that otherwise might remain undetected. To further facilitate the community genetics or genes-to-ecosystem concept, we propose four community genetics postulates that allow for the conclusion of a causal relationship between the gene and its effect on the ecosystem. Although most current studies do not satisfy these criteria completely, several come close and, in so doing, begin to provide a genetic-based understanding of communities and ecosystems, as well as a sound basis for conservation and management practices.

I. Introduction

Genetic differences among individuals within a species can lead to differences in associated community composition and ecosystem processes. An understanding of these effects generates improved predictions regarding impacts of environmental pressures, such as climate change, invasive species and pollution. This concept is referred to as genes-to-ecosystems, or community and ecosystem genetics, which is a trait-based approach (Suding *et al.*, 2003; Gross *et al.*, 2009; Shipley, 2009) similar to quantitative trait analysis. It is defined as the study of genetic interactions between species and the abiotic environment within a context of a community or ecosystem (Shuster *et al.*, 2006; Whitham *et al.*, 2006), which typically involves hundreds or even thousands of species. This approach has been specifically tested and reviewed using systems with more integrated genetics and ecological databases (e.g. Whitham *et al.*, 2003, 2006; Johnson & Stinchcombe, 2007; Wade, 2007; Hughes *et al.*, 2008; Bailey *et al.*, 2009). This approach, however, has yet to be broadly applied, because the breadth of disciplines involved in integrating genes, populations, communities and ecosystems often goes beyond the skill set of any individual and requires a multidisciplinary and collaborative effort.

The major goal of this review is to explore how this concept applies to systems for which this approach has not been explicitly employed, yet, are sufficiently developed to explore broader basic and applied issues. We develop our ideas in the context of global change associated with commonly occurring, ecosystem-impacting events, including invasive species, climate and pollution. For example, in conifers, we explore how the interactions of foundation species (trees and squirrels) and climate can affect a much larger community. With examples from two highly invasive species that have become foundation species in their new environments, we explore how a single mutation in one example and a single haplotype in another example can have cascading effects to redefine their respective ecosystems. Similarly, with the release of endocrine-disrupting chemicals from human contraceptives into aquatic ecosystems, we explore how pollution can alter the gene expression of foundation species, which, in turn, may redefine these ecosystems. Thus, a community genetics perspective on interacting foundation species, exotics and pollution can broaden our understanding of how the genetics of foundation species can have unexpected consequences, and remind us of the complex connections that exist in both natural and exotic systems.

II. Fundamental principles and the community genetics equivalent of Koch's postulates

The genes-to-ecosystem framework is built on four major principles that are crucial for confirming or rejecting the hypothesis that genes can have predictable ecological and evolutionary 'footprints' at community and ecosystem levels. (1) Genotypes have traditional, community and ecosystem phenotypes. The traditional phenotype is defined as the observable properties of an organism that are produced by the interaction of the genotype and the environment (Ridley, 2004). Community and ecosystem phenotypes, on the other hand, represent the effects of genes at levels higher than the population, which largely result from interspecific indirect genetic effects (Shuster *et al.*, 2006; Whitham *et al.*, 2006; Allan *et al.*, 2011). (2) Community and ecosystem phenotypes can be heritable. Community heritability is the tendency for related individuals to support similar communities of organisms and ecosystem processes (e.g. Johnson & Agrawal, 2005; Bailey *et al.*, 2006; Shuster *et al.*, 2006; Schweitzer *et al.*, 2008a; Keith *et al.*, 2010). (3) Community and ecosystem phenotypes can result in feedbacks, affecting the fitness of individual genotypes of the foundation species (Schweitzer *et al.*, 2008a,b, 2011). Such feedbacks can lead to community evolution, which is defined as a genetically based change in the ecological interactions that occur between species over time (Whitham *et al.*, 2006). (4) Community and ecosystem phenotypes are likely to be most important when expressed in a foundation species. Foundation species are defined as those that structure a community by creating locally stable conditions for other species, and by modulating and stabilizing fundamental ecosystem processes (Dayton, 1972). Foundation species are synonymous with keystone species, ecosystem engineers and other similar terms (reviewed by Ellison *et al.*, 2005).

Therefore, what does it take to observationally and/or experimentally demonstrate a genetic effect on the community and ecosystem? Similar to Koch's postulates for demonstrating the causal relationship between a microbe and a disease, we propose four community genetics postulates that provide a framework for the development of a causal relationship between gene(s) and their ecosystem consequences (Table 1). Postulate 1 argues that for a genes-to-ecosystem effect to be detected, the target organism must affect other species in the same or different trophic levels. As the magnitude of these community effects increase, so should the probability of detecting the impacts of genetic differences among individuals of the target organism on the associated community and ecosystem. For example, several studies have shown that, with the removal of a foundation species, diverse community members can be either positively or negatively impacted (e.g. Dickson &

Table 1 Four community genetics postulates to establish a causal relationship between genes and their community and ecosystem consequences

1.	A target species must have a significant effect on the community and ecosystem
2.	The trait in question must be genetically based and heritable
3.	Different genotypes must have quantifiable different effects on the community and ecosystem processes
4.	When the gene(s) of interest or its expression is manipulated, a predictable effect on the community and ecosystem must occur

Whitham, 1996; Gehring *et al.*, 1997; Wimp & Whitham, 2001; Crawford *et al.*, 2007; Kane *et al.*, 2011). The degree to which other community members and trophic levels are impacted is probably caused by key quantitative traits of the foundation species, such as condensed tannins in cottonwoods, which, in turn, may have cascading effects on the community structure and ecosystem processes (Schweitzer *et al.*, 2008a,b).

Postulate 2 requires that the trait whose effect is being studied must be genetically based, and those traits with higher heritability would be expected to show larger effects. For example, Barbour *et al.* (2009) found that the bark characteristics (i.e. quantity and type of decorticating bark) varied greatly among races of *Eucalyptus globulus*. Common garden trials showed that these bark traits were under strong genetic control, in which some tree genotypes had shaggy trunks, whereas others were nearly smooth.

Postulate 3 requires that genes, in their different states, should affect either dependent communities or ecosystem processes in significantly different ways. In the above eucalypt example, differences in bark traits had a major effect on an arthropod community composed of 180 taxa that lived and foraged in the crevices and underneath the bark. The authors found that 60% of the variation in community composition was linked to genetically based variation in these bark traits.

Postulate 4 requires that a causal relationship be demonstrated, such that, when the gene(s) of interest or its expression is manipulated, predictable effects will be observed. Knock-ins, knock-outs, and up- and down-regulation are molecular methods that are becoming increasingly feasible. Genetically modified organisms represent a test of this postulate on a massive scale (Lawrence, 2008) when genes of known function are inserted into isogenic lines. When the community and ecosystem phenotypes of modified and nonmodified controls are compared, the differences can be attributed solely to the inserted genes and their potential interactions with other genes.

We reviewed the literature and selected several studies, which illustrate the genes-to-ecosystem concept in key areas that have received little attention from community geneticists. For each example, we discuss how the research demonstrates this approach, and test it against our four postulates. Lastly, we discuss how this approach can result in novel management solutions, in addition to enhancing the fundamental understanding of how complex biological systems function.

III. Genes, invasions and competition

Invasive genotypes can have an impact on ecosystem processes and community composition. Common reed (*Phragmites australis*) is a native foundation aquatic plant associated with marsh communities in North America, Europe, Asia and Africa (Saltonstall, 2002). Historically, common reed had a sparse, yet widespread, distribution throughout North America (Fig. 1a; Saltonstall, 2002). However, in the past 150–200 yr, common reed has increased in abundance, its distribution changing from a relatively rare to a dominant wetland species (Chambers *et al.*, 1999; Fig. 1a). Saltonstall (2002, 2003) evaluated two noncoding chloroplast DNA markers in samples collected from current populations and historical specimens from North America and worldwide. Analyses revealed three lineages consisting of 11 haplotypes native to North America, one haplotype (I) found along the Gulf of Mexico and South America, and a nonnative haplotype (M) with a cosmopolitan distribution spanning North America, Europe and Asia. Haplotype M has expanded widely throughout North America, replacing native haplotypes regionally along the Atlantic coast (Fig. 1a). The expansion of the common reed in North America may be a result of the invasion of ‘aggressive genotypes’ (Chambers *et al.*, 1999).

Howard *et al.* (2008) demonstrated one potential mechanism for the success of the nonnative M haplotype in North America (Fig. 1b). They took advantage of a restoration project that included both the nonnative M haplotype and the Gulf Coast I haplotype. Comparisons of common reed haplotypes along the coast of Louisiana revealed that the nonnative M haplotype exhibited significantly higher vegetative growth rates compared with the Gulf Coast I haplotype. After 14 months of growth, the final coverage of the nonnative M haplotype was more than four times that of the Gulf Coast I haplotype. The study also demonstrated a shift in genetic composition from an equal representation of the two haplotypes towards a composition dominated by the nonnative M haplotype.

Several studies have demonstrated physiological differences between the nonnative haplotype and native common reed, which may explain the success of the nonnative haplotype (Vasquez *et al.*, 2005; Holdredge *et al.*, 2010; Mozdzer & Zieman, 2010). The nonnative haplotype exhibits greater salt tolerance than does native common reed, as evidenced by its higher survival and growth rates (Vasquez *et al.*, 2005). Holdredge *et al.* (2010) demonstrated that increased nutrients (fertilization) favored nonnative haplotypes through increased lateral growth, above-ground biomass and rhizome biomass. Mozdzer & Zieman (2010) studied common reed in the field and laboratory, demonstrating that the nonnative haplotype of common reed had significantly higher plant density, biomass, percentages of carbon and nitrogen (N), and photosynthesis rates compared with native haplotypes. These studies suggest that the nonnative haplotype has the ability to exploit habitats previously impenetrable to native common reed, probably through greater tolerance of environmental conditions, such as increased salinity and

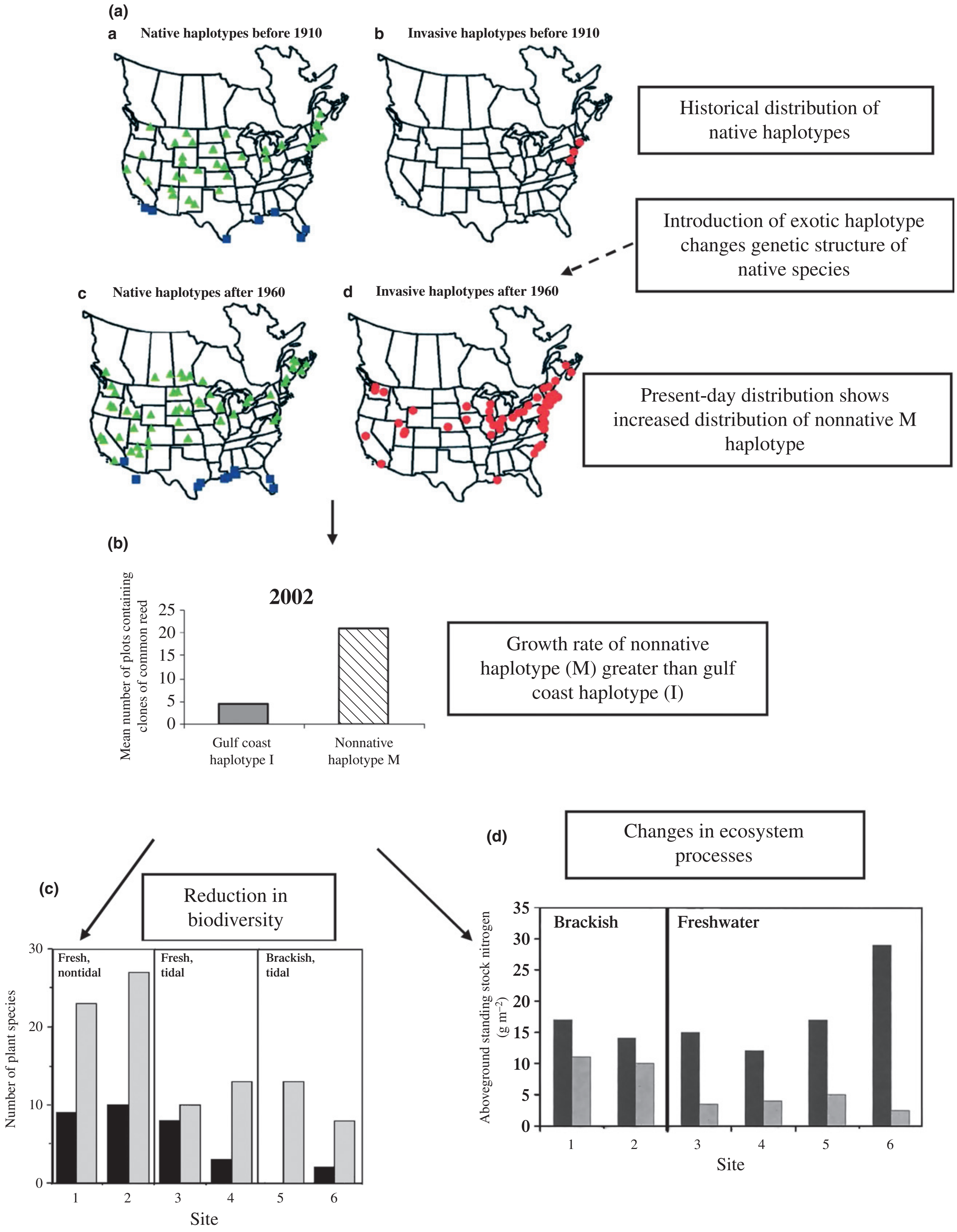

(a)
a Native haplotypes before 1910
b Invasive haplotypes before 1910
Historical distribution of native haplotypes
Introduction of exotic haplotype changes genetic structure of native species
c Native haplotypes after 1960
d Invasive haplotypes after 1960
Present-day distribution shows increased distribution of nonnative M haplotype
(b)
2002
Mean number of plots containing clones of common reed
25
20
15
10
5
0
Gulf coast haplotype I
Nonnative haplotype M
Growth rate of nonnative haplotype (M) greater than gulf coast haplotype (I)
(c)
Reduction in biodiversity
Number of plant species
30
20
10
0
Fresh, nontidal
Fresh, tidal
Brackish, tidal
1
2
3
4
5
6
Site
(d)
Changes in ecosystem processes
Aboveground standing stock nitrogen (g m⁻²)
35
30
25
20
15
10
5
0
Brackish
Freshwater
1
2
3
4
5
6
Site

Fig. 1 A nonnative haplotype invades wetlands with community- and ecosystem-level effects. (a) Historically common reed was distributed throughout North America at low abundance. Within the past 150–200 yr, common reed became invasive, as a result of a nonnative haplotype, shown as red circles on the distribution map of North America. The blue squares represent haplotype I (the Gulf Coast haplotype) and the green triangles represent native haplotypes. An exact test of population differences revealed significant shifts in haplotype frequencies ($P < 0.001$). (b) After a 14-month period, the nonnative M haplotype showed significantly higher growth rates compared with the Gulf Coast I haplotype in a re-vegetation project conducted along the Gulf Coast states. There was a significant difference in the ratio of change in growth before and after 14 months for the two haplotypes ($P < 0.0001$). (c) Studies of marsh sites in Connecticut and New Jersey show that plant species' diversity is higher at marsh sites without common reed compared with sites invaded by common reed. The noncommon reed-dominated sites were dominated by *Typha* for sites 1, 3 and 4, *Carex* for site 2, and *Spartina patens* for sites 5 and 6. Black bars, common reed-dominated marsh sites; gray bars, noncommon reed-dominated marsh sites. (d) Wetlands dominated by common reed show higher levels of above-ground standing stocks of nitrogen (SSN) compared with wetlands without common reed. For example, the above-ground SSN of common reed was 428% of *Typha angustifolia* and 158% of *Spartina patens* in freshwater tidal and brackish marshes, respectively. Sites 1 and 2 were located in New Jersey, sites 3 and 4 were located in New York, and sites 5 and 6 were located in Connecticut. (d) Black bars, common reed-dominated marsh sites; gray bars, noncommon reed-dominated marsh sites. Figures courtesy of: (a) Saltonstall (2002), Copyright 2002 National Academy of Sciences, USA; (b) Howard *et al.* (2008); (c) Meyerson *et al.* (2000); (d) Windham & Meyerson (2003), (b–d) reproduced with kind permission from Springer Science+Business Media B.V.

eutrophication, which are commonly brought about by anthropogenic changes to the environment.

Many studies have shown that marsh communities dominated by common reed are associated with cascading effects at the community (Benoit & Askins, 1999; Keller, 2000; Silliman & Bertness, 2004) and ecosystem (Meyerson *et al.*, 2000; Windham & Meyerson, 2003) levels, although few have attributed such impacts specifically to the nonnative haplotype (but see Maerz *et al.*, 2010). Nevertheless, such impacts are important to consider as the nonnative haplotype has increased in abundance and range across North America (Saltonstall, 2002; Fig. 1a), and clearly shows an enhanced capability to invade new habitats relative to native common reed, as detailed above.

The impacts of common reed on biodiversity are often negative, yet there is some variation depending on the taxa studied (see the review by Meyerson *et al.*, 2009). Meyerson *et al.* (2000) reported that the total number of plant species in marsh habitat dominated by common reed is lower than that in marsh habitat without common reed (Fig. 1c), and that plant species' richness may increase following restoration efforts to remove common reed. Studies conducted along the Atlantic coast, an area of high invasion by the nonnative haplotype of common reed, also showed that plant species' richness declined to only one-third that found in marshes without common reed (Silliman & Bertness, 2004). Studies of the impacts of common reed on other taxa have shown decreased fish abundance (Able *et al.*, 2003), but minimal impacts on macroinvertebrate diversity (Holomuzki & Klarer, 2010). In some cases, common reed may benefit native species, such as land birds (Meyer *et al.*, 2010).

The influence of common reed also extends to ecosystem processes (Fig. 1d). The plant's presence in wetlands is associated with higher levels of above-ground standing stocks of N, comparatively higher rates of N uptake and subsequent impacts on N fluxes in marsh habitats in which it dominates (Windham & Meyerson, 2003). Although earlier studies of ecosystem impacts did not test explicitly for differences between the native and nonnative common reed haplotypes, recent studies have demonstrated intraspecific differences in ecophysiology, such as significant differences in C : N ratios and N requirements (Maerz *et al.*, 2010; Mozdzer & Zieman, 2010), which could lead to changes in ecosystem processes.

The common reed system fulfills the first and third postulates. Common reed has significant effects on its community and ecosystem through high vegetative growth that reduces biodiversity and increases available N in the ecosystem. The focal trait, higher vegetative growth rate, is linked to the nonnative M haplotype that is genetically based and may allow for important changes in gene expression, rather than different isoforms. However, to address the second postulate, further research needs to investigate the heritability of the higher vegetative growth rate in common garden experiments. Although the specific gene in the M haplotype of common reed that is responsible for its increased competitive abilities has not been investigated, the introduction of this nonnative haplotype is a natural potential knock-in experiment. This natural experiment could potentially address postulate 4, as the predicted effect of haplotype M on its new community and ecosystem can be compared with similar, noninvaded ecosystems and communities. This example is especially interesting in that it focuses on an invasive exotic haplotype rather than an invasive species; in other words, it appears that individual genes matter at whole-community and ecosystem levels.

Of additional concern is the possibility of hybridization between native and nonnative haplotypes. Meyerson *et al.* (2010) demonstrated that native and nonnative haplotypes were capable of producing viable offspring. F1 seeds had germination rates of 50% compared with nonnative seeds. Although there has been little evidence of hybridization in nature (Saltonstall, 2003; Howard *et al.*, 2008; but see Paul *et al.*, 2010), the possibility of new allelic combinations in viable, hybrid offspring exists (Meyerson *et al.*, 2010), and may be significant for the conservation of communities (Wimp *et al.*, 2004) and processes of speciation (Evans *et al.*, 2008).

IV. Mutation, resistance and ecosystem consequences

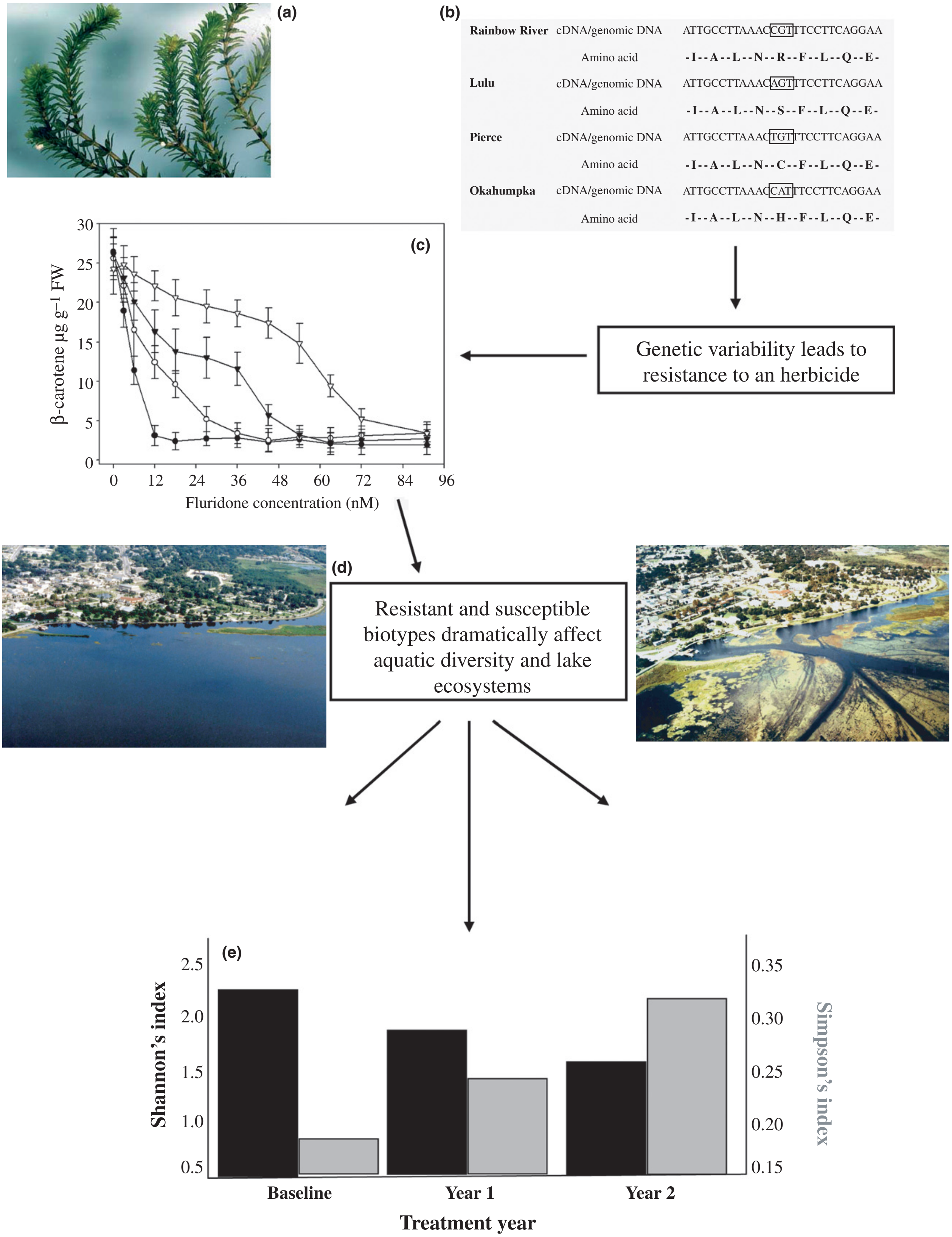
The evolution of herbicide resistance is thought to be unlikely in the absence of sexual reproduction; yet, the story of hydrilla (*Hydrilla verticillata*) demonstrates that somatic mutations can result in rapid evolution and have major community- and ecosystem-level consequences. Hydrilla (Fig. 2a), an aquatic monocotyledon native to Asia, was introduced to Florida in the 1950s and has subsequently become the most abundant submerged aquatic plant in Florida. This has resulted in one of the greatest weed problems in the southeastern USA (Michel *et al.*, 2004). A management response to hydrilla is the herbicide fluridone (Arnold, 1979; Fox *et al.*, 1994). Fluridone works by inhibiting the enzyme phytoene desaturase (PDS), a rate-limiting enzyme in the biosynthesis of carotenoid (Chamovitz *et al.*, 1993). PDS is produced via the nuclear genome and is active in the chloroplast. The PDS pathway is critical, as carotenoids absorb excess activation energy that protects plants from photosaturation and photobleaching. When lakes are treated with fluridone, photobleaching and the death of hydrilla occur, and, within several weeks, can convert clogged lakes into open waterways (Netherland & Getsinger, 1995; Fox *et al.*, 1996; Michel *et al.*, 2004).

After a decrease in the effectiveness of fluridone in lakes in which the herbicide had been used the longest (*c.* 7 yr), a major sampling effort was conducted in 200 Florida lakes to determine the nature of susceptible and resistant forms of hydrilla (Michel *et al.*, 2004). From these samples, PDS genes were cloned and sequenced using polymerase chain reaction. Multiple mutations were located at codon 301 (Fig. 2b). This codon is highly conserved across cyanobacteria, microalgae and higher plants, and produces arginine (CGT) in the wild-type hydrilla. In the study, three distinct biotypes were discovered, each originating from a different lake, indicating three separate somatic mutation events. Two different single point mutations were identified, resulting in a serine substitution (AGT) and a cysteine substitution (TGT), and a third double point mutation conferring a histidine (CAT). The three novel variations had activity levels similar to that of the wild-type enzyme (Fig. 2c); yet, they were two to five times less sensitive to fluridone, required higher concentrations of fluridone for complete bleaching and had higher resistance to sensitivity ratios (Michel *et al.*, 2004). No intra-lake variation was found, suggesting that, once the resistant biotypes appeared, they effectively spread throughout the lakes.

The ecosystem-level consequences of the resistant biotypes can be significant for aquatic systems (Fig. 2d). Lakes with abundant hydrilla became stratified, had lower dissolved oxygen concentrations, pH levels and phosphorus concentrations, and showed increases in carbon dioxide concentration. These changes in water chemistry and biogeochemistry led to weight and size reduction in some fish, decreases in phytoplankton abundance and changes in zooplankton diversity (Richard *et al.*, 1983; Schmitz *et al.*, 1993; Gordon, 1998). With treatment of herbicide to reduce hydrilla, measurements of community diversity (e.g. Shannon and Simpson indices) changed significantly (Fig. 2e). Changes in these diversity metrics are often thought to reflect community stability over time. However, similar to the cottonwood–tamarix controversy (i.e. the invasive tamarix provides a suitable habitat for the endangered southwestern willow fly catcher; Sogge *et al.*, 2008), higher levels of hydrilla are positively correlated with bird species' richness, including the American coot (*Fulica americana*) and pied-billed grebes (*Podilymbus podiceps*). Decreases in bird numbers occurred with the experimental removal of hydrilla (Esler, 1990).

The hydrilla point mutation example meets at least three of the four genes-to-ecosystem postulates. The first postulate is supported by hydrilla's ability to dominate whole aquatic systems, making its effects widespread. The second postulate is maintained by the genetic basis for the PDS enzyme. Although somatic mutations are not normally thought to be heritable (especially in animals with integrated organ systems), in organisms with repeating module structure, such as plants, it has long been known that somatic mutations can be heritable via both sexual and asexual modes of reproduction (Whitham & Slobodchikoff,

Fig. 2 Somatic point mutations led to herbicide resistance in hydrilla (*Hydrilla verticillata*), causing numerous lakes in Florida to experience community- and ecosystem-level changes. (a) Hydrilla was introduced to Florida in the 1950s and has become a ubiquitous aquatic weed. (b) Multiple point mutations from different lakes have been documented conferring substitutions at codon 301. (c) Genetic variation has led to an increased concentration of carotenoid pigments in the presence of the herbicide fluridone. Data are means ± SD β-carotene content in hydrilla shoot apices. Systems represent different phenotypes: closed circles, susceptible; open circles, low resistance; closed triangles, intermediate resistance; open triangles, high resistance. (d) Resistant biotypes have significant effects on lake ecosystems; lake colonized by susceptible genotypes (left) and lake colonized by resistant genotypes (right). (e) Community-level effects occur when treated with the herbicide. Shannon's (black bars) and Simpson' (gray bars) indices both show significant changes over time as a result of herbicide treatments. Data are annual means from Lake Mann, Florida, and are adapted from Richard *et al*. (1983) (Kruskal–Wallis; $P < 0.05$). These diversity indices are considered to be measures of community stability and the patterns reveal significant changes in the zooplankton community and a change in the lake's food base. A decreased Shannon's index indicates lower species' richness, and an increased Simpson's index indicates lower diversity. Figures courtesy of: (a) South Carolina Department of Natural Resources: http://www.dnr.sc.gov/invasiveweeds/hydrilla.html; (b–d) Michel *et al.* (2004), reproduced with kind permission from John Wiley & Sons, Inc; (e) adapted from Richard *et al.* (1983), with kind permission from Springer Science+Business Media B.V.


(a)
(b)
Rainbow River cDNA/genomic DNA ATTGCCTTAAACCGTTTCCTTCAGGAA
Amino acid -I--A--L--N--R--F--L--Q--E-
Lulu cDNA/genomic DNA ATTGCCTTAAACAGTTTCCTTCAGGAA
Amino acid -I--A--L--N--S--F--L--Q--E-
Pierce cDNA/genomic DNA ATTGCCTTAAACTGTTTCCTTCAGGAA
Amino acid -I--A--L--N--C--F--L--Q--E-
Okahumpka cDNA/genomic DNA ATTGCCTTAAACCATTTCCTTCAGGAA
Amino acid -I--A--L--N--H--F--L--Q--E-
Genetic variability leads to resistance to an herbicide
(c)
β-carotene μg g−1 FW
30
25
20
15
10
5
0
0
12
24
36
48
60
72
84
96
Fluridone concentration (nM)
(d)
Resistant and susceptible biotypes dramatically affect aquatic diversity and lake ecosystems
(e)
Shannon's index
2.5
2.0
1.5
1.0
0.5
Simpson's index
0.35
0.30
0.25
0.20
0.15
Baseline
Year 1
Year 2
Treatment year

1981; Buss, 1983; Gill *et al.*, 1995). The third postulate is met as the different biotypes (i.e. genetic variants) of hydrilla can affect significantly associated ecosystems. The fourth postulate could easily be met by propagating the three biotypes in a glasshouse and observing their effects in a highly controlled setting. This example is remarkable in its mechanistic understanding at the molecular level. The research identified a somatic point mutation which confers resistance to a herbicide with a known pathway of interactions. Most gene-to-ecosystem examples lack such genetic detail and tend to be most thoroughly developed at higher levels of the continuum (e.g. quantitative traits), which is often associated with where the research first started and then expanded to other levels.

V. Heritable traits, pine cones and climate

The level of serotiny, a heritable trait in lodgepole pine (*Pinus contorta*) stands, is influenced by climate, fire and seed predators, and, in turn, affects forest composition and dependent species' evolution (Fig. 3). The lodgepole pine is a common foundation species throughout western North America. An important cone characteristic of these trees is cone serotiny: the capacity to release seeds in response to an environmental trigger rather than spontaneously at seed maturation (Lamont *et al.*, 1991). The cone scales of lodgepole pines are sealed shut with a resin that melts when heated. Seed release in lodgepole pines is usually triggered by temperatures above 50°C, as during a forest fire (Teich, 1970). Lodgepole pines are likely to display serotiny if they grow in fire-prone habitats and experience stand-replacing fire within their average life-span (Lamont *et al.*, 1991). Because seeds from several years are released from the heat of a fire, serotiny allows trees to regenerate in extremely dense stands after a stand-replacing fire, thus excluding other species. Levels of serotiny vary among populations, and common garden experiments with Jack pine (*Pinus backsiana*) have shown that this trait is heritable (Rudolph *et al.*, 1959). Teich (1970) determined the frequencies of lodgepole pine trees bearing serotinous, nonserotinous, and both serotinous and nonserotinous cones in several populations. Taking into account selection and possible misclassification of heterozygotes, he concluded that cone serotiny is probably governed by two alleles of a single gene. However, the genes responsible for this trait have not yet been identified.

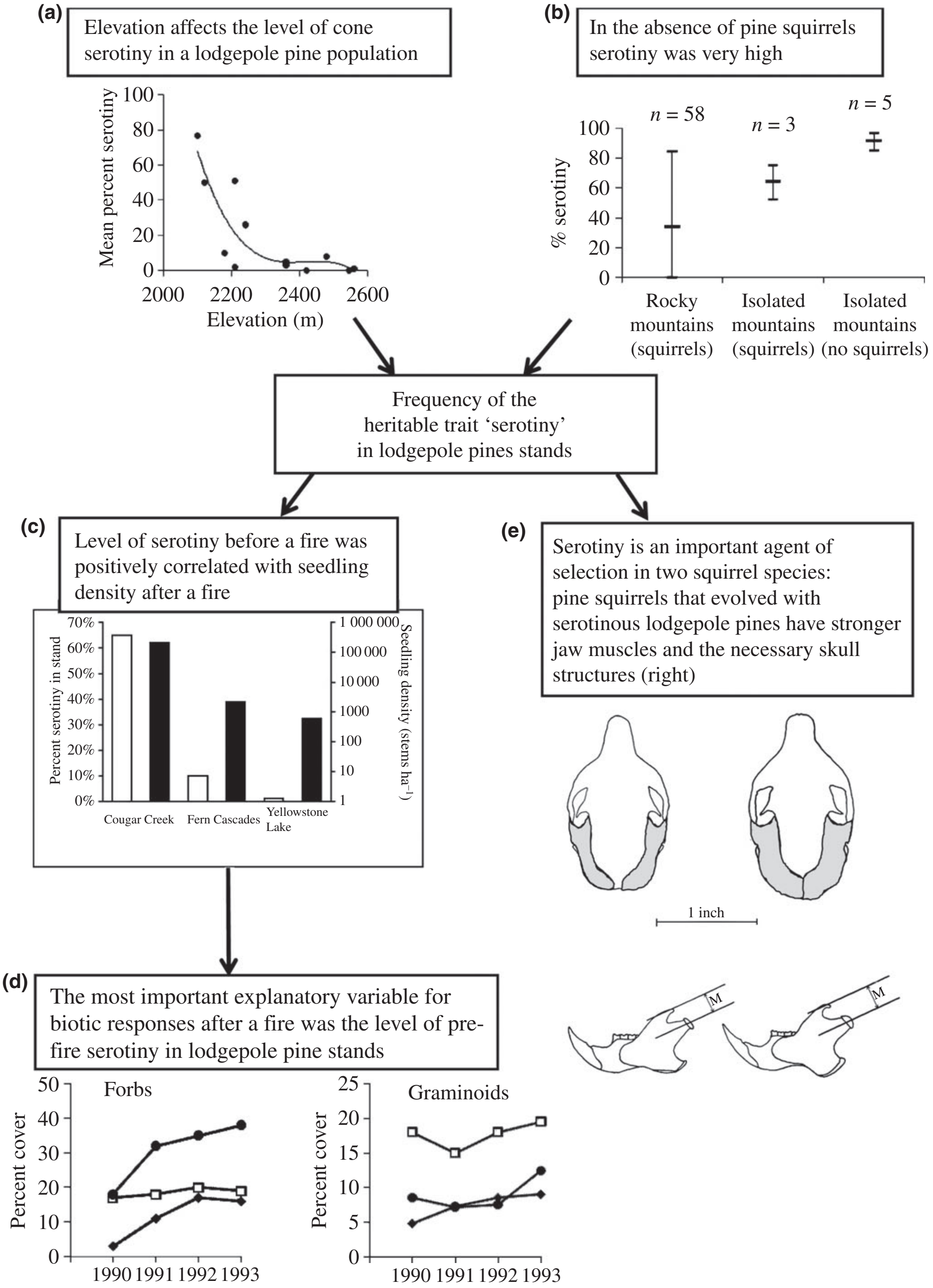
Climate, through its effect on fire regimes, appears to exert a major selection pressure that acts on serotiny. Elevation influences climate and thus fire regimes; at low elevation in Yellowstone National Park, fire occurred historically at 135–185-yr intervals, but, at high elevation, fire occurred at 280–310-yr intervals (Schoennagel *et al.*, 2003). As a result of the different fire regimes, more trees were serotinous at low and middle elevations than at high elevations (Fig. 3a; Tinker *et al.*, 1994). On a larger scale, the distribution of serotinous and nonserotinous lodgepole pines in the western USA also reflects the influence of climate. In the moist, less fire-prone forests along the Pacific Coast, lodgepole pines are nonserotinous. However, on the dry slopes of the Rocky Mountains and the intermountain areas of British Columbia and the Yukon, lodgepole pines are serotinous (Smith, 1970).

Seed predators also influence the level of serotiny in lodgepole pine stands (Fig. 3b). American red squirrels (*Tamiasciurus hudsonicus*) eat a large fraction of the seeds held in the canopy before dispersal occurs. This predispersal loss of seeds represents a strong selection pressure for the evolution of plant traits that would counter this reduction in fitness. Benkman & Siepielski (2004) compared the levels of serotiny in lodgepole pine stands in isolated mountain ranges in which American red squirrels had been absent for the last 12 000 yr with stands in mountain ranges with American red squirrels present. In the absence of American red squirrels, almost 100% of lodgepole pines were serotinous, whereas the frequency of serotiny in 341 different stands in the northern Rocky Mountains, where American red squirrels were present, was variable (0–90%) and much lower. Seventy-six per cent of the stands had a frequency of serotiny of 50% or less (Fig. 3b). The level of serotiny in pines decreases when seed predators are present because the latter feed on stored seeds from past years and thus continuously diminish the seed bank. When a fire occurs that could trigger the mass release of stored seeds, the seed bank is depleted. Therefore, serotiny is not as advantageous when seed predators are present.

The interaction of fire, herbivory and serotiny cascades to affect the whole forest ecosystem through sapling density after a fire. In Yellowstone National Park, in forest stands with many serotinous pine trees before a fire, seedling density after a stand-replacing fire was very high, whereas stands with few serotinous trees produced few seedlings (Fig. 3c; Turner *et al.*, 2003).

Geographic location and pre-fire levels of serotiny also explained much of the observed variation in biotic responses, including species' richness, abundance of opportunistic species, and cover and density of pine seedlings, forbs, graminoids and shrubs post-fire (Fig. 3d; Turner *et al.*, 1997). At a site that was characterized by a very low lodgepole pine seedling density (Yellowstone Lake), the percentage cover of forbs was very high; whereas, at a site with an extremely high lodgepole pine seedling density (Cougar Creek), the percentage cover of graminoids was much higher than at the other sites (Fig. 3d). Thus, the level of lodgepole pine serotiny in a stand affected post-fire seedling density and community composition.

The level of serotiny in a population also affects the evolution of individual species. Smith (1970) showed that American red squirrels living east of the Cascades in forests



(a) Elevation affects the level of cone serotiny in a lodgepole pine population

(b) In the absence of pine squirrels serotiny was very high

Frequency of the heritable trait ‘serotiny’ in lodgepole pines stands

(c) Level of serotiny before a fire was positively correlated with seedling density after a fire

(e) Serotiny is an important agent of selection in two squirrel species: pine squirrels that evolved with serotinous lodgepole pines have stronger jaw muscles and the necessary skull structures (right)

(d) The most important explanatory variable for biotic responses after a fire was the level of pre-fire serotiny in lodgepole pine stands

Fig. 3 The level of serotiny in lodgepole pine (*Pinus contorta*) stands is influenced by elevation and seed predators, and, in turn, affects forest productivity, community composition and dependent species' evolution. (a) Percentage serotiny decreased with an increase in elevation, which determines fire frequency. (b) In the absence of squirrels, the percentage serotiny is higher than when squirrels are present. Presented are the sample size, median and range of percentage serotiny in lodgepole pine stands. (c) Post-fire lodgepole pine seedlings grew more densely when the level of pre-fire stand serotiny was high. Open bars, pre-fire serotiny; closed bars, post-fire seedling density. Note the logarithmic scale of the seedling density. (d) The level of pre-fire stand serotiny in three locations (Cougar Creek, squares; Fern Cascades, diamonds; Yellowstone Lake, circles) in Yellowstone National Park affected the percentage cover of forbs and graminoids. (e) Dorsal view of the skull and lateral view of the lower jaw of a Douglas squirrel (*Tamiasciurus douglasii*) (left) and a red squirrel (*T. hudsonicus*) (right). The shaded area of the skull is the surface of attachment of the temporal muscles. M is the distance of the moment arm of the force applied by the temporal muscles. Its greater distance in the red squirrel allows a greater force to be applied by the teeth. Figures courtesy of: (a) adapted from Tinker *et al.* (1994), reproduced with kind permission from NRC Research Press; (b) after Benkman & Siepielski (2004); (c) after Turner *et al.* (2003); (d) after Turner *et al.* (1997); (e) Smith (1970), (b–e) Copyright by the Ecological Society of America.

with serotinous lodgepole pines were adapted to eating serotinous cones with hard bracts. These American red squirrels had 16% greater average body weight and a 25% greater temporal jaw muscle weight and associated skull structures than Douglas squirrels (*Tamiasciurus douglasii*) living west of that mountain range in forests with nonserotinous lodgepole pines (Fig. 3e). It appears that, because serotinous cones have thicker and harder scales, squirrels that feed on these cones must have greater jaw strength to open them (Smith, 1970). The effects of serotiny are also visible within one squirrel species. American red squirrels living in lodgepole pine forests had jaw musculature that weighed, on average, one-third more than that of American red squirrels in forests without lodgepole pines (Smith, 1970).

To summarize, climate affects fire regimes, which, together with seed predators, select for or against the heritable trait of serotiny in lodgepole pine stands. The percentage serotiny influences pine seedling density and thus forest productivity, which consecutively shape numerous ecosystem characteristics and processes, and the evolution of dependent species. An understanding of these relationships can help to mitigate the effects of climate change on the important foundation species: lodgepole pine.

The lodgepole pine system fulfills three of the four postulates. Lodgepole pine is a foundation species that has significant effects on the ecosystem. Serotiny is heritable. Recruitment and productivity after a stand-replacing fire are much higher when pre-fire serotiny levels are high. However, the fourth postulate has not been tested. This would require a knowledge of the serotiny gene(s) sequence and a controlled long-term landscape-scale experiment, or, alternatively, common garden experiments with serotinous and nonserotinous trees.

VI. Gene expression, fish and pollution

Not only can the genotype(s) of an individual or a population of organisms affect an ecosystem, but the variable expression of this genetic material may also play a profound role. The field of ecotoxicology and its implications from an individual to community level have been reviewed recently by Shugart *et al.* (2010). They suggest that exposure to chemical pollutants may have impacts on populations through the induction of mutations, selection against specific genotypes and/or actions at the level of gene expression. Although our emphasis has been on plant examples, as they are the basis of food chains and expected to frequently be foundation species (Ellison *et al.*, 2005), vertebrates are often foundation species and can interact with foundation plant species to define community structure. For example, the interactions of two foundation species, beavers and willows, can determine whether a community develops as a wetland or a dry grassland with all the differences in species associated with these two very different communities (Chadde & Kay, 1991). Here, we develop an animal-based example in which changes in levels of gene expression can have an impact on the entire ecosystem. After our previous plant-based examples, it is important to emphasize that a genes-to-ecosystem approach can be applied at different trophic levels, such that the cascading effects can be top–down, bottom–up and/or lateral.

Gene expression is susceptible to many natural environmental factors, including seasonal and daily fluctuations (Gozdowska *et al.*, 2006), chemicals in the environment (Lange *et al.*, 2009) and climate (Baroiller *et al.*, 1999). Some genes are regulated by hormones, specifically sex steroids, and are therefore additionally susceptible to anthropogenic chemicals that mimic or block endogenous hormones. This class of chemicals is referred to as endocrine-disrupting chemicals (EDCs) (Kavlock *et al.*, 1996). Because aquatic ecosystems act as a sink for anthropogenic compounds, they are used to assess the impacts of EDCs on wildlife, with fish the best-studied organism (Scholz & Mayer, 2008). This example focuses on the effects of an EDC on fish gene expression, and how these effects cause ecosystem-wide consequences.

One particular EDC, 17β-ethinylestradiol (EE2), is a chemical used in contraceptives and released into many ecosystems throughout the world via wastewater effluent. Designed to mimic natural estrogen, this chemical has been shown to alter the expression of genes in estrogen-signaling pathways in numerous fish species. Lange *et al.* (2009) have shown how exposure to an environmentally relevant dose of EE2 changes the expression of genes in a sex-dependent manner in roaches (*Rutilus rutilus*), a species of fish (Fig. 4a). One of the genes studied (*cyp19ala*) is responsible for an enzyme essential to the production of the sex steroid estrogen, which plays a critical role in the process and timing of development and sexual differentiation of these fish. These chemicals can have further effects by altering the expression of genes regulating behavior (Saaristo *et al.*, 2009).

The effects of altered gene expression extend to the physiology of the fish in both laboratory and natural communities. As a result of exposure to this EDC and the subsequent changes in gene expression, many genetic males had feminized reproductive ducts or were physiologically female in the aforementioned experiment (Lange *et al.*, 2009). This sex reversal can affect the sex ratio of a fish population, sometimes resulting in the loss of all males. Jobling *et al.* (2006) found that the presence of intersex fish in wild populations was strongly influenced by the level of exposure to estrogenic chemicals in their environment (Fig. 4b). In environments exposed to higher concentrations of EDCs, intersex fish were more prevalent. The sex ratio was feminized in these areas as well, although this trend was not statistically significant.

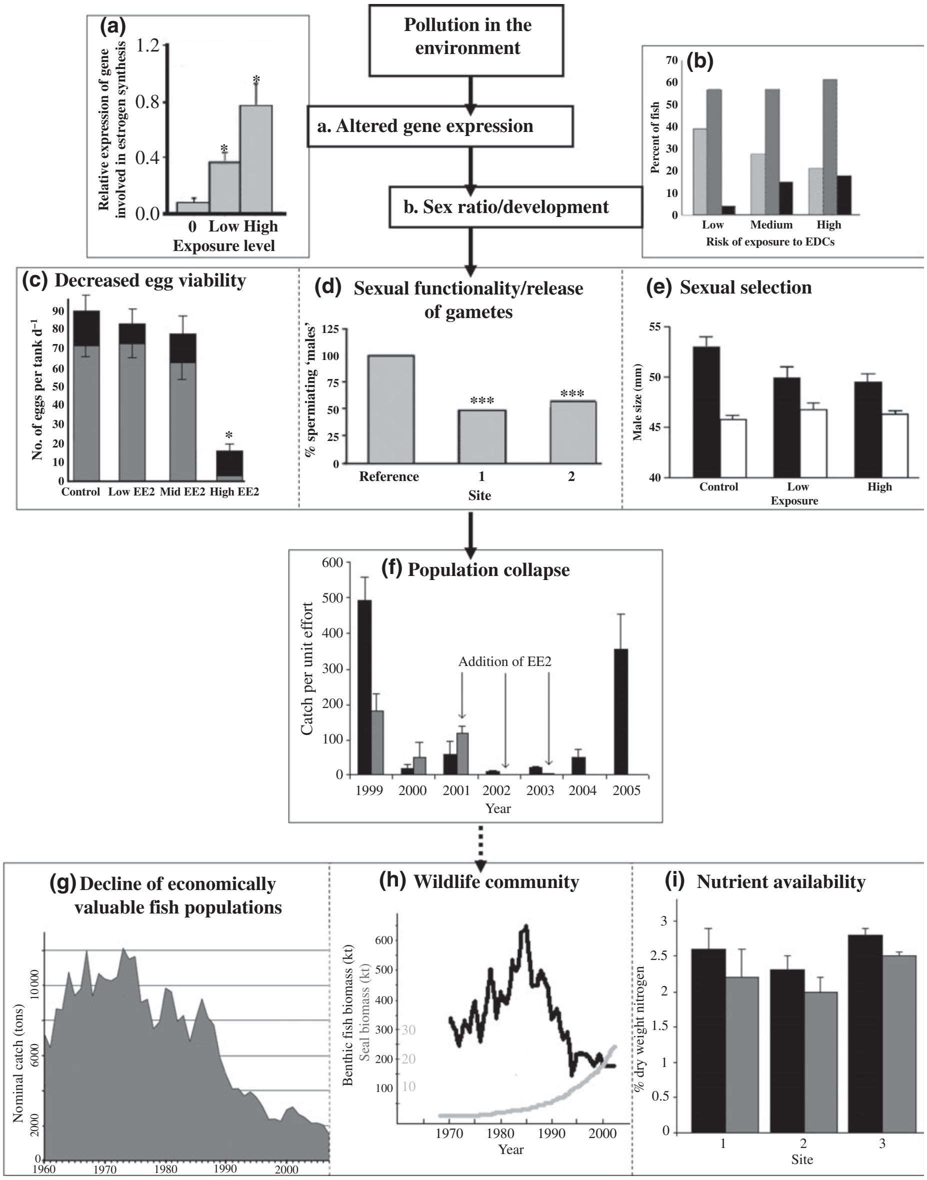


Fig. 4 Pollution has been shown to affect gene expression in fish, inducing population-level changes. (a) 17β-Ethinylestradiol (EE2) exposure to young life stages of a fish called the roach alters the expression of an important gene in estrogen signaling pathways (*cyp19ala*). Asterisks denote statistical significance: *, $P = 0.05$. (b) More male roach have oocyte-testes and feminized reproductive ducts in sites with a higher chance of containing endocrine-disrupting chemicals (EDCs). Pale gray bars, male; dark gray bars, female; black bars, intersex. (c) Zebrafish exposed to EE2 for 6–10 d lay fewer eggs (total bar on graph) and, of the eggs laid, more nonviable (black fraction) than viable (gray fraction). Asterisks denote statistical significance: *, $P = 0.01$. (d) Fewer roach release sperm when exposed to wastewater. Asterisks denote statistical significance: ***, $P < 0.0001$. (e) Female sand gobies exposed to EE2 select smaller mates. Mated males are larger than unmated males in all treatments ($P < 0.001$), yet the difference in size between mated and unmated males in the control treatment was larger than that of either EE2 treatment ($P = 0.014$). Closed bars, mated males; open bars, unmated males. (f) A population of fathead minnows in a Canadian lake collapses when exposed to EE2 for 3 yr. Black bars, control; gray bars, exposed to EE2. Given the endocrine-disrupting chemical EDC-induced population-level declines, greater community- and ecosystem-level effects are expected to occur. (g) Reported nominal catch of salmon in the North Atlantic from 1960 to 2007. (h) When benthic fish populations collapse, the pressure on their prey base is relieved, allowing the grey seal population to increase exponentially. (i) Nutrient availability in the ecosystem is higher when salmon are present. The concentrations of nitrogen are higher in streams with salmon compared to streams without salmon in every case ($P < 0.05$). Black bars, ecosystem with salmon; gray bars, without salmon. Modified figures courtesy of: (a) Lange *et al.* (2009), reproduced with kind permission from the American Chemical Society; (b) Jobling *et al.* (2006); (c) Nash *et al.* (2004), (b–c) reproduced with kind permission from *Environmental Health Perspectives*; (d) Saaristo *et al.* (2009), reproduced with kind permission from Elsevier; (e) adapted from Jobling *et al.* (2002), reproduced with kind permission from the Society for the Study of Reproduction; (f) adapted from Kidd *et al.* (2007), Copyright 2005 National Academy of Sciences, USA; (g) graph and axis labels only are adapted with kind permission from the International Council for Exploration of the Seas (ICES) (2008); (h) adapted from Frank *et al.* (2005), reprinted with kind permission from AAAS; (i) Naiman *et al.* (2002), reproduced with kind permission from John Wiley & Sons, Inc.

Altered sexual development and sex ratios can decrease the reproductive success of a population. Nash *et al.* (2004) found that fish exposed to EE2 had decreased fertility, laying fewer eggs, and, of those eggs, fewer were viable (Fig. 4c). Furthermore, because exposure to EE2 reduces the number of functional males in a population through full or partial sex reversal, there are fewer males to release sperm (Fig. 4d). Even those affected males who maintained their reproductive functionality released less sperm than males in uncontaminated environments (Jobling *et al.*, 2002). Reproductive success can also be impaired by alterations in behavior induced by a change in gene expression. Female fish exposed to a high dose of EE2 were less able to choose superior mates than those exposed to low doses or no EE2 (Fig. 4e; Saaristo *et al.*, 2009). A higher dose of EDC not only induced the selection of smaller mates, but changed the expression of key genes, including vitellogenin, reducing the quality of reproducing individuals.

By causing a reduction in reproductive success, environmental contaminants, such as EE2, have been shown to decrease overall population size, potentially causing the collapse of an entire population (Kidd *et al.*, 2007). Populations of fathead minnows (*Pimephales promelas*) were monitored in a reference lake and a lake given a 3-yr treatment of EE2. Although there were natural population fluctuations in both lakes, there was no recovery of numbers after treatment with EE2 in the experimental lake (Fig. 4f; Kidd *et al.*, 2007).

Given that EE2 can cause the collapse of an entire population in a natural environment, exposure to EDCs is presumed to have effects extending throughout the ecosystem. The negative impacts of EDCs, in conjunction with other stresses in the environment, such as overfishing, may contribute to the decline of economically valuable fish populations (Kime, 1995) (Fig. 4g). The removal of a fish population from an ecosystem, regardless of its economic value, will have an impact on community structure through trophic interactions. Removing cod from an ecosystem caused an increase in both a competing species, grey seals, and their prey, shrimp and snow crabs (Fig. 4h; Frank *et al.*, 2005). However, the resulting increase in these prey species caused a decrease in their own prey, large zooplankton. Thus, pollution-induced changes in gene expression in foundation fish species can alter their abundance, which, in turn, can cascade to other trophic levels, including primary producers. Naiman *et al.* (2002) showed that nutrients available to plants and other organisms are increased when salmon are present within the community (Fig. 4i). Streams with spawning salmon (*Oncorhynchus* spp.) have been linked to greater growth of both aquatic plants and terrestrial vegetation (Carlson *et al.*, 2011), including sitka spruce (22.93 ± 3.07 $\mathrm{cm^2\ yr^{-1}}$ basal area growth in streams with salmon, compared with 6.39 ± 1.82 $\mathrm{cm^2\ yr^{-1}}$ in streams without salmon; Naiman *et al.*, 2002). Therefore, the reduction of fish populations as a result of exposure to EDCs would reduce the availability of these important nutrients and could reduce the growth of both the floral and faunal communities.

The pollution–fish system almost fulfills all four postulates. As fish can play important roles within an ecosystem, changes in fish populations can have diverse effects on the entire ecosystem (Horppila *et al.*, 2003), thus fulfilling the first postulate. Although the traits studied in this example are genetically based, it might be argued that expression levels and their consequences are not heritable, as they can be altered by natural and anthropogenic factors in the environment. However, there are several ways in which these changes can have a genetic impact on future generations, thus fulfilling the second postulate. First, gene expression is altered by additional epigenetic factors (i.e. inherited changes in gene expression via mechanisms other than changes to the genetic code), including the pattern of cytosine methylation of genes. In addition to being susceptible to alteration by environmental chemicals, methylation patterns are heritable in many species (Aniagu *et al.*, 2008). In fish, exposure to EE2 has been shown to cause genomic hypermethylation of genes key to gonad development and carcinogenesis, thus providing a heritable source of EDC-induced effects scaling from genes to the entire ecosystem. This point is further supported by the increase in susceptibility to EDCs in the offspring of fish exposed to these chemicals (Nash *et al.*, 2004). A mechanism of vulnerability to these chemicals is somehow passed on to the offspring of exposed organisms. Secondly, parental behavior is controlled by hormones, and thus susceptible to changes in gene expression. Altered behavior in parents has been shown to affect the offspring and their subsequent parental behavior (Crews *et al.*, 2007). Third, as discussed above, different genotypes may contribute to the level of response to an endocrine disruptor. Given the genetic basis of these responses, these traits are heritable and these forms of heritability could satisfy the second postulate.

Although the third postulate asserts that different genotypes can have measurable effects on the ecosystem, the series of studies presented in Fig. 4 demonstrates that gene expression, too, can have measurable effects. In addition, future research on this topic could measure the vulnerability of different genotypes (short nucleotide polymorphisms, etc.) to effects of EDCs. Although the fish in the experiments mentioned in Fig. 4 were exposed to the same doses of EDC, they were affected to different degrees. For example, some males developed intersex gonads and others did not. This implies that certain genotypes may be less susceptible to the effects of EDCs, and a knowledge of the genotypes within a population could be used to predict the effects of chemicals within the ecosystem. The fourth postulate is fulfilled, because the pollutants themselves manipulate the expression of genes, causing a predictable effect in the populations, community and ecosystem. The use of the proposed postulates can be incorporated into an ecotoxicological approach for the evaluation of impacts of exposure among genotypes within and across generations of exposed foundation species. Such an approach can be linked with concomitant shifts in population structure that may ultimately radiate throughout an ecosystem.

VII. An emphasis on foundation species and their biotic and abiotic interactions

By focusing on the genetics and genomics of foundation species (i.e. strong interactors), the application of community genetics provides a way to study networks in ecosystems without being overwhelmed by their complexity (Brose *et al.*, 2005; Bascompte *et al.*, 2006; Shuster *et al.*, 2006; Whitham *et al.*, 2006; Bascompte, 2009). By incorporating interspecific indirect genetic effects, the interactions among species are emphasized, especially those interactions that include foundation species that may structure whole communities and ecosystems (Shuster *et al.*, 2006; Allan *et al.*, 2011; Ohgushi *et al.*, 2011). This emphasis on foundation species, which are a small subset of the total species in an ecosystem, should capture much of the variation in community structure and ecosystem processes that could be nearly impossible to obtain if a knowledge of all species in the system was required (i.e. community genetics and genomics without tears).

An emphasis on the genetics of foundation species recognizes their central role as community 'drivers', such that the analysis of genetic effects for one or a few species can reveal surprisingly strong and predictable impacts on communities and ecosystems (Whitham *et al.*, 2003, 2006). Differences among genotypes of foundation species, such as a common tree, can affect communities of arthropods (Shuster *et al.*, 2006), aquatic fungi (LeRoy *et al.*, 2007), the soil microbial community (Schweitzer *et al.*, 2008a,b), trophic interactions (Bailey *et al.*, 2006), community diversity (Johnson & Agrawal, 2005), community stability (Keith *et al.*, 2010), ecosystem processes, such as nutrient cycling (Schweitzer *et al.*, 2008a,b) and primary production (Hughes & Stachowicz, 2004; Crutsinger *et al.*, 2006), and the evolution of dependent species (Evans *et al.*, 2008). A meta-analysis based on 22 *Populus* studies, and a second meta-analysis based on 11 other systems including marine seagrass and terrestrial herbaceous and woody plants, suggests that the gene-to-ecosystem approach is widely applicable to diverse communities and ecosystems (Bailey *et al.*, 2009).

Because most species are rare, we would expect that their removal would have little demonstrable impact on the rest of the community. For example, in an analysis of 63 652 arthropods representing 19 orders, Bridgeland *et al.* (2010) found 689 arthropod morphospecies on cottonwoods growing in a common garden. Of these, 428 species were considered to be rare as they were found less than six times. Taken together, these rare species contributed only 1.6% of the total abundance and 9.8% of the total biomass. By contrast, as few as two species comprised 56% of the total biomass (W. Bridgeland, unpublished data). Such patterns, in which few species comprise most of the biomass, are common (Polis, 1991; Schwartz *et al.*, 2000). Although biomass is one indicator of a species' importance, other characteristics, such as interaction strengths and expert knowledge, can be important in deciding which species should be the focus of limited research dollars. Thus, from a foundation species perspective, most species are so rare that their removal would probably have a small, if even detectable, effect on the community or ecosystem. This does not mean that they are unimportant; it just means that they are less likely to be community 'drivers' and that the genetic differences among individuals within such species are unlikely to have community or ecosystem phenotypes.

To predicatively understand the functioning of whole ecosystems, it is important to quantify the number of foundation species in a given ecosystem and to empirically test and model their biotic and abiotic interactions. By understanding such interactions, we can detect hidden or unexpected cascading effects that might otherwise be missed, which could increase the probability of erroneous conclusions and important management errors. For example, Orians & Fritz (1996) found that individual willows resistant to herbivory at low nutrient levels became susceptible at high nutrient levels. These findings show that a genetic–environmental interaction of a foundation willow species fundamentally switched with fertilization. Thus, a widespread agricultural practice of fertilizer use could have unexpected consequences, as emphasized in the mycorrhizal–plant interaction studies of Johnson *et al.* (1997). Similarly, van Ommeren & Whitham (2002) found that, when the interactions of mistletoe and juniper were analyzed as a two-way interaction, the relationship was a parasitic–host interaction. However, when birds that disperse the seeds of both juniper and mistletoe were added to the analysis in a three-way interaction, they concluded that mistletoe could be a mutualist of juniper as it attracted more birds, which enhanced juniper seedling recruitment. Thus, the addition of just one more species to the analysis could switch the relationship from parasitic to mutualistic. Such examples have been referred to as 'switches', in which the outcome of an interaction can fundamentally change from negative to positive, or positive to negative, with the addition of a single variable.

In their review of switches, Bailey & Whitham (2007) found that switches occurred with much higher frequency as studies included more species in their analyses, as studies increased from short to long term, and as studies progressed from local to regional scales. Switches are especially important for land managers and policy makers when the outcome of their decisions can have effects opposite to what is intended. It appears that only with a system-wide approach that crosses scales and incorporates the biotic and abiotic interactions of foundation species are we likely to understand these complexities and avoid costly economic and conservation mistakes that may be impossible to reverse.

In studies of agroecosystems, genetic changes in foundation species can have unintended outcomes that will benefit from a genes-to-ecosystem analysis. For example, genetically modified corn (Bt corn) can have unintended impacts that extend beyond the corn fields to an adjacent aquatic ecosystem. When focusing on the two-way interaction between Bt corn and the corn pest species, the desired effect of pest control is achieved; however, studies of the effects of the inserted Bt genes on the ecosystem revealed undesired effects. Rosi-Marshall *et al.* (2007) showed that pollen and detritus from the Bt genotype were responsible for reduced growth and increased mortality in nontarget stream caddisflies (Trichoptera). Caddisflies are key aquatic insects occupying diverse functional groups from filtering collectors to carnivores (Wallace & Merritt, 1980), and their decline will have cascading effects of their own. This research connects the genes of a genetically modified crop to stream biota and food webs. The design of experiments without considering the whole system can result in misleading environmental conclusions and management mistakes.

Genes-to-ecosystem studies of diverse foundation species can also help us to understand important 'emergent properties' of ecosystems that are regarded as not being deducible from single species or lower order processes. Although community diversity, stability and/or productivity are generally viewed as emergent properties, findings from the poplar, goldenrod and seagrass systems show that these properties can be genetically based (Hughes & Stachowicz, 2004; Wimp *et al.*, 2004; Crutsinger *et al.*, 2006; Keith *et al.*, 2010). For example, Hughes & Stachowicz (2004) showed that an increase in intraspecific genetic diversity in seagrass (*Zostera marina*) enhanced resistance to disturbance and decreased recovery time to predisturbance densities. Thus, a genes-to-ecosystem approach shows that these emergent properties can be derived from lower order processes that are subject to natural selection and evolution. Such information could also be used in restoration designs that seek to manage these traits.

VIII. Applications to the human condition

A genes-to-ecosystem approach can also be used to understand and prevent problems concerning human health. For example, exposure to low, ecologically relevant doses of bisphenol-A (BPA), a widely used chemical found in many plastics and epoxy resins, has been shown to change the expression of over 300 human genes by two-fold or more (Singleton *et al.*, 2006). These alterations, in turn, have been shown to have serious consequences in comparative animal systems, including upsetting the development of male and female reproductive tracts, the feminization of males (Singleton *et al.*, 2006) and increased body weight even after exposure ceased (Rubin *et al.*, 2001). Indeed, BPA exposure has been correlated directly with cardiovascular problems and diabetes in humans (Lang *et al.*, 2008). Dichlorodiphenyltrichloroethane (DDT) exposure during early life is correlated with an increased risk of breast cancer (Cohn *et al.*, 2007). Because studies of the impacts of exposure to pollutants in humans necessarily involve a correlative approach, a genes-to-ecosystem approach may be used to better identify whether these correlations have underlying causative relevance. BPA and many other seemingly beneficial chemicals are used in products or applied directly to the environment (e.g. DDT) without considering how their impact on selection and gene expression of nontarget organisms can drive processes at the community and ecosystem level. If we find these processes disrupted in exposed ecosystems, the argument that impacts on humans are causative becomes stronger.

Recent studies have argued that there is a relationship between bacterial gut microbiota communities and the genetics of both mice and humans that may have an impact on numerous metabolic diseases, such as obesity and diabetes. The transfer of the gut microbiota from obese (*ob/ob*) mice to germ-free wild-type (WT) recipients led to an increase in fat mass in the recipients (Turnbaugh *et al.*, 2006). This increase in fat mass in genetically obese mice is associated with a shift in the relative abundance of two dominant bacterial phyla in the gut, the *Bacteroidetes* and the *Firmicutes* (Turnbaugh *et al.*, 2009). Vijay-Kumar *et al.* (2010) have shown that the toll-like receptor (TLR) 5 is a transmembrane protein in the intestinal mucosa that recognizes bacterial flagellin. These studies suggest that the gut microbiota of obese and wild-type mice differ in their ability to extract energy from ingested food, which ultimately leads to obesity in one group, but not in the other. Thus, genetic differences among mice affect the composition of the gut community, which, in turn, may play an important role in these important diseases.

IX. Conclusions

In summary, it seems that John Muir (1911) might have been correct when he stated that, 'When we try to pick out anything by itself, we find it hitched to everything else in the Universe.' Numerous examples have emerged from diverse systems that make the case that the genes-to-ecosystem approach can provide an important perspective for the understanding of complex systems, for informing land managers and even for evaluating the effect on the human condition where the genetic impacts of pollution can have unintended effects on the food supply and human health. Similar to Koch's postulates, we present four community genetics postulates for confirming or rejecting the hypothesis of a genetic effect on the community and ecosystem (Table 1): (1) the demonstration of a target species' impact on the community and ecosystem; (2) the demonstration of key traits that are heritable; (3) the demonstration of genotypic variation in the communities they support and ecosystem processes; and (4) the manipulation of target gene(s) or their expression to experimentally evaluate a community and ecosystem effect. The last of these is the least well documented (but see the exotic hydrilla example of Michel *et al.*, 2004; Fig. 2). Nevertheless, as we genetically engineer and release organisms, the fourth postulate will be evaluated on a global scale.

In complex systems involving many interacting species, we believe that there are three main advantages to this approach. First, the incorporation of a genetically based model places community and ecosystem ecology within an evolutionary framework subject to natural selection. Second, because a genes-to-ecosystem approach studies species within a community context, it is more realistic and less likely to result in management errors compared with a single species' approach. Third, the use of the genes-to-ecosystem concept can reveal important interspecific indirect genetic effects among species, thus generating meaningful applications for the conservation of biodiversity, restoration, bioengineering, climate change and even the understanding of important human diseases.

Acknowledgements

The manuscript benefited from discussions in the 'Genes-to-Ecosystem' course of Northern Arizona University. In particular, we thank H. Cooper, M. K. Lau, T. McHugh, S. Shuster and A. Whipple. Three anonymous reviewers also contributed significantly to the manuscript. A.S. Wymore, A.T.H. Keeley, K.M. Yturralde and M.L. Schroer are funded by the National Science Foundation (NSF) Integrative Graduate Education and Research Traineeship (IGERT) program. C.R. Propper is funded by an Integrative Organismal Systems (IOS) NSF grant, and T.G. Whitham is funded by an NSF Frontiers in Integrative Biological Research (FIBR) grant focused on community genetics.

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