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Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals

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Large-scale exploitation of wild animals and plants through fishing, hunting and logging often depends on augmentation through releases of translocated or captive raised individuals. Such releases are performed worldwide in vast numbers. Augmentation can be demographically and economically beneficial but can also cause four types of adverse genetic change to wild populations: (1) loss of genetic variation, (2) loss of adaptations, (3) change of population composition, and (4) change of population structure. While adverse genetic impacts are recognized and documented in fisheries, little effort is devoted to actually monitoring them. In forestry and wildlife management, genetic risks associated with releases are largely neglected. We outline key features of programs to effectively monitor consequences of such releases on natural populations.

Occurrence of large-scale releases

The continued large-scale exploitation of wild animals and plants through activities such as fishing, hunting, and logging is frequently dependent on extensive releases of translocated, captive bred, or cultivated individuals. The scale of these releases is enormous, especially within the fields of forestry, fisheries, and wildlife management [1–3]. Each year worldwide, billions of individuals are translocated and released into settings, where wild populations ‘receive’ these massive inflows of alien species, populations, and gene pools. Despite the staggering scale of these releases, their potential effects on native biodiversity are largely neglected in research and policy.

Releases are of four categories: (1) species that do not occur naturally at the release site (alien species), (2) individuals whose DNA has been artificially manipulated (genetically modified organisms; GMOs), (3) non-local populations of a species that occurs naturally at the release

site (genetically exotic populations), or (4) local populations from which captive-bred individuals are derived (so-called supportive breeding; [4]). Typically, research and political attention has focused on effects of Category 1 and 2 releases on native biodiversity, even though in many areas the most extensive releases are Category 3 and 4. Furthermore, potential effects of all four categories on gene-level biodiversity of native populations are largely ignored.

Potentially harmful effects on aquatic gene pools and the need for monitoring of such effects were pointed out almost three decades ago [5] and have been stressed repeatedly in subsequent scientific literature [6–8]. A similar scientific discussion appears largely absent with respect to commercial releases within forestry and wildlife management (but see Ref. [9]), even though the scale of releases and potential risks to natural populations are comparable to those for aquatic species.

Our primary objectives are to: (i) draw attention to the global extent of mass releases and the urgent need for understanding the consequences for natural ecosystems, (ii) review documented genetic effects of releases, (iii) compare the field of fisheries to forestry and wildlife management with respect to the scale and genetic monitoring of releases, and (iv) recommend actions to address identified concerns. We note a general lack of research and monitoring of genetic and ecological impacts of large-scale releases, even in fisheries where the risks have been widely recognized for so long. After briefly describing Category 1 and 2 releases, we focus on Category 3 because commercial releases of this type are poorly studied, but conducted on a large scale. We also give examples of Category 4 releases in fisheries, where this type of program has become common following recognition of the potential adverse genetic effects of Category 3 releases.

Large-scale releases can have positive demographic consequences in some cases and can provide economic or other societal benefits. In such situations, it is important to

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Box 1. The emerging markets of large-scale releases

While the aquaculture and forestry industries have conducted large-scale releases for decades, several emerging markets have the potential to rapidly become economically important, leading to a plethora of unmonitored releases. Two such markets are biofuels and carbon sequestration.

Biofuels

Biofuels are fuels derived from plant materials including seeds, grains and woody debris. In the United States, corn ethanol comprises 99% of biofuels, amounting to 3.4 billion gallons of ethanol per year [44]. Although corn ethanol is currently the dominant biofuel, a booming industry is searching for more efficient species for production, with perennial rhizomatous grasses leading in potential [45]. Unfortunately, some leading candidates for biofuel production (and thus for large-scale releases outside their native geographic range) have high invasive potential and are known to hybridize with endemic species. For example, cordgrass (*Spartina* spp.) not only hybridizes with native species but the hybrids have become highly invasive in the United Kingdom and North America [46].

It is critical that any plants used for biofuels are sterile hybrids since non-sterile grasses have been notoriously difficult to eradicate or even control once established [45]. Barney and Ditomaso [47] assessed three leading U.S. biofuel candidates and found that two of the species (switchgrass *Panicum virgatum* L. and giant reed *Arundo donax* L.) had high invasive potential in some environments. In contrast, giant reed posed a low risk if sterile. One missing element to the biofuel “food, energy, and environment trilemma” [48] is the impact these biofuels can have on native gene pools.

Carbon sequestration

Carbon sequestration is a technique used for long-term capture and storage of carbon dioxide and other forms of carbon to mitigate global warming. One popular tool for this technique has been reforestation of degraded or non-performing crop or pasture lands. Large-scale tree-planting efforts occur in the tropics partially for carbon sequestration, and are currently worth billions of US dollars. However, chosen tree species are often exotics (frequently *Eucalyptus* and *Pinus* spp.) which have desired traits of fast growth, high yield,

known site preference and high reproduction [49]. Neither the ecological nor genetic impacts of these approaches have been well studied, nor have genetic monitoring programs been established to watch for impacts on native populations. However, recently there has been growing momentum in the international carbon market to have certification standards that require the consideration of native tree species that have positive biodiversity impacts both on and offsite, and that implement biodiversity monitoring (Figure 1, [50]).



TRENDS in Ecology & Evolution

Figure 1. A reforestation project in Panama undertaken partially for carbon sequestration purposes, implemented by Futuro Forestal S.A. and ClearSky Climate Solutions, LLC (photo courtesy of Keegan Eisenstadt). Native species are used here (large leaves – *Hyeronima alchorneoides*, small leaves – *Swietenia macrophylla*), with attention to genetic origin. Where local seed sources remain, individuals are members of the same gene pool as the surrounding naturally occurring populations. Where seed sources have been locally extirpated, they are acquired from other areas within Panama, or in neighboring Costa Rica.

balance potential conservation benefits of releases (demographic or genetic rescue [10]) against potentially detrimental, micro-evolutionary changes to native populations that run counter to international goals of conserving and sustainably using genetic diversity. We emphasize that effective monitoring of these risk–benefit tradeoffs is essential to ensure informed decision making, and we stress the need to develop and evaluate protocols for such conservation genetic monitoring.

Alien species (Category 1)

Commercial releases commonly use alien species. Eucalypts, comprising over 800 species endemic to Australia and surrounding islands, have been spread widely for timber production [9]. Extensive tropical reforestation and carbon sequestration projects cost millions of dollars and often use exotic plantation species adjacent to natural forests (Box 1). Large-scale commercial releases of exotics are not restricted to agriculture and forestry: in Great Britain, 20–35 million game birds are released annually, over 95% of which are pheasants (*Phasianus colchicus*) and red-legged partridge. Both of these are non-native species in Great Britain [11]. As a further example, Chile, a leading salmon producer, bases its aquaculture industry on introduced Atlantic salmon [12].

Alien species are recognized as a major threat to biodiversity worldwide and considerable research and political

attention has focused on their effects [13]. However, this attention has not stopped widespread use of alien species for commercial purposes, e.g. in agroforestry, causing major problems with invasions of natural and semi-natural ecosystems [14]. Alien species hybridizing with native species represent a particular threat to genetic diversity; introgression of alien gene pools compromises natural genetic variability patterns and can cause outbreeding depression [15].

GMO (Category 2)

Considerable discussion has focused on methods for assessing and monitoring risks of releasing GMOs into nature [16], especially spread of modified DNA segments into natural populations [17]. Further, as GMOs typically originate from populations that are genetically distinct from native ones near GMO release sites, GMOs also pose risks typical of Category 3 releases (see below). However, these latter risks are rarely discussed in the context of GMOs.

Conspecific populations (Category 3)

Commercial releases of genetically distinct populations of species that already exist naturally in the release area are conducted on massive scales worldwide, with the species involved including various forest trees and shrubs, game birds and mammals, fish, insects, grasses and other vascular plants (Table 1). In Sweden alone, over 30 billion

Table 1. Examples of large-scale releases of animals and plants in areas where native populations of the same or closely related species occur.

Species	Geographic region or locality of release	Scale and time frame of release	Reason for release	Origin of released individuals	Systematic monitoring programs of genetic effects	Studies or documentation of effects	Source
Fishes							
Atlantic salmon (<i>Salmo salar</i>)	13 Swedish rivers	Over 2 million annually	Commercial and sports fishing	Hatchery populations	No	90% of Baltic salmon of hatchery origin.	[18]
Black sea bream (<i>Acanthopragus schlegelii</i>)	Hiroshima Bay, Japan	20 million juveniles annually	Commercial fisheries	Hatchery stocks	No	Reduced number of alleles in hatchery fish.	[77]
Pacific herring (<i>Clupea pallasii</i>)	Akkeshi Lake and Bay, Japan	4.3 million during 1987–2005	Commercial fisheries	Hatchery fish	Yes, to some extent	Number of rare alleles decreased.	[61,78]
Pacific salmon species: chum (<i>Onchorhynchus keta</i>), pink (<i>O. gorbuscha</i>), masu (<i>O. masou</i>)	Hokkaido Island, Japan	1.2 billion juveniles annually	Commercial fisheries	Hatchery fish	No	Dramatic increased catches of some species, reduced catches in others.	[79]
Pacific salmon species: chum, pink, sockeye (<i>O. nerka</i>), coho (<i>O. kisutch</i>)	North Pacific	Around 4.4 billion annually	Commercial and sport fisheries	Hatchery fish	No	Replacement of several wild populations by hatchery fishes.	[80]
Red sea bream (<i>Pagrus major</i>)	Kagoshima Bay, Japan	20.8 million during 1974–2002	Commercial fisheries	Hatchery fish	Yes, genetic diversity	Reduction of number of rare alleles.	[61,81]
Birds							
Gray partridge (<i>Perdix perdix</i>)	Great Britain	200 000–700 000 birds annually	Sports hunting	Captive bred birds	No	No	[11]
Mallard duck (<i>Anas platyrhynchos</i>)	Southern and central Sweden France	Over 100 000 annually Around 1 million annually	Sports hunting Sports hunting	Captive stocks, imported birds Captive stock, imported birds	No No	No No	[18] [82]
Red-legged partridge (<i>Alectoris rufa</i>)	Rural Spain	3–4 million birds annually	Sports hunting	Farmed birds including hybrids	No	Introgression of <i>Alectoris chukar</i> genes in 28.7% of wild <i>A. rufa</i> . Hybrids have lower survival. Released birds transferred parasites.	[25,83,84]
Insects							
Bumblebee (<i>Bombus terrestris</i>)	Southern, western Europe	Tens of thousands of colonies	Commercial pollination	Subspecies (<i>B. t. sassaricus</i>) from Sardinia	No	Genetic differences between native and released bees indicated.	[85]
Forest trees							
Blue gum (<i>Eucalyptus globulus</i>)	Forest areas of Australia	70 000 ha annually turned into plantations of <i>E. globulus</i> and non-native <i>Pinus radiata</i>	Increase forest productivity	Selectively bred non-local populations	No	Yes (Box 3)	[24,86,87]
Norway spruce (<i>Picea abies</i>)	Sweden	30 billion imported plants during 20 th century	Increase forest productivity	Various parts of Europe and Russia	No	No. Central European spruce have lower genetic variation than native spruce.	[18]

Norway spruce have been imported from various regions in Europe, but documentation is sparse and programs to monitor possible effects are nonexistent [1,18]. The situation is similar in Norway. During 1960–1980 over 17 million central European Norway spruce were imported and spread in southeastern Østlandet, directly affecting one-third of the local spruce populations. Monitoring efforts have focused exclusively on timber productivity [19], which has an uncertain relationship to long-term fitness in the wild. Furthermore, it is important to evaluate other effects on the genetic composition of native gene pools. Other than in fisheries, little attention has been paid to examining effects of Category 3 releases on biodiversity, although the risks have long been known [9,15].

Local populations: supportive breeding (Category 4)

Supportive breeding, in which part of a natural population is brought into captivity for reproduction and resulting offspring released into the wild [4], is commonly used in fisheries management, where potential adverse effects are recognized. Category 4 releases minimize risks associated with alien populations but have potentially serious effects on fitness and levels of diversity in native populations [4].

New markets for releases

We note that several new markets for large-scale releases have emerged recently (Box 1). Also, genetically alien gene pools are widely used for gardening and park management,

where commercial mixes of seeds from different populations and species of grasses are spread. For example, 2000 tons of grass seeds and 160 tons of legume seeds of unclear origin were imported to Sweden during 2004–2005 alone to be used for lawns, golf courses, roadsides and pastures.

Genetic effects of releases

Category 3 releases have four major potential consequences for natural populations: loss of genetic variation, breakdown of adaptations, changes to genetic composition within populations, and breakdown of population structure (genetic differences between populations; Box 2).

Even releases that do not result in gene flow can have genetic consequences if they reduce local population size – for example, through competition or disease transmission, or through wasted reproductive effort by native individuals that mate with captive-bred individuals but do not produce viable offspring. The main concern in these cases is that changes to naturally existing genetic diversity within and among populations can reduce viability and productivity of exploited populations. This could be a problem both in the short term by reducing individual fitness and in the long term by reducing the capacity for populations to evolve and adapt to future conditions [20].

Introgression from genetically alien populations has been documented in a number of species subject to large-scale releases (Table 2). Although risks to native

Box 2. Evidence for genetic effects of large-scale releases on fish populations

Large-scale commercial releases of fishes have been widespread for over a century [2,15]. Recently, intensive genetic monitoring programs for aquatic species have documented each of the major effects illustrated in Figure 1.

Among populations

Genetic structure. Massive releases of coho salmon (*Oncorhynchus kisutch*) have reduced the level of genetic differentiation between natural populations in Puget Sound, USA [51,52]. In the Central Valley of California, extensive habitat modification and large hatchery programs with release strategies that promote widespread straying have genetically homogenized the metapopulation of fall-run Chinook salmon (*Oncorhynchus tshawytscha*) [53]. After widespread recruitment failure in 2008, the U.S. imposed the most severe restrictions in history on west coast salmon fisheries. Lindley *et al.* [53] concluded that a significant contributing factor to the collapse was loss of environmental buffering provided by a diverse array of natural populations.

Within populations

Genetic composition. Complete replacement of native gene pools of Mediterranean brown trout with introduced populations of Atlantic origin occurs over large areas [54]. Slovenian populations of Adriatic grayling (*Thymallus thymallus*) have been stocked with Danubian fish for over four decades, and levels of introgression are so high (40–50%) that few indigenous populations can be identified [55]. Atlantic salmon (*Salmo salar*) in the Swedish River Vindelälven, which supports one of the few remaining native populations in the Baltic, are becoming increasingly genetically similar to non-native hatchery stocks [56].

Adaptations. A 37-year study of Atlantic salmon in Ireland [57] found that naturally spawning farmed fish depress wild recruitment and disrupt the capacity of natural populations to adapt to higher water temperatures associated with climate change. Hansen *et al.* [58] examined Danish populations of brown trout subject to hatchery supplementation for 60 years and found evidence for selection in the wild against alleles associated with non-native hatchery fish. Muhlfeld

et al. [59] showed that non-native rainbow trout (*Oncorhynchus mykiss*) that hybridized with native cutthroat trout (*Oncorhynchus clarkii lewisii*) in Montana, USA, had high F₁ reproductive success. However, in subsequent generations fitness declined by nearly 50% (compared to fitness of native trout) following 20% introgression of non-native genes.

Genetic diversity. Unintended introduction of the parasite *Gyrodactylus salaris* with Atlantic salmon from Sweden used in aquaculture caused the collapse of wild salmon populations in many Norwegian rivers [60], exemplifying loss of diversity not associated with gene flow from introduced populations. Loss of alleles in the natural population following gene flow from commercial releases is reported for red sea bream in Japan [61].

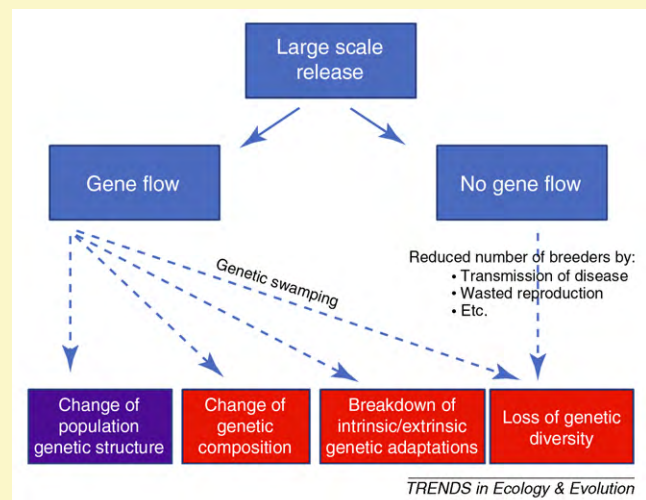


Figure 1. Primary pathways by which large-scale releases can change genetic characteristics within (red boxes) and between (purple box) natural populations.

Table 2. Examples of documented gene flow from genetically alien populations released into native populations

Native species	Geographic region or locality of release	Species or population released	Reason for release	Observation	Sources
<i>Acacia saligna lindleyi</i>	Southwestern Australia	<i>Acacia saligna saligna</i>	Agroforestry	Gene flow rate of 32% from planted agroforestry into native population. Small remnant populations of subsp. <i>lindleyi</i> exposed to high levels of hybridization.	[88]
Black poplar (<i>Populus nigra</i> L.)	Europe	Black 'lombardy' poplar (<i>Populus nigra italica</i>), hybrids between <i>P. nigra</i> and exotic poplar species.	Ornamental plantings	Black poplar highly threatened in western Europe by habitat reductions and genetic pollution from plantings. Planted trees represent a narrow gene pool spread on a wide scale.	[9,89–91]
Brown hare (<i>Lepus europaeus</i>)	Greece	Captively reared brown hares imported from Italy, Yugoslavia and Bulgaria	Maintain hunting opportunities	Introgression of genes from released hares into natural populations detected.	[92]
California tiger salamander (<i>Ambystoma californiense</i>)	Gonzales, Monterey County, California, USA	The congener tiger salamander <i>Ambystoma tigrinum</i>	Production of fish bait	Native species hybridize with released congener. Less than 10% remaining pure, native animals detected in six pools and ponds studied.	[93]
Common quail (<i>Coturnix coturnix coturnix</i>)	Spain, Portugal, France, Greece	The subspecies Japanese quail (<i>C. c. japonica</i>) and hybrids.	Game bird hunting	Thousands of captive bred quails are released annually. Hybrids observed in the wild in France and Portugal. In Italy and Spain 9% of sampled wild quails were of hybrid origin.	[94,95]
European wild rabbit (<i>Oryctolagus cuniculus</i>)	Spain	Mixture of two evolutionary distinct lineages of <i>O. cuniculus</i> .	Sports hunting and conservation	Genetically exotic rabbits occur in nature.	[96]
Silver fir (<i>Abies alba</i>)	Bialowieza, Poland	Exogenous <i>A. alba</i>	Forestry	Gene flow from planted exogenous populations threatens genetic distinctiveness of small, native relict population.	[9,97]

gene pools have been recognized for a variety of species [20,21], the most intense attention has focused on salmonids such as Pacific salmon, Atlantic salmon and brown trout (Box 2, [3]). In Denmark, these concerns have resulted in a ban of all releases of salmonids originating from anything but the local population (i.e. only Category 4 releases are allowed [22]). However, this is the exception even for salmonids. Surprisingly little monitoring of the effects of mass releases has occurred in forestry and wild-life management, but examples are beginning to accumulate such as Eucalypt populations used in Australian forestry (Box 3 [9,23,24]) and exotic game birds in Southern Europe (Tables 1 and 2).

Loss of genetic variation

Genetic swamping occurs when there is a strong inflow of genes from alien populations into wild ones, a process that can destroy unique gene pools (Box 2, Tables 1 and 2). Wild populations might also lose genetic variation if their effective population size (N_e) is reduced due to increased mortality caused by parasites or diseases transmitted by released individuals. A classic example refers to the effects of the unintended introduction of the parasite *Gyrodactylus salaris* (an ectoparasite living on the skin of Atlantic salmon) into Norway with juvenile salmon imported from Sweden in the early 1970 s (Box 2). Substantial mortality

in wild populations following spread of parasites through alien populations has been observed in salmon in Japan [3], red partridge in Spain, and rabbits in France and southern Europe [25,26]. Similarly, lower abundance and survival of wild salmon has been observed in areas with aquaculture compared to areas without such activities [27].

With Category 4 releases, genetic diversity can be lost by reduction of overall (wild plus captive) N_e . Typically, relatively few parents are brought into captivity for reproduction; these parents often contribute disproportionately large numbers of genes to the next generation, potentially resulting in increased rates of inbreeding and genetic drift in the total population. Reduced genetic variation has been observed in populations of salmonid fishes subject to supportive breeding [28]. Parameters required to predict the effects of supportive breeding include the effective sizes of the captive and wild population segments, their relative contributions to the managed population, and the duration of the support program (Box 4, [4]).

Breakdown of adaptations

Releases can reduce adaptation by causing loss of extrinsic or intrinsic adaptation. Loss of fitness can occur when alleles that confer local adaptation are replaced by ones that are locally non-adaptive. This extrinsic type of fitness

Box 3. Genetic contamination of eucalypts in Australia

Genetic risks from large-scale commercial releases appear to be only marginally recognized in forestry. One exception is the considerable research focused on monitoring genetic pollution from Eucalypt species translocated across Australia to establish commercial plantations [9,23,24,62].

Eucalyptus nitens has been extensively introduced from continental Australia to a Tasmanian forestry expanding from 5000 to 117 000 ha during 1980–2000 [63]. Of 29 native Tasmanian eucalypt species, 16 are potentially at risk of hybridization [9], and gene flow from plantations into natural stands has been monitored using morphological techniques. Rates of first generation hybridization (F_1) from *E. nitens* pollen dispersal into native *Eucalyptus ovata* forests were around 7% within 100 m of the plantation, and around 1% within 0.2–1.6 km. F_1 hybrids exhibit reduced height and higher levels of mortality, disease and insect damage. F_2 hybrids and backcrosses have been produced in the lab but due to the long generation length of these trees will not occur in the wild until 1–2 decades from now [62]. The rare, native Tasmanian species *Eucalyptus perriniana* is at risk of introgression, perhaps even extinction, from *E. nitens* plantations [24], and is genetically monitored. Similar observations occur in Western Australia where gene flow from an agroforest plantation of non-native *Eucalyptus loxophleba lissophloia* to en-

demically remnant populations of the native subspecies *supralaevus* was estimated at 40% within 0.5 km of the plantation [64].

Spread of non-native genes can result in loss of adaptation to local environments. Wilkinson [65] collected *Eucalyptus oblique* from several adjacent, but ecologically distinct, native forests in Tasmania and raised them in common environments. He found genetic differences in survival, growth and susceptibility to fungi and browsing, reflecting adaptation to micro-geographic habitat. Thus, large-scale spread of seed from a genetically narrow base across a mosaic of ecological patches can constrain local adaptation.

Genetic composition of plants can affect associated communities of other organisms. Barbour *et al.* [66,67] examined the effects of genetic variation in *Eucalyptus globulus* on dependent biodiversity. They studied 160 trees representing eight races in a 15-year-old common garden, and showed that genetic composition of trees affects species occurrence and composition of a number of other groups of organisms including arthropods, fungi, snails and spiders, not only on the living trees but also in the associated litter. For instance, a twofold difference in species richness (from 7 to 14 species) and abundance (from 22 to 55 individuals) was observed when comparing bark litter from different genetic groupings. Thus, introgression of alien gene pools can affect biodiversity at species and ecosystem levels.

loss is frequently observed in the F_1 generation (Box 3, [10]). Gene flow from a non-local source population can cause breakup of co-adapted gene complexes, i.e. alleles at multiple loci that work synergistically to increase fitness (intrinsic adaptation). Because this breakup is caused by recombination, loss of adaptation generally occurs only in the F_2 generation and beyond and can be much more

difficult to detect than loss of extrinsic adaptation. Empirical examples from wild populations show that both types of adaptation can be lost by gene flow from genetically divergent populations [29]. Fitness effects can be insidious: in some studies, increased F_1 fitness due to heterosis has been followed by decreased fitness in F_2 or later generations as co-adapted gene complexes are eroded (Box 2).

Box 4. Genetic monitoring of commercial releases: red drum in southeastern U.S.

Marine stock enhancement is conducted on a large scale worldwide [68] and is a good example of Category 4 releases, which artificially enhance local populations in captivity and release offspring into the wild [4,36]. Large enhancement efforts have been conducted for over two decades for red drum (*Sciaenops ocellatus*) in both the Gulf of Mexico and the Atlantic. As many as 25–30 million fingerlings are released each year in Texas alone [69]. State-of-the-art genetic monitoring programs associated with these enhancement efforts have provided key information about effects on natural populations:

- Wild populations exhibit a weak pattern of isolation by distance. Estimated N_e for local populations is roughly 10^2 – 10^3 compared to a census size on the order of 10^6 adults [70–72].
- Individual broodstock programs typically use 40–200 adults [71–73], but non-random contributions of different parents leads to relatively low hatchery N_e [69,71,72]. A detailed study of one Texas hatchery in one year estimated the hatchery N_e to be 28–47 [71].
- Hatchery fish had habitat usage similar to wild fish in Florida [74] but not in Texas [69].
- Hatchery releases comprised an estimated 1–12% of the wild population in Texas and Florida and up to 78% in South Carolina [69,73].
- In Texas, adults used for broodstock had comparable levels of genetic diversity to wild fish, but released fish had lower genetic diversity [69]. No reductions in levels of genetic diversity were detected in wild populations [70].

Most monitoring efforts provide information about within-population genetic diversity (Figure 1 in Box 2). If hatchery-reared fish make only modest contributions to the overall population (cf. Florida and Texas studies), effects on wild genetic diversity might also be relatively modest (cf. Figure 1). However, a program with 50 or fewer effective parents, that produces a substantial fraction of individuals in the next generation (as estimated for at least one program), could greatly

reduce overall N_e . No before and after data are available, so only weak inferences can be made about reductions in population structure. Furthermore, no studies have evaluated effects on wild population fitness. This is an important information gap; adaptation to captivity has been demonstrated for a wide variety of taxa [75], and studies for red drum have found moderately high heritabilities for traits that likely would respond to selection in captivity [76].

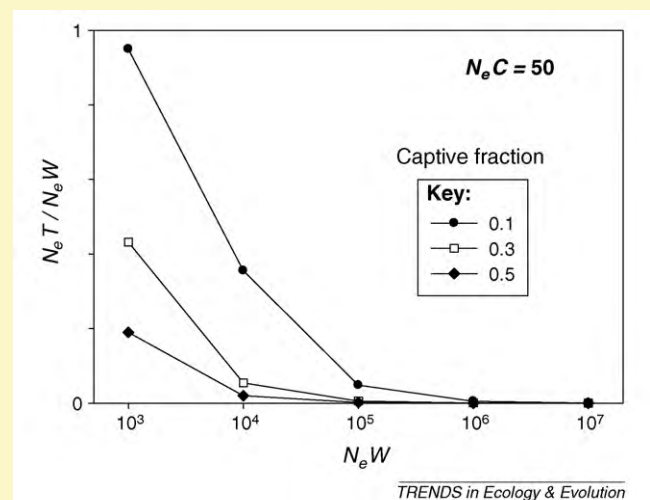


Figure 1. Overall effective size ($N_e T$) of a captive–wild system compared to the unsupplemented wild effective size ($N_e W$). Supportive breeding can severely reduce the $N_e T / N_e W$ ratio unless 1) $N_e W$ is already low, or 2) captive-bred individuals contribute only a small fraction of genes to the next generation (captive fraction < about 0.1). This example assumes that captive effective size ($N_e C$) is 50, which is at least as high as values that have been estimated for red drum.

Change of genetic composition

Releases can result in a change of the genetic make-up of individual populations if alien alleles establish as a result of gene flow. Several examples exist of natural gene pools being replaced by those of released populations (Boxes 1–3, and Tables 1 and 2). A well-known example involves release of sheepshead minnows (*Cyprinodon variegatus*) as baitfish in the Pecos River in Texas, with subsequent massive introgression into native Pecos pupfish (*Cyprinodon pecosensis*) populations in about half the geographic range of this endemic species [20].

Change of population genetic structure

Most natural animal and plant species are structured into genetically distinct populations because of restricted gene flow, genetic drift and local adaptation. Since large-scale releases can affect these microevolutionary processes, they can alter genetic structuring of natural populations, but such effects have rarely been monitored (but see Box 2).

Changed genetic attributes affect species and ecosystem diversity

Genetic changes to native populations can have consequences that extend beyond the affected species. Evidence is accumulating to show that genetic changes to one species can affect other species as well as entire communities and ecosystems [30]. For instance, genetic characteristics of individual plant populations can affect the composition and/or species richness of arthropods (Boxes 2 and 3, [31]), and foraging behavior of beavers (*Castor canadensis*) is affected by genetic makeup of the *Populus* species on which they feed [32].

New evidence indicates that high levels of genetic diversity increase resilience of species and ecosystems, and that genotypic diversity can complement the role of species diversity in a species-poor coastal ecosystem, and thus help buffer against extreme climatic events. Genetic variation was positively correlated with recovery of seagrass ecosystems following overgrazing and climatic extremes [33]. Reusch *et al.* [34] conducted manipulative field experiments and found that increasing genotypic diversity of the cosmopolitan seagrass *Zostera marina* enhanced biomass production, plant density, and invertebrate faunal abundance, despite near-lethal water temperatures.

The native California common cordgrass (*Spartina foliosa*) introgressed with non-native genes from smooth cordgrass (*Spartina alterniflora*, Box 1) produces hybrids with up to 400 times the seed and pollen productivity of native plants. Hybrid populations also show altered distribution patterns: they invade marshes, and change the entire community dynamics of those ecosystems, several of which are subject to conservation efforts [35]. Ecosystem effects of genetic introgression from large-scale releases can be particularly devastating in light of current rapid climate change (Box 2).

Why are lessons so slowly learned?

If potentially deleterious genetic effects of releases on native gene pools have been recognized for several decades, why are these programs still conducted on such a gigantic scale with (in the vast majority of cases) little or no genetic

monitoring? One explanation is that potential benefits of rapidly enhancing populations are so easy to visualize, while appreciation of long-term effects on biodiversity and sustainability require a more nuanced understanding of biology. Large release programs are typically supported by influential stakeholders, and these are historically proven to be extremely resistant to change [2]. In the field of fisheries, steady progress has been facilitated particularly by increasingly strong empirical documentation of all of the potential risks outlined above (Table 1, Boxes 2 and 4), as well as consistent conclusions by several high-level science panels (e.g. [36]) that long-term sustainability depends on conserving a diverse array of natural populations. Despite this, hatchery issues remain controversial and a source of polarization within the fisheries community [7,8].

Although the major genetic concerns identified for fisheries also apply to forestry and game management, those disciplines have been slow to incorporate genetic considerations for natural populations into plans for large-scale releases. This might in part reflect the research traditions of university faculties, which in many countries are strongly related to the goal of increasing forest productivity or hunting opportunities. In Sweden, forestry research managers explicitly state that spread of translocated Norway spruce and Scots pine is necessary to maintain forest production and that monitoring the genetic effects on wild populations is not warranted [37].

Poor implementation of international policy on genetic diversity

The pervasive lack of genetic monitoring of commercial releases reflects a general neglect of gene-level biodiversity associated with implementation of international conservation policy. The Convention on Biological Diversity (CBD) is the most important international political instrument dealing with biodiversity loss. Guidelines for reducing spread of alien species and populations were adopted in 2002 (COP 6 Decision VI/23; www.cbd.int), stating that effects of spread should be monitored, as should biological diversity in general at the levels of ecosystems, species, and genes.

The CBD affects international and national conservation efforts worldwide and although genetic diversity is clearly included in the convention, practical implementation has failed to recognize this sufficiently [38]. Part of the problem is that genetic variation is largely 'invisible' to the human eye. This diversity cannot be readily observed without advanced molecular techniques, making it difficult to generate an understanding of this level of diversity among non-scientists. Conceptually challenging theoretical concepts (such as effective population size) add to this difficulty.

Goals for monitoring large scale releases

Genetic monitoring of releases should aim to provide answers to the following key questions. (1) What are the genetic characteristics of the natural population(s) prior to the release? (2) Do releases alter these characteristics? If so, (3) what are the biological consequences?

Ideally, monitoring should include genetic screening and statistical evaluation of (i) native population genetic

structure and level of diversity prior to releases, (ii) natural rates of genetic change of these parameters, (iii) genetic composition of the population(s) used for release, and (iv) genetic structure and amount of diversity of natural population(s) on repeated occasions during and after the release(s). Such monitoring should be included as a basic part of any program for commercial or other releases. Molecular genetic and statistical techniques are readily available [39], although sampling strategies (e.g. number of populations, individuals and loci) need to be evaluated for individual cases to provide acceptable statistical power.

Assessments of risk–benefit tradeoffs are most effective if conducted prior to release activities. Waples and Drake [3] outline a framework for elements of comprehensive risk–benefit analysis that should be conducted prior to fish stock enhancement programs. Similarly, Barbour *et al.* [23,24] discuss strategies for assessing risks of pollen-mediated gene flow from translocated species and hybrids of *Corymbia* and *Eucalyptus globulus* plantations into native populations. These studies show that different risk–benefit assessment protocols are needed for different taxa and should be refined to fit particular species.

For releases that have already been carried out, an idealized monitoring design often cannot be followed. Sometimes, however, archived material can help addressing questions of genetic composition prior to release. Within forestry, so-called provenance trials have been used since the 19th century to identify populations with economically important characteristics. Such traditional tree breeding programs are aimed at examining performance of trees from different geographic localities (provenances) to find the best sources of seed for selective breeding and planting. Geographic source materials for provenance trials are thus known, and existing trial stands can be used to study long-term effects of plantations, such as gene flow into neighboring, native populations [40].

Genomics and monitoring large scale releases

The field of genomics provides new insights and influences the study of large-scale releases in several ways. First, genomics will reduce bias and increase precision and power in estimates of relatedness, population substructure, genetic distance, hybridization and introgression [41]. Using thousands of single nucleotide polymorphisms (SNPs) will provide more power for studies of micro-evolutionary dynamics. Secondly, genomics will allow identifying and monitoring of genes under selection, enabling more direct assessments of the effects of large-scale releases on fitness and long-term evolutionary potential [42]. Third, genomics can help identify the mechanisms of adaptation. If it is possible to investigate how genomic structure of separate individuals influences how well-suited they are for particular environments, this will allow predictions of their survival and fitness as conditions change. Fourth, genomics will provide more sensitive tools to monitor populations under threat from large-scale releases. Ouborg *et al.* [42] suggest that it will soon be possible to design microarrays that allow detection of specific gene-expression profiles for monitoring purposes. Sample analysis is becoming faster and less expensive. This means microarrays could be designed to detect presence of gene-express-

ion products that are specific to strays or hybrids from large-scale releases. Finally, genomics will facilitate development of community genetics, allowing us to monitor not only changes in individual species, but how such changes affect diversity of entire communities [43].

Summary and conclusions

Our review has established that commercial releases of many taxa occur globally on an enormous scale. The genetic risks associated with such releases have been known for several decades but are seldom incorporated into management actions. Recent research provides increasing evidence of deleterious effects, and empirical results increasingly document that genetic composition of one species can affect other species and entire ecosystems. Powerful tools, including both molecular genetic techniques (such as genomics) and statistical methods, exist to facilitate genetic monitoring. Nevertheless, only a tiny fraction of releases are monitored for effects on natural populations.

The lack of monitoring efforts is particularly true for forestry and wildlife management. In fisheries, risks are more widely recognized and monitoring efforts better developed, but still inadequate to protect natural populations. The absence of adequate monitoring also reflects a more general neglect of gene-level biodiversity in national and international conservation policy implementation. The Convention on Biological Diversity (CBD) calls for conserving and monitoring gene-level biodiversity, and acknowledges risks from spread of genetically alien populations, but implementation is mostly non-existent. This extreme disconnection between acknowledged risks and actions is probably due in part to the highly visible potential benefits of large-scale releases and the more nuanced effects on natural populations. Genetic variation is largely invisible to the human eye; there is a need for molecular and statistical conceptualization most non-researchers find difficult to grasp. Further, with few exceptions genetic researchers participate to only a very limited extent in CBD and other policy work.

We stress that there is an urgent need for genetic monitoring of the massive commercial releases within forestry, fisheries and wildlife management. Without adequate monitoring, deleterious effects on native genetic diversity can go unnoticed over huge geographic areas. Monitoring is essential not only for maintenance of biodiversity, but also for social, economic and ecological reasons, given that large-scale releases can have long-term effects on ecosystem function and sustainability of living natural resources.

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