



Accidental experiments: ecological and evolutionary insights and opportunities derived from global change

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Humans are the dominant ecological and evolutionary force on the planet today, transforming habitats, polluting environments, changing climates, introducing new species, and causing other species to decline in number or go extinct. These worrying anthropogenic impacts, collectively termed global change, are often viewed as a confounding factor to minimize in basic studies and a problem to resolve or quantify in applied studies. However, these ‘accidental experiments’ also represent opportunities to gain fundamental insight into ecological and evolutionary processes, especially when they result in perturbations that are large or long in duration and difficult or unethical to impose experimentally. We demonstrate this by describing important fundamental insights already gained from studies which utilize global change factors as accidental experiments. In doing so, we highlight why accidental experiments are sometimes more likely to yield insights than traditional approaches. Next, we argue that emerging environmental problems can provide even more opportunities for scientific discovery in the future, and provide both examples and guidelines for moving forward. We recommend 1) a greater flow of information between basic and applied subfields of ecology and evolution to identify emerging opportunities; 2) considering the advantages of the ‘accidental experiment’ approach relative to more traditional approaches; and 3) planning for the challenges inherent to uncontrolled accidental experiments. We emphasize that we do not view the accidental experiments provided by global change as replacements for scientific studies quantifying the magnitude of anthropogenic impacts or outlining strategies for mitigating impacts. Instead, we believe that accidental experiments are uniquely situated to provide insights into evolutionary and ecological processes that ultimately allow us to better predict and manage change on our human-dominated planet.

Synthesis

Humans have an increasingly large impact on the planet. In response, ecologists and evolutionary biologists are dedicating increasing scientific attention to global change, largely with studies documenting biological effects and testing strategies to avoid or reverse negative impacts. In this article, we analyze global change from a different perspective, and suggest that human impacts on the environment also serve as valuable ‘accidental experiments’ that can provide fundamental scientific insight. We highlight and synthesize examples of studies taking this approach, and give guidance for gaining future insights from these unfortunate ‘accidental experiments’.

Humans are the dominant ecological and evolutionary force on our planet, with our activities altering populations, communities and ecosystems on a global scale (Vitousek et al. 1997, Palumbi 2001). For example, human-induced habitat loss and fragmentation impact virtually all terrestrial habitats (Sala et al. 2000, Hoekstra et al. 2005). Advances in agriculture, medicine, energy and industry have resulted in widespread changes to existing biogeochemical cycles (e.g. nitrogen, phosphorus, carbon dioxide) as well as the introduction of novel chemicals to the environment (e.g.

agrochemicals, CFC's, antibiotics: Tilman et al. 2001, Smith et al. 2006, Martinez 2009). Anthropogenic alterations of the carbon cycle have already resulted in global climate change, with even greater change expected in the future (IPCC, Climate Change Synthesis Report 2007). The globalization of trade has led to an enormous reshuffling of biotas and a rapid rise in invasive species (Levine and D'Antonio 2003). All of these activities, coupled with increased harvesting of species for food or natural resources, intensified illegal hunting, and protection of human assets

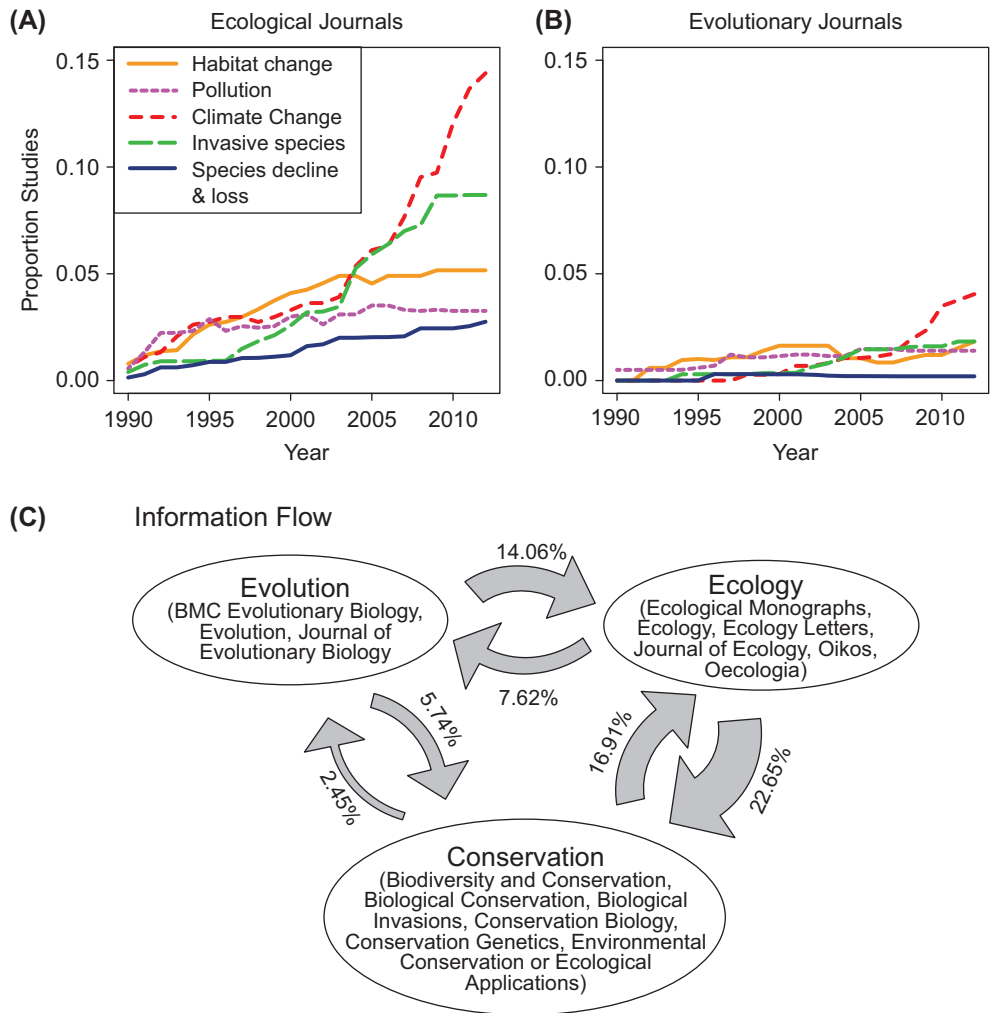


Figure 1. Citation history of global change terms in the last 23 years (A, B), showing an increasing interest by the scientific community that appears greater in ecological (A) than evolutionary (B) fields. Plotted is the proportion of studies (of all published in select ecological and evolutionary journals that year) including specific keywords in the title, abstract or keyword list that relate to the five global change factors. The flow of information (according to number of citations) between ‘basic’ and ‘applied’ journals may explain these differences (C); it is greater in the field of ecology than the field of evolution. The size of each arrow and percentage indicates the proportion of articles (published between 2008–2013 in select journals) in one subdiscipline (that the arrow is pointing to) that cite at least one article published in journals in the other subdiscipline in 2008 (that the arrow is pointing from). More details on Web of Science search parameters used to generate these figures are in Supplementary material Appendix A1 (for Fig. 1A–B) and Supplementary material Appendix A2 (for Fig. 1C).

are dramatically influencing the diversity and structure of ecosystems around the world (Reid et al. 2005).

The magnitude of environmental problems faced by humanity has not escaped the attention of the scientific community, with many studies documenting the impacts of global change on individual species or ecosystems (Fig. 1A–B, Edmondson 1970, Vitousek and Walker 1989, Laurance et al. 2002, Parmesan and Yohe 2003, Ripple and Beschta 2006). Global change has even resulted in the development of entirely new ecological and evolutionary subdisciplines and journals (e.g. Conservation Genetics, Restoration Ecology). Traditionally, a dichotomy existed between these ‘applied’ research directions and more fundamental studies, with anthropogenic global change often viewed as a problem to quantify or resolve in the former or as a confounding factor to minimize in the latter. Despite the increased attention on global change factors in both ecological and evolutionary fields (Fig. 1A–B), we believe

this dichotomy still exists to some extent, as reflected by the lack of cross-citations between traditionally ‘basic’ ecological and evolutionary journals and those ‘applied’ journals addressing the biological impacts of global change (Fig. 1C).

We argue that fundamental insights into ecological and evolutionary processes can be gained by considering global change factors as ‘accidental experiments’, much as Diamond argued that ‘natural experiments’ are an important complement to lab and field experiments (1983). Scientists going back to Darwin, who used naturalized species to suggest competition is most severe between close relatives (1859), and Grinnell, who proposed that the introduced English sparrow be used to investigate ecotypic adaptation (1919), have made similar suggestions for specific case studies. More recently, Sax et al. made a parallel argument for introduced species (2007). In this paper, we expand on these arguments by providing a retrospective view on ecological and

Box 1. Examples of key ecological and evolutionary insights from the study of five global change factors, including studies on habitat transformation (Galetti et al. 2013), pollution (Vonlanthen et al. 2012), climate change (Harsch et al. 2009), introduced species (Rogers et al. 2012), and the recovery of a species from low population numbers (Duckworth and Badyaev 2007).

Global change factor	Example ecological/evolutionary insight
	<i>Habitat transformation:</i> deforestation and defaunation in Brazil has led to the local extinction of large-gaped seed dispersers like the channel-billed toucan ¹ . Galetti et al. (2013) studied palm populations in these forests and found a reduction in their seed size in fragments without these large-gaped seed dispersers, consistent with altered selective pressures on seed size with disperser loss.
	<i>Pollution:</i> eutrophication of Swiss lakes ² leads to hypoxia, eliminating spawning habitat for deep-dwelling whitefish. Vonlanthen et al. (2012) demonstrated that this decline in reproductive isolation relaxed divergent selection between deep- and shallow-dwelling whitefish, and increased gene flow between previously distinct types, leading to a loss of diversity (termed 'reverse speciation').
	<i>Climate change:</i> most of the globe has warmed in the last 50–100 years. Using a meta-analysis, Harsch et al. (2009) examined the relationship between warming and the position of treelines ³ globally, demonstrating the importance of climate as well as other factors for the establishment of this ecotone.
	<i>Introduced species:</i> The introduction of the non-native brown tree snake to Guam has resulted in the functional extirpation of the native avifauna. Rogers et al. (2012) used this extinction to demonstrate that birds have strong top-down effects on spider abundances ⁴ when they found 40× greater spider densities on Guam than on neighboring islands with intact avifauna.
	<i>Extinction/population decline:</i> western bluebirds ⁵ are recolonizing their historic range after rebounding from low populations (due to habitat loss). Using this range expansion, Duckworth and Badyaev (2007) demonstrated that aggressive behavior is coupled with dispersal in expanding populations of this species, facilitating the displacement of mountain bluebirds by western bluebirds.

¹The channel-billed toucan *Ramphastos vitellinus* is capable of eating and dispersing large palm seeds. Picture courtesy of Guto Balieiro.

²The River Rhone entering Lake Geneva, one of the lakes studied by Vonlanthen et al. Rama / Wikimedia Commons / CC-BY-SA-2.0-FR

³*Nothofagus* treeline in Takahē Valley, Murchinson Mountains, New Zealand. Picture courtesy of Melanie Harsch.

⁴Spider webs on Guam. Picture courtesy of Isaac Chellman.

⁵A western bluebird *Sialia mexicana*. Picture courtesy of Alexander Badyaev.

evolutionary insights gained by all global change factors, and a prospective view by outlining a path to maximize continued insight. Specifically, we first summarize important ecological and evolutionary insights that five broad global change factors have already provided (e.g. Box 1), and discuss when such insights are uniquely gained from accidental experiments (as opposed to more traditional observational studies or manipulative experiments). Next, we argue that accidental experiments created by ongoing or emerging global change factors will yield additional ecological and evolutionary insights in the future, and we provide suggestions on how both to identify such opportunities and design scientific studies that maximize insight from these opportunities.

A retrospective view: insights already gained from the study of global change factors

Habitat transformation

Nearly a fifth of the world's land surface has been converted to human use (Hoekstra et al. 2005). These habitat transfor-

mations cause a wide variety of changes to the environment that can be viewed as 'treatments' (Table 1). For example, deforestation, urbanization and agriculture have reduced the amount of habitat available for most species, as well as increased habitat fragmentation and disturbance rates. Thus, the direct effects of habitat transformation provide biologists with the opportunity to investigate the impacts of habitat size and quality, habitat isolation, and the effects of edges and disturbances on gene flow, populations, species, communities and ecosystems (Fukami and Wardle 2005, Laurance 2008). Through these direct effects, habitat transformation can dramatically increase local extinction rates, providing biologists with additional opportunities to examine, for example, how changes in biotic components of communities influence community and ecosystem structure (Table 1).

Evolutionary biologists and ecologists have already gained tremendous insight into population, community and ecosystem-level processes by studying these 'treatments.' For example, fragmented habitats are frequently used to establish that small population sizes and isolation generally negatively influence gene flow and increase inbreeding depression

Table 1. Treatments resulting from global change factors, the evolutionary and ecological processes altered by these unintentional ‘treatments’, and example insights that would have been difficult to achieve with more traditional experimental or observational approaches.

Global change factor Potential ‘treatments’	Evolutionary/ecological processes affected	Example insights ³
Habitat transformation Less habitat area More isolated habitats Less connectivity Altered habitat quality	Lower dispersal and gene flow ¹ Altered population sizes ¹ Loss of species and genetic diversity ² Loss of biotic interactors ² Altered competitive hierarchies ² Altered selective regimes ²	Studies supporting and refuting elements of theories of island biogeography and meta-population ecology are largely provided by fragmented habitats (Hanski 1998, Laurance 2008).
Pollution Increased resources Toxins (poisons) Endocrine disruptors Antibiotics Radioactive materials	Greater productivity ¹ Altered population sizes ¹ Altered sex ratios ¹ Increased mutation rates ¹ Loss of species and genetic diversity ² Loss of biotic interactors ² Altered competitive hierarchies ² Altered selective regimes ²	The concept of alternative stable states, although long recognized as a theoretical possibility (May 1977), first gained empirical support from studies of eutrophied lakes (Scheffer et al. 1993).
Climate change Warmer temperatures Altered precipitation regimes Greater variability in climate Sea-level rise Ocean acidification Loss/gain of habitats	Altered distributions (range shifts) ¹ Altered phenological timing ¹ Loss and gain of biotic interactors ² Altered competitive hierarchies ² Altered selective regimes ² Succession ²	Range limits are a classic ecological topic (Darwin 1859, MacArthur 1972). Studies documenting range shifts consistent with recent warming (Chen et al. 2011) support climatic controls over range limits.
Introduced species Small populations Lower/higher genetic diversity Loss of interactions Novel interactions	Small population sizes ¹ Founder effects ¹ Inbreeding depression ¹ Hybridization (heterosis) ¹ Loss and gain of biotic interactors ¹ Range expansions ¹ Adaptive radiation ² Altered competitive hierarchies ² Altered selective regimes ²	Recognition that rapid evolutionary change in ecologically relevant traits (e.g. food acquisition traits, defense against predation or herbivory) can occur over short time scales was fostered by studies of introduced species (Carroll et al. 2007).
Species loss and decline Small populations Loss of interactions Gain of interactions	Greater demographic stochasticity ¹ Loss of species and genetic diversity ¹ Altered competitive hierarchies ² Altered selective regimes ²	Top-down control of ecosystems by apex predators is convincingly demonstrated by anthropogenic extinctions (Estes et al. 2011).

¹Direct responses to global change factors.

²Indirect responses to global change factors that have themselves been used to gain fundamental insight.

³Several of these insights are not unique to the global change factor in question – for example, rapid evolutionary changes have been documented in introduced species as well as species responding to climate change.

(Madsen et al. 1996, Westemeier et al. 1998, Saccheri et al. 1998, Morgan 1999, Buza et al. 2000, Templeton et al. 2001, Jump and Penuelas 2006). One recent study illustrates that selective pressures may also be altered in transformed habitats by documenting reduced seed size of palms in forest fragments where their large-gaped seed dispersers have become locally extinct (Box 1, Galetti et al. 2013). Many aspects of the theories of island biogeography and metapopulation dynamics (e.g. relationships between habitat size and diversity, habitat size and extinction, habitat isolation and colonization) have largely been clarified by the characteristics of populations occurring in habitats reduced and fragmented through anthropogenic disturbances (Bierregaard et al. 1992, Hanski and Ovaskainen 2000, Ricketts et al. 2001, Laurance et al. 2002). These studies have illustrated that responses are often species and population specific, with generalizations possible based

on functional traits (e.g. average movement, body size). Another classic ecological topic – succession – has largely been explored in studies examining the response of populations, species, communities and biogeochemical cycling to areas varying in time since agriculture or other human activities (Bard 1952, Bazzaz 1968, Gleeson and Tilman 1990, De Deyn et al. 2003, Goulden et al. 2011). Community and ecosystem responses to habitat transformation have also generated fundamental insights. For example, ecological studies on coffee plantations suggest a link between diversity and ecosystem functioning (Philpott et al. 2008), islands created by a dam in Venezuela helped address a classic ecological question “Why is the world green?” (Hairston et al. 1960, Terborgh et al. 2001), and the creation of the Panama Canal allowed for a test of the importance of dispersal versus competition in large-scale biogeographic patterns of diversity (Smith et al. 2004).

Pollution

Pollution caused by environmental toxins (e.g. antibiotics, PCB's), anthropogenic nutrient sources (e.g. nitrogen and phosphorus) and environmental disasters (e.g. oil spills, nuclear disasters like Chernobyl and Fukushima) provide many unintended 'treatments', both evolutionary and ecological (Table 1). For example, radioactive pollutants can increase mutation rates (generally lowering fitness) and endocrine disrupters can alter sex-ratios (Stoker et al. 2003), potentially allowing physiological or behavioral ecologists to determine the influence of such 'treatments' on population dynamics and behavior. Pollutants that are plant resources (e.g. N and P) can alter competitive hierarchies, eliminating some species and genotypes from populations and communities while allowing others to become abundant. These resources also influence productivity and nutrient cycling, allowing for a better understanding of ecosystem dynamics (Suding et al. 2005, Smith et al. 2006). Finally, the indirect effects of these treatments further allow ecologists to examine the community- and ecosystem-level impacts of individual species (when lost or gained) and allow evolutionary biologists to study how environmental pressures alter selection on certain traits (e.g. antibiotic resistance), as well as the spatial and temporal scales over which these traits are fixed or eliminated (Martinez 2009).

The biological impacts of pollution have clearly changed the way scientists think about ecological and evolutionary processes. Kettlewell's seminal study, for example, demonstrated that traits (such as a dark color) can sweep through a population after selective pressures are changed, with pollution altering the relative camouflage benefits of peppered moth morphs on lichen-covered versus sooty trees (Kettlewell 1955). This example has been reproduced in virtually every introductory biological textbook (Rudge 2005). Many studies since have used pollution gradients to investigate rates of evolution and the traits that confer fitness under changing environmental conditions (Hairston et al. 2005, Antonovics 2006, Saccheri et al. 2008, Eranen et al. 2009, Brede et al. 2009). Aquatic eutrophication has also been used to demonstrate the importance of visual mate choice and ecological opportunity for sexual selection or reproductive isolation in cichlids, sticklebacks and whitefish (Box 1, Seehausen et al. 1997, Candolin et al. 2007, Engstrom-Ost and Mattila 2008, Vonlanthen et al. 2012). Additionally, a breakdown in the relationship between coloration and immune function in barn swallows near Chernobyl allowed evolutionary biologists to speculate that the link between sexual selection linked and secondary sexual characters weakens under extreme environmental stress (Camplani et al. 1999, Møller and Mousseau 2006).

For ecologists, Edmondson's seminal study of Lake Washington and more recent studies of systems experiencing anthropogenic nutrient loading have provided insight into the relative importance of nitrogen and phosphorus in limiting terrestrial and aquatic productivity (Edmondson 1970, Ryther and Dunstan 1971, Smith et al. 2006). Additionally, the importance of resource niches for species diversity and coexistence has been examined with studies documenting relationships between the deposition of nitrogen and phosphorus and the loss of terrestrial plant diversity (Stevens et al. 2004, Wassen et al. 2005). The concept

of alternative stable states was also strongly influenced by the study of eutrophication in lakes, when scientists noticed that small changes in an external driver (in this case, nutrients) could result in large changes in ecosystems (clear versus turbid water) that could not be reversed without large decreases in the same external driver (Scheffer et al. 1993, Carpenter and Brock 2006).

Climate change

Atmospheric carbon dioxide and methane levels are higher now than at any other time in the last 650 000 years, and will continue to rise (IPCC, Climate Change Synthesis Report 2007). Climate change resulting from these gases is expected to increase surface temperatures, alter precipitation regimes, and cause ocean warming and acidification at unprecedented rates (IPCC, Climate Change Synthesis Report 2007). All of these abiotic factors are likely to directly influence the genetic make-up, physiology and abundance of organisms, and thus, the diversity of communities (Table 1). Indirect effects are also possible – for example, global warming has already increased glacial melting, which can create new, previously uncolonized habitat where succession can proceed (Cannone et al. 2008). In addition, altered biotic interactions can result from climate-induced species range shifts, declines, and extinctions, including expansions of infectious diseases or pathogens (Harvell et al. 2002), phenological mismatches (Harrington et al. 1999), and novel or 'no-analog' climates (Williams and Jackson 2007).

Despite the challenges of attributing biological responses to the long-term impacts of climate change, this global change factor has already resulted in many ecological and evolutionary insights. For example, warming has caused rapid genetic changes in populations, providing insights into the potential speed of evolutionary changes in response to environmental changes (Bradshaw and Holzapfel 2001, Reale et al. 2003, Balanya et al. 2006). There are also many studies documenting shifts in species distributions and phenology in response to recent warming (reviewed by Parmesan and Yohe 2003, Parmesan 2006, Chen et al. 2011). This implies a fundamental role for climatic factors in determining range limits (Crozier 2004, Beckage et al. 2008, Lenoir et al. 2008, Moritz et al. 2008, Chen et al. 2009, Harsch et al. 2009, Tingley et al. 2012) and the timing of phenological events (Fitter and Fitter 2002, Cotton 2003, Kausarud et al. 2008, Miller-Rushing and Primack 2008, Altermatt 2010, Bartomeus et al. 2011). However, it is also clear that species are responding to climate change idiosyncratically, stimulating many recent studies on the importance of phenological timing for species interactions (Visser et al. 1998, Both and Visser 2001, Edwards and Richardson 2004, Winder and Schindler 2004, Post and Forchhammer 2008, Both et al. 2009, Thackeray et al. 2010) as well as the role of species interactions or traits in slowing or facilitating range shifts (Box 1, Harsch et al. 2009, Harley 2011, Pateman et al. 2012). We have also learned that phenotypic plasticity can play a central role in modulating species responses to changes in their environment (Charmantier et al. 2008, Lane et al. 2012), and that the degree to which species can track environmental shifts may determine the long-term survival of a population or species during periods of rapid change (Willis et al. 2008).

Introduced species

The purposeful or unintended movement of organisms into novel habitats has many consequences that can be studied by ecologists and evolutionary biologists (Table 1). Introduced species are initially at small population sizes and often have reduced genetic variation relative to populations in their native ranges, allowing the study of founder events, Allee effects, demographic stochasticity and genetic drift. Multiple introductions can bring together genotypes from very different native regions in introduced regions, and can provide insight into the potential role of genetic reshuffling in the establishment of successful genotypes (Roman and Darling 2007). Those introduced species that establish and spread also represent excellent opportunities to understand the drivers and rates of range expansions (Hastings et al. 2005) and the potential importance of ecosystem engineers and/or top predators (Fukami and Wardle 2005). As introduced species generally leave behind the competitors, natural enemies, consumers, pathogens, and predators with which they interact in their native ranges, the study of introduced species also allows us to study the importance of coevolution for species' interactions (Callaway and Maron 2006, Strauss et al. 2006b). Over longer time scales, introduced species offer biologists the chance to observe how species evolve in response to novel climates and interactors, and the loss of native interactors (Strauss et al. 2006b). In addition to studying the introduced species, the invaded community can also become the target of study – lending itself to research on the relationship between disturbance, diversity, invasibility, the trophic and ecosystem level impacts of individual invaders on the habitats they invade, and the manner in which native species evolve in response to these novel interactors (Strauss et al. 2006b, Callaway and Maron 2006, Sax et al. 2007).

The insights gained from the study of introduced species have been diverse and far ranging (reviewed by Fukami and Wardle 2005, Strauss et al. 2006b, Callaway and Maron 2006, Sax et al. 2007). On the evolutionary side, multiple introductions of common non-native species have resulted in novel genotypes relative to their native state (Kolbe et al. 2004, Roman 2006, Facon et al. 2008), which in some cases, appear responsible for the overwhelming success of the invader (Lavergne and Molofsky 2007). Introduced species have also supported the idea that evolutionary change can occur extremely rapidly, both in the introduced species and the native species responding to their introduction (Phillips and Shine 2004, Carroll et al. 2005, Zangerl and Berenbaum 2005, Siemann et al. 2006, Phillips et al. 2006, Montesinos et al. 2012). Finally, introduced species have provided several examples of speciation dynamics mediated through reproductive isolation, ecological opportunity and/or hybridization (Bush 1969, Filchak et al. 2000, Hendry 2001, Salmon et al. 2005, Fitzpatrick and Shaffer 2007, Ward et al. 2012).

Ecologists have also gained insight from introduced species. Early applied ecological work on biological control was based on the assumption that host-specific natural enemies can strongly regulate population sizes (Murdoch et al. 1985), and more recent studies indeed suggest that the loss of natural enemies in the invaded range is sometimes, but not always, correlated with invasive success (Mitchell and Power 2003,

Torchin et al. 2003, Reinhart and Callaway 2004, Hawkes et al. 2006, Callaway et al. 2011). Introduced species have also been studied in the context of ecosystem engineers and trophic cascades, illustrating that the impacts of individual species on populations, communities and ecosystems can be enormous (Box 1, Vitousek and Walker 1989, D'Antonio and Vitousek 1992, O'Dowd et al. 2003, Kurle et al. 2008, Baiser et al. 2008, Kimbro et al. 2009, Rogers et al. 2012). These studies have also convincingly demonstrated that species interactions are enormously complex (Stinson et al. 2006, Edgell et al. 2009, Green et al. 2011) and often depend on the evolutionary history of the interacting species (Parker et al. 2006, Strauss et al. 2006a, Desurmont et al. 2011).

Species decline and loss

Anthropogenic activities remove species from a variety of ecosystems through local extirpation or global extinction. According to the International Union for Conservation of Nature (IUCN), 16 928 species are threatened (critically endangered, endangered or vulnerable) and global extinction rates are currently 100–1000 times greater than background levels (Dirzo and Raven 2003, Vie et al. 2009). The decline or loss of each population and species allows ecologists and evolutionary biologists to address a variety of questions (Table 1), including the dynamics of small populations (demographic stochasticity, genetic drift, population bottlenecks) and the role individual species play in structuring communities and ecosystems. For example, removing a species can sever interspecific interactions (competition, predation, mutualism, etc.) and illuminate the importance of these interactions for remaining species. If a species' removal results in a large change to its community or ecosystem, that species can be identified as a strong ecological interactor (e.g. keystone species or ecosystem engineer). Recovering or reintroduced populations of previously decimated species can provide additional insights into population spread and dynamics, and the influence of individual species on community and ecosystem processes.

Loss of strong interactors, reduction in population density, and loss of genetic diversity represent accidental experiments that have already been used to gain insight into basic questions in community ecology, population biology, evolutionary genetics, and life history evolution. For example, species experiencing population declines due to overharvesting or active culling have been observed to evolve life history traits in response to these anthropogenic impacts (Coltman et al. 2003, Olsen et al. 2009, Sasaki et al. 2009, Darimont et al. 2009). These small populations have also demonstrated Allee effects may be common (Courchamp and Macdonald 2001). Additionally, the negative impacts of inbreeding depression and the loss of genetic variability on population fitness have been clarified by studies of rare species (Westemeier et al. 1998, Vila et al. 2003). Studies of declining populations have allowed ecologists to identify controls over population dynamics, exploring, for example, the relative importance of intrinsic versus extrinsic mechanisms, and the importance of biotic and abiotic controls over population fluctuations (Jackson et al. 2001, Olsen et al. 2004, Ims et al. 2008, Anderson et al. 2008). The loss

(or reintroduction) of top predators has also convincingly demonstrated the importance of top-down control for communities and ecosystems (Leopold et al. 1947, Estes et al. 1998, Ripple et al. 2001, Myers et al. 2007, Johnson and VanDerWal 2009, reviewed by Estes et al. 2011). Finally, a recent study demonstrated a role for dispersal and behavioral aggression in the re-expansion of western bluebirds into their historic range as their populations rebounded from low numbers (Box 1, Duckworth and Badyaev 2007).

Summary

How critical have studies of the impacts of global change been for fundamental insights into ecological and evolutionary topics (e.g. Box 1)? We suspect there are many insights uniquely gained by accidental experiments, including the existence of ‘alternative stable states,’ the rapidity with which evolutionary change can occur, and the role of apex predators in community structure and ecosystem function (Table 1). In our opinion, there are several factors that contribute to the role of accidental experiments in scientific discovery. First, accidental experiments often result in treatments that are extreme in magnitude (e.g. the eutrophication of lakes) or cover large spatial and temporal scales (e.g. climate change), often difficult or impossible to impose experimentally (Table 2). Thus, accidental experiments that are repeatedly used to examine a particular

hypothesis (e.g. the role of climate in setting range limits), can allow for the kind of generalization (Parmesan 2006, Harsch et al. 2009, Chen et al. 2011) that might otherwise be difficult to achieve without highly coordinated networks of scientists replicating the same set of experiments. Similarly, accidental experiments can validate whether findings from smaller-scale manipulative experiments scale up (e.g. species loss when nutrient limitation is overcome – Stevens et al. 2004, Suding et al. 2005, Wassen et al. 2005). Finally, when accidental experiments result in treatments that are simply unethical to intentionally impose (e.g. the introduction of thousands of species to environments with novel selection pressures, the extirpation of apex predators from large numbers of ecosystems), they can allow scientists to empirically validate hypotheses that otherwise might primarily have remained in the realm of theory (e.g. top-down control of ecosystems: Hairston et al. 1960, Estes et al. 2011, rapid evolution: Carroll et al. 2007).

Moving forward: can additional ecological and evolutionary insights be gained from anthropogenic change?

The five broad global change factors we describe have already provided critical insight on a diverse array of evolutionary and ecological topics (Box 1). The influence of humans on the planet is increasing (Sala et al. 2000, Tilman et al. 2001, IPCC Climate Change Synthesis Report 2007), and ecologists

Table 2. Advantages and disadvantages of ‘Accidental experiments’ compared to more traditional approaches for studying ecological and evolutionary processes.

Characteristic	Traditional approaches		Accidental experiments
	Observational studies	Manipulative experiments	
Control over treatments/perturbations (strength of inference)	Low (unobserved/unmeasured confounding variables)	High	Intermediate (‘treatments’ covary with other factors and may themselves be responses to global change)
Magnitude of treatment	Low (depends on spatial or temporal variability)	Can be high (if manipulations allow)	Often high (may vary over time)
Appropriate control (‘null’ treatment)	Can be challenging (absent, or depends on an appropriate choice of spatial or temporal observations)	Easy to impose (in a well-designed experiment)	Can be challenging (imposed by scale of anthropogenic perturbation or ability to foresee anthropogenic change)
Spatial scale (of treatment)	Can be large	Generally small	Can be large (sometimes uneven)
Temporal scale (of treatment)	Based on time span of observations	Generally short, applied in a step fashion (i.e. a pulse experiment)	Can be long-term (often already imposed), applied in a step or gradual fashion (i.e. a pulse or press experiment), sometimes uneven
Difficulty of imposing treatments	Easy (no treatments as such)	Often difficult	Easy (treatment already imposed)
Relative cost (equipment, supplies, labor)	Low (only requires sampling)	High (in addition to sampling, treatments have to be imposed and maintained)	Low (only requires sampling)
Main advantages	Large spatio-temporal scale possible; can help quantify semi-equilibrium dynamics; inexpensive and logistically simple	Control over experimental treatments; strength of inference	Treatments often over large spatial and long temporal scales; access to ‘treatments’ that are otherwise inaccessible
Main disadvantages	Covariates and magnitude of perturbations often makes inference weak	Chance of experimental ‘failure’ (treatment doesn’t work); small spatial and temporal scale of ‘treatments’; often expensive and challenging logistically	‘Treatments’ infrequently applied in isolation (compromising inference); desired experimental design difficult to impose

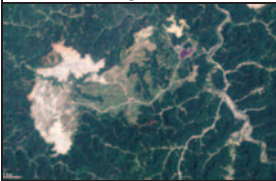


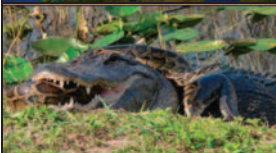

and evolutionary biologists will undoubtedly continue to focus on global change factors, perhaps at even higher rates (Fig. 1). But would explicitly considering emerging global change factors as accidental experiments make fundamental insights more likely in the future? Identifying *all* insights that could be gained is challenging (we suggest a few in Box 2), but studies that have already considered global change factors as accidental experiments can provide direction (e.g. Box 1). Here we outline approaches allowing ecologists and evolutionary biologists to 1) identify emerging opportunities in global change; 2) determine whether the ‘accidental experiment’ approach is superior to more traditional approaches for gaining fundamental insight; and 3) overcome the likely challenges associated with the ‘accidental experiment’ approach.

Increase awareness of opportunities for basic research associated with emerging or ongoing environmental problems

More communication between the ‘applied’ and ‘basic’ subfields of ecology and evolution might help achieve the

transformation of perspective necessary to highlight the diverse research opportunities associated with global change. Others have made similar arguments based on the observation that our globe is increasingly human-dominated (Hobbs et al. 2006, Marris 2009). Despite the many insights described here (e.g. Box 1), as well as papers advocating the use of global change factors to gain fundamental insights (Fukami and Wardle 2005, Strauss et al. 2006a, Sax et al. 2007), we believe that it may still not occur to many that ongoing global change factors can be used to test basic theory, perhaps because the negative impacts of these perturbations makes the study of applied solutions seem more immediate. For example, mountain top mining is a habitat disturbance that affects > 8000 km² of southern Appalachian forests and streams (Box 2). Most ecologists and evolutionary biologists are probably aware of the environmental destruction mountaintop mining brings, and the concomitant need for restoration projects. Yet there are few studies, to our knowledge, utilizing the opportunity to gain insights into basic ecological questions by documenting the long-term community or

Box 2. Potential ecological and/or evolutionary insights that might be gained from recent or upcoming impacts of habitat transformation (Bernhardt and Palmer 2011), pollution (Lubchenco et al. 2012), climate change (Perovich and Richter-Menge 2009), introduced species (Dorcas et al. 2012) and species extinctions or declines (Wake and Vredenburg 2008).

Global change factor	Example ecological/evolutionary insight
	<i>Habitat transformation</i> : mountain top mining ¹ results in large scale removal of vegetation. This disturbance could be used to investigate (for example) evolutionary changes in life history traits of initially colonizing species and the interplay of species interactions and the environment during community assembly.
	<i>Pollution</i> : the explosion of the Deepwater Horizon drilling rig ² in 2010 resulted in one of the largest oil spills ever recorded. This disturbance could be used to investigate (for example) how the resulting oil spill altered selection regimes for sea floor microbes and the dynamics of succession in areas barren of sea life.
	<i>Climate change</i> : warming in the Arctic will likely result in an ice free north passage by the year 2020 ³ . The elimination of this geographic barrier will increase migration between the Pacific and Atlantic Oceans biotas, altering community composition and competitive dynamics, and thus, evolutionary dynamics.
	<i>Introduced species</i> : pythons have invaded the Everglades in Florida, resulting in many novel interactions ⁴ . This invasion could be used to examine when/how behavioral responses to snake predation are selected for, and whether decreased herbivory by deer whose numbers have declined due to python predation influences ecosystem functioning.
	<i>Extinction / population decline</i> : dramatic declines in amphibian diversity and abundance ⁵ are occurring world-wide (due to the effects of an emerging pathogen). These declines could be used to investigate the ecological role of frogs in food webs, and the evolutionary responses of prey to the loss of an important biotic interaction.

¹A NASA Landsat satellite image of a surface mine in Boone County, West Virginia. This picture is in the public domain.

²The remnants of the Deepwater Horizon on 20 April 2010. This picture was taken by a USGS employee and is in the public domain.

³A NASA satellite image of Arctic sea ice in 2005. This image is in the public domain.

⁴A non-native Burmese python and an American alligator in the Florida Everglades National Park. This image was taken by Lori Overhofer (NPS employee) and is in the public domain.

⁵A frog infected by Chytridiomycosis (photo taken by Forrest Brem). This picture was first published in PLoS Biology (Gewin 2008), and is therefore under Creative Commons Attribution 2.5 license.

evolutionary dynamics following these large disturbances. Similarly, with a few exceptions we are not aware of studies that have used the ongoing decline of amphibians to document their role in aquatic foodwebs or ecosystems (Box 2, but see Colon-Gaud et al. 2009, 2010). Being aware of the environmental pressures facing particular study organisms or systems, through scientific literature, conferences, and dialogue between natural resource managers and academic scientists, could allow ecologists and evolutionary biologists to better identify the unique opportunities embedded in ongoing global change.

In fact, we were surprised by the low flow of information between traditionally basic versus applied journals in both fields (Fig. 1C), especially in the field of evolutionary biology. Has this resulted in a lower number of fundamental insights gained from studying global change in evolutionary biology relative to ecology? This is a difficult question to answer, but it does seem to us that it might have – we had a much harder time finding examples of evolutionary accidental experiments in our literature searches for most global change factors (introduced species being the exception, Strauss et al. 2006a, Callaway and Maron 2006, Sax et al. 2007). This is a subjective conclusion, and it is of course possible that the search terms we used to indicate studies of global change are less used by evolutionary biologists in titles and abstracts (Supplementary material Appendix A1, A2). Alternatively, perhaps evolutionary changes in response to the global change factors in question really are rarer than ecological responses, influencing citation patterns. Regardless of the ultimate reason for these patterns, we believe ‘accidental experiments’ provides a useful and underused framework for integrating applied and basic research in both ecology and evolutionary biology.

Consider the advantages and disadvantages of ‘accidental experiments’, and seek them out when desired treatments would be difficult or unethical to impose

When might accidental experiments better provide us fundamental insights than traditional approaches, like observational monitoring and manipulative experiments? This will depend on the costs (disadvantages) and benefits (advantages) of all potential approaches relative to each other (Table 2), as well as the specific question being asked. For example, understanding whether a terrestrial grassland community is more limited by the top-down effects of herbivores or the bottom up effects of soil nutrients is probably more easily ascertained from a manipulative experiment than a landscape scale survey of productivity relative to the density of herbivores and nutrient deposition, because treatments in such a manipulative experiment are straightforward to apply (fences, fertilizer; Gruner et al. 2008), while herbivore density and nutrient deposition regimes across landscapes are potentially confounded with many other (anthropogenic) variables. In many cases, pairing accidental experiments with manipulative experimental studies (Pateman et al. 2012) can allow for stronger inference while incorporating the larger spatio-temporal scale and complexity that accidental experiments allow (a similar argument for pairing observational monitoring and manipulative experiments is present in Hewitt et al. 2007).

Most useful is when ongoing global change provides opportunities to study numerous contemporary ecological

and evolutionary questions that might not otherwise be possible (Box 2). For example, the perturbations introduced by mountain top mining and global amphibian declines are relevant to ecological or evolutionary topics of great contemporary interest including community assembly (Ackerly and Cornwell 2007, Cavender-Bares et al. 2009, HilleRisLambers et al. 2012) and the adaptive repercussions of altered species interactions for ecosystems (Whitham et al. 2006). Direct experimental approaches for these topics do exist at smaller scales (e.g. rapid evolution in response to predator-prey dynamics: Yoshida et al. 2003, experimental community assembly: Fukami et al. 2005), but the resources required to impose these experimental treatments at the spatial (and temporal) scale of most human-induced changes (e.g. climate change) are beyond the scope of most ecology and evolutionary biology funding sources. Finally, many experimental manipulations that could elucidate the ecological and evolutionary dynamics of our study systems or species are simply unethical (for example, the virtual elimination of frogs or the introduction of a new apex predator – Box 2).

Foresee and plan for the challenges inherent in studying accidental experiments

Once a scientist decides a particular global change factor will be used to explore a particular ecological or evolutionary topic (i.e. an ‘accidental experiment’ is identified), there are still important challenges to consider (Table 2). Most obviously, the investigator has little to no control over where, when, or over what spatial extent global change factors are imposed, making many desirable aspects of experimental design impossible. It may therefore be difficult to obtain sufficient replicates of the treatment and avoid pseudo-replication (e.g. when studying a point-source pollutant). Controls are unlikely to be ideal, and the timing and location of sampling will probably be dictated by accessibility (both temporal and spatial). Finally, because global change factors are inherently correlated with the extent of human influence on a landscape, global change ‘treatments’ will almost always covary in ways that make the identification of driving forces difficult - for example, the impacts of temperature on range limits are difficult to disentangle from the ongoing influence of elevated CO₂ and habitat transformation.

In many cases, the challenges above can be addressed. For one, accidental experiments can often be anticipated. For example, mining companies (and other resource extraction agencies) have to submit detailed management plans in many countries, allowing scientists to survey processes of interest both before and after the inevitable disturbance (Laurance et al. 2002, Wu et al. 2003, Bernhardt and Palmer 2011). Thanks to monitoring efforts by countless conservation agencies and citizen scientists (e.g. IUCN, the Christmas Bird Count), the impending invasion of introduced species as well as the decline of certain species or functional groups can frequently be predicted in advance (Colon-Gaud et al. 2009, Dorcas et al. 2012). Conservation and restoration efforts, often years in planning, can themselves provide critical opportunities for insight (Hobbs et al. 2006, Schulte et al. 2009, Araiza et al. 2012). Where advance notice is impossible, long-term monitoring efforts, historical data sets, museum specimens and citizen science can provide information on ‘pre-treatment’ conditions (LaDeau et al. 2007, Moritz et al. 2008,

Dietl and Flessa 2011, Pateman et al. 2012). Small numbers of replicates and multivariate environmental stressors, while undesirable, are already familiar to ecologists and evolutionary biologists studying unique events and increasingly better accommodated by more sophisticated statistical approaches (Clark 2005).

Conclusions

Our influence on the planet continues to grow, increasingly blurring the boundary between 'natural' and 'human-dominated' environments (Hobbs et al. 2006, Marris 2009). We believe that the accidental experiments imposed by these intentional and unintentional human activities have and will continue to provide unique opportunities to understand ecological and evolutionary dynamics (Fukami and Wardle 2005, Sax et al. 2007). We want to be clear that we do not revel in the massive and often negative impacts of human activities, nor do we discount the importance and value of studies documenting global change or outlining valuable approaches to manage or mitigate their negative consequences. Instead, we view accidental experiments as complementary to the observational studies and manipulative experiments ecologists and evolutionary biologists often rely on for fundamental insight. We firmly believe that accidental experiments will also provide guidance to management; for example, conservation efforts to reintroduce apex predators to protected areas have been influenced by our understanding that they can have strong top-down effects on ecosystem function (Estes et al. 2011, Araiza et al. 2012). We therefore believe that viewing inevitable global change as a scientific opportunity can afford us insights that will ultimately allow us to better manage and predict change on our human-dominated planet.

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References

- Ackerly, D. D. and Cornwell, W. K. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. – *Ecol. Lett.* 10: 135–145.
- Altermatt, F. 2010. Climatic warming increases voltinism in European butterflies and moths. – *Proc. R. Soc. B* 277: 1281–1287.
- Anderson, C. N. K. et al. 2008. Why fishing magnifies fluctuations in fish abundance. – *Nature* 452: 835–839.
- Antonovics, J. 2006. Evolution in closely adjacent plant populations X: long-term persistence of prereproductive isolation at a mine boundary. – *Heredity* 97: 33–37.
- Araiza, M. et al. 2012. Consensus on criteria for potential areas for wolf reintroduction in Mexico. – *Conserv. Biol.* 26: 630–637.
- Baiser, B. et al. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. – *Biol. Invas.* 10: 785–795.
- Balanya, J. et al. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. – *Science* 313: 1773–1775.
- Bard, G. E. 1952. Secondary succession on the Piedmont of New Jersey. – *Ecol. Monogr.* 22: 195–215.
- Bartomeus, I. et al. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. – *Proc. Natl Acad. Sci. USA* 108: 20645–20649.
- Bazzaz, F. A. 1968. Succession on abandoned fields in Shawnee Hills southern Illinois. – *Ecology* 49: 924–936.
- Beckage, B. et al. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. – *Proc. Natl Acad. Sci. USA* 105: 4197–4202.
- Bernhardt, E. S. and Palmer, M. A. 2011. The environmental costs of mountaintop mining valley fill operations for aquatic ecosystems of the central Appalachians. – *Year Ecol. Conserv. Biol.* 1223: 39–57.
- Bierregaard, R. O. et al. 1992. The biological dynamics of tropical rain-forest fragments. – *Bioscience* 42: 859–866.
- Both, C. and Visser, M. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. – *Nature* 411: 296–298.
- Both, C. et al. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? – *J. Anim. Ecol.* 78: 73–83.
- Bradshaw, W. and Holzapfel, C. 2001. Genetic shift in photoperiodic response correlated with global warming. – *Proc. Natl Acad. Sci. USA* 98: 14509–14511.
- Brede, N. et al. 2009. The impact of human-made ecological changes on the genetic architecture of *Daphnia* species. – *Proc. Natl Acad. Sci. USA* 106: 4758–4763.
- Bush, G. 1969. Sympatric host race formation and speciation in frugivorous flies of genus *Rhagoletis* (Diptera, Tephritidae). – *Evolution* 23: 237–251.
- Buza, L. et al. 2000. Genetic erosion, inbreeding and reduced fitness in fragmented populations of the endangered tetraploid pea *Swainsona recta*. – *Biol. Conserv.* 93: 177–186.
- Callaway, R. M. and Maron, J. L. 2006. What have exotic plant invasions taught us over the past 20 years? – *Trends Ecol. Evol.* 21: 369–374.
- Callaway, R. M. et al. 2011. Effects of soil biota from different ranges on *Robinia* invasion: acquiring mutualists and escaping pathogens. – *Ecology* 92: 1027–1035.
- Camplani, A. et al. 1999. Carotenoids, sexual signals and immune function in barn swallows from Chernobyl. – *Proc. R. Soc. B* 266: 1111–1116.
- Candolin, U. et al. 2007. Changed environmental conditions weaken sexual selection in sticklebacks. – *J. Evol. Biol.* 20: 233–239.
- Cannone, N. et al. 2008. Accelerating climate change impacts on alpine glacier forefield ecosystems in the European Alps. – *Ecol. Appl.* 18: 637–648.
- Carpenter, S. and Brock, W. 2006. Rising variance: a leading indicator of ecological transition. – *Ecol. Lett.* 9: 308–315.
- Carroll, S. P. et al. 2005. And the beak shall inherit – evolution in response to invasion. – *Ecol. Lett.* 8: 944–951.
- Carroll, S. P. et al. 2007. Evolution on ecological time-scales. – *Funct. Ecol.* 21: 387–393.
- Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. – *Ecol. Lett.* 12: 693–715.
- Charmantier, A. et al. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. – *Science* 320: 800–803.
- Chen, I. et al. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. – *Proc. Natl Acad. Sci. USA* 106: 1479–1483.
- Chen, I. et al. 2011. Rapid range shifts of species associated with high levels of climate warming. – *Science* 333: 1024–1026.

- Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. – *Ecol. Lett.* 8: 2–14.
- Colon-Gaud, C. et al. 2009. Assessing ecological responses to catastrophic amphibian declines: patterns of macroinvertebrate production and food web structure in upland Panamanian streams. – *Limnol. Oceanogr.* 54: 331–343.
- Colon-Gaud, C. et al. 2010. Stream invertebrate responses to a catastrophic decline in consumer diversity. – *J. N. Am. Benthol. Soc.* 29: 1185–1198.
- Coltman, D. et al. 2003. Undesirable evolutionary consequences of trophy hunting. – *Nature* 426: 655–658.
- Cotton, P. 2003. Avian migration phenology and global climate change. – *Proc. Natl Acad. Sci. USA* 100: 12219–12222.
- Courchamp, F. and Macdonald, D. 2001. Crucial importance of pack size in the African wild dog *Lycyon pictus*. – *Anim. Conserv.* 4: 169–174.
- Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. – *Ecology* 85: 231–241.
- D'Antonio, C. M. and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass fire cycle and global change. – *Annu. Rev. Ecol. Syst.* 23: 63–87.
- Darimont, C. T. et al. 2009. Human predators outpace other agents of trait change in the wild. – *Proc. Natl Acad. Sci. USA* 106: 952–954.
- Darwin, C. R. 1859. On the origin of species by means of natural selection. – John Murray.
- De Deyn, G. et al. 2003. Soil invertebrate fauna enhances grassland succession and diversity. – *Nature* 422: 711–713.
- Desurmont, G. A. et al. 2011. Evolutionary history predicts plant defense against an invasive pest. – *Proc. Natl Acad. Sci. USA* 108: 7070–7074.
- Diamond, J. M. 1983. Ecology – laboratory, field and natural experiments. – *Nature* 304: 586–587.
- Dietl, G. P. and Flessa, K. W. 2011. Conservation paleobiology: putting the dead to work. – *Trends Ecol. Evol.* 26: 30–37.
- Dirzo, R. and Raven, P. 2003. Global state of biodiversity and loss. – *Annu. Rev. Environ. Resour.* 28: 137–167.
- Dorcas, M. E. et al. 2012. Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. – *Proc. Natl Acad. Sci. USA* 109: 2418–2422.
- Duckworth, R. A. and Badyaev, A. V. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. – *Proc. Natl Acad. Sci. USA* 104: 15017–15022.
- Edgell, T. C. et al. 2009. Experimental evidence for the rapid evolution of behavioral canalization in natural populations. – *Am. Nat.* 174: 434–440.
- Edmondson, W. 1970. Phosphorus, nitrogen and algae in Lake Washington after diversion of sewage. – *Science* 169: 690–691.
- Edwards, M. and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. – *Nature* 430: 881–884.
- Engstrom-Ost, J. and Mattila, J. 2008. Foraging, growth and habitat choice in turbid water: an experimental study with fish larvae in the Baltic Sea. – *Mar. Ecol. Progr. Ser.* 359: 275–281.
- Eranen, J. K. et al. 2009. Mountain birch under multiple stressors – heavy metal-resistant populations co-resistant to biotic stress but maladapted to abiotic stress. – *J. Evol. Biol.* 22: 840–851.
- Estes, J. et al. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. – *Science* 282: 473–476.
- Estes, J. A. et al. 2011. Trophic downgrading of planet Earth. – *Science* 333: 301–306.
- Facon, B. et al. 2008. High genetic variance in life-history strategies within invasive populations by way of multiple introductions. – *Curr. Biol.* 18: 363–367.
- Filchak, K. et al. 2000. Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. – *Nature* 407: 739–742.
- Fitter, A. and Fitter, R. 2002. Rapid changes in flowering time in British plants. – *Science* 296: 1689–1691.
- Fitzpatrick, B. M. and Shaffer, H. B. 2007. Hybrid vigor between native and introduced salamanders raises new challenges for conservation. – *Proc. Natl Acad. Sci. USA* 104: 15793–15798.
- Fukami, T. and Wardle, D. 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. – *Proc. R. Soc. B* 272: 2105–2115.
- Fukami, T. et al. 2005. Species divergence and trait convergence in experimental plant community assembly. – *Ecol. Lett.* 8: 1283–1290.
- Galetti, M. et al. 2013. Functional extinction of birds drive rapid evolutionary changes in seed size. – *Science* 340: 1086–1090.
- Gewin, V. 2008. Riders of a modern-day Ark. – *PloS Biol.* 6: 18–21.
- Gleeson, S. K. and Tilman, D. 1990. Allocation and the transient dynamics of succession on poor soils. – *Ecology* 71: 1144–1155.
- Goulden, M. L. et al. 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. – *Global Change Biol.* 17: 855–871.
- Green, P. T. et al. 2011. Invasional meltdown: Invader-invader mutualism facilitates a secondary invasion. – *Ecology* 92: 1758–1768.
- Grinnell, J. 1919. The English sparrow has arrived in Death Valley – an experiment in nature. – *Am. Nat.* 53: 468–472.
- Gruner, D. S. et al. 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. – *Ecol. Lett.* 11: 740–755.
- Hairston, N. G. et al. 1960. Community structure, population control and competition. – *Am. Nat.* 94: 421–425.
- Hairston, N. et al. 2005. Species-specific *Daphnia* phenotypes: a history of industrial pollution and pelagic ecosystem response. – *Ecology* 86: 1669–1678.
- Hanski, I. 1998. Metapopulation dynamics. – *Nature* 396: 41–49.
- Hanski, I. and Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape. – *Nature* 404: 755–758.
- Harley, C. D. G. 2011. Climate change, keystone predation and biodiversity loss. – *Science* 334: 1124–1127.
- Harrington, R. et al. 1999. Climate change and trophic interactions. – *Trends Ecol. Evol.* 14: 146–150.
- Harsch, M. A. et al. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. – *Ecol. Lett.* 12: 1040–1049.
- Harvell, C. et al. 2002. Ecology – climate warming and disease risks for terrestrial and marine biota. – *Science* 296: 2158–2162.
- Hastings, A. et al. 2005. The spatial spread of invasions: new developments in theory and evidence. – *Ecol. Lett.* 8: 91–101.
- Hawkes, C. et al. 2006. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. – *Plant Soil* 281: 369–380.
- Hendry, A. 2001. Adaptive divergence and the evolution of reproductive isolation in the wild: an empirical demonstration using introduced sockeye salmon. – *Genetica* 112: 515–534.
- Hewitt, J. E. et al. 2007. The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale-dependent systems. – *Am. Nat.* 169: 398–408.
- HilleRisLambers, J. et al. 2012. Rethinking community assembly through the lens of coexistence theory. – *Annu. Rev. Ecol. Syst.* 43: 227–248.
- Hobbs, R. et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. – *Global Ecol. Biogeogr.* 15: 1–7.

- Hoekstra, J. et al. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. – *Ecol. Lett.* 8: 23–29.
- Ims, R. A. et al. 2008. Collapsing population cycles. – *Trends Ecol. Evol.* 23: 79–86.
- IPCC, Climate Change Synthesis Report 2007. IPCC, Climate Change Synthesis Report, Fourth Assessment Report. Core Writing Team, Pauchari, R. and Reisinger, A. (eds). – IPCC.
- Jackson, J. et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. – *Science* 293: 629–638.
- Johnson, C. N. and VanDerWal, J. 2009. Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. – *J. Appl. Ecol.* 46: 641–646.
- Jump, A. S. and Penuelas, J. 2006. Genetic effects of chronic habitat fragmentation in a wind-pollinated tree. – *Proc. Natl Acad. Sci. USA* 103: 8096–8100.
- Kausrud, H. et al. 2008. Mushroom fruiting and climate change. – *Proc. Natl Acad. Sci. USA* 105: 3811–3814.
- Kettlewell, H. 1955. Recognition of appropriate backgrounds by the pale and black phases of *Lepidoptera*. – *Nature* 175: 943–944.
- Kimbro, D. L. et al. 2009. Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. – *Oecologia* 160: 563–575.
- Kolbe, J. et al. 2004. Genetic variation increases during biological invasion by a Cuban lizard. – *Nature* 431: 177–181.
- Kurle, C. M. et al. 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. – *Proc. Natl Acad. Sci. USA* 105: 3800–3804.
- LaDeau, S. L. et al. 2007. West Nile virus emergence and large-scale declines of North American bird populations. – *Nature* 447: 710–713.
- Lane, J. E. et al. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. – *Nature* 489: 554–557.
- Laurance, W. F. 2008. Theory meets reality in fragmented forests. – *Anim. Conserv.* 11: 364–365.
- Laurance, W. et al. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. – *Conserv. Biol.* 16: 605–618.
- Lavergne, S. and Molofsky, J. 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. – *Proc. Natl Acad. Sci. USA* 104: 3883–3888.
- Lenoir, J. et al. 2008. A significant upward shift in plant species optimum elevation during the 20th century. – *Science* 320: 1768–1771.
- Leopold, A. et al. 1947. A survey of over-populated deer ranges in the United States. – *J. Wildlife Manage.* 11: 162–177.
- Levine, J. and D'Antonio, C. 2003. Forecasting biological invasions with increasing international trade. – *Conserv. Biol.* 17: 322–326.
- Lubchenco, J. et al. 2012. Science in support of the deepwater horizon response. – *Proc. Natl Acad. Sci. USA* 109: 20212–20221.
- MacArthur, R. H. 1972. Geographical ecology; patterns in the distribution of species. – Harper and Row.
- Madsen, T. et al. 1996. Inbreeding depression in an isolated population of adders *Vipera berus*. – *Biol. Conserv.* 75: 113–118.
- Marris, E. 2009. Ecology: ragamuffin Earth. – *Nature* 460: 450–453.
- Martinez, J. L. 2009. The role of natural environments in the evolution of resistance traits in pathogenic bacteria. – *Proc. R. Soc. B* 276: 2521–2530.
- May, R. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. – *Nature* 269: 471–477.
- Miller-Rushing, A. J. and Primack, R. B. 2008. Global warming and flowering times in Thoreau's concord: a community perspective. – *Ecology* 89: 332–341.
- Mitchell, C. E. and Power, A. G. 2003. Release of invasive plants from fungal and viral pathogens. – *Nature* 421: 625–627.
- Møller, A. and Mousseau, T. 2006. Biological consequences of Chernobyl: 20 years on. – *Trends Ecol. Evol.* 21: 200–207.
- Montesinos, D. et al. 2012. Neo-allopatry and rapid reproductive isolation. – *Am. Nat.* 180: 529–533.
- Morgan, J. 1999. Effects of population size on seed production and germinability in an endangered, fragmented grassland plant. – *Conserv. Biol.* 13: 266–273.
- Moritz, C. et al. 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. – *Science* 322: 261–264.
- Murdoch, W. et al. 1985. Biological-control in theory and practice. – *Am. Nat.* 125: 344–366.
- Myers, R. A. et al. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. – *Science* 315: 1846–1850.
- O'Dowd, D. et al. 2003. Invasional 'meltdown' on an oceanic island. – *Ecol. Lett.* 6: 812–817.
- Olsen, E. et al. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. – *Nature* 428: 932–935.
- Olsen, E. M. et al. 2009. Nine decades of decreasing phenotypic variability in Atlantic cod. – *Ecol. Lett.* 12: 622–631.
- Palumbi, S. 2001. Evolution – humans as the world's greatest evolutionary force. – *Science* 293: 1786–1790.
- Parker, J. D. et al. 2006. Opposing effects of native and exotic herbivores on plant invasions. – *Science* 311: 1459–1461.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Syst.* 37: 637–669.
- Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – *Nature* 421: 37–42.
- Pateman, R. M. et al. 2012. Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. – *Science* 336: 1028–1030.
- Perovich, D. K. and Richter-Menge, J. A. 2009. Loss of sea ice in the Arctic. – *Annu. Rev. Mar. Sci.* 1: 417–441.
- Phillips, B. and Shine, R. 2004. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. – *Proc. Natl Acad. Sci. USA* 101: 17150–17155.
- Phillips, B. L. et al. 2006. Invasion and the evolution of speed in toads. – *Nature* 439: 803–803.
- Philpott, S. M. et al. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds and trees. – *Conserv. Biol.* 22: 1093–1105.
- Post, E. and Forchhammer, M. C. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. – *Phil. Trans. R. Soc. B* 363: 2369–2375.
- Reale, D. et al. 2003. Genetic and plastic responses of a northern mammal to climate change. – *Proc. R. Soc. B* 270: 591–596.
- Reid, W. et al. 2005. Millennium ecosystem assessment: ecosystems and human well-being. Synthesis. – Millennium Ecosystem Assessment Board.
- Reinhart, K. and Callaway, R. 2004. Soil biota facilitate exotic *Acer* invasions in Europe and North America. – *Ecol. Appl.* 14: 1737–1745.
- Ricketts, T. et al. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. – *Conserv. Biol.* 15: 378–388.
- Ripple, W. J. and Beschta, R. L. 2006. Linking a cougar decline, trophic cascade and catastrophic regime shift in Zion National Park. – *Biol. Conserv.* 133: 397–408.
- Ripple, W. et al. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. – *Biol. Conserv.* 102: 227–234.
- Rogers, H. et al. 2012. 'Natural experiment' demonstrates top-down control of spiders by birds on a landscape level. – *PloS ONE* 7: e43446.

- Roman, J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader's range. – *Proc. R. Soc. B* 273: 2453–2459.
- Roman, J. and Darling, J. A. 2007. Paradox lost: genetic diversity and the success of aquatic invasions. – *Trends Ecol. Evol.* 22: 454–464.
- Rudge, D. 2005. The beauty of Kettlewell's classic experimental demonstration of natural selection. – *Bioscience* 55: 369–375.
- Ryther, J. and Dunstan, W. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. – *Science* 171: 1008–1013.
- Saccheri, I. et al. 1998. Inbreeding and extinction in a butterfly metapopulation. – *Nature* 392: 491–494.
- Saccheri, I. J. et al. 2008. Selection and gene flow on a diminishing cline of melanic peppered moths. – *Proc. Natl Acad. Sci. USA* 105: 16212–16217.
- Sala, O. et al. 2000. Biodiversity – global biodiversity scenarios for the year 2100. – *Science* 287: 1770–1774.
- Salmon, A. et al. 2005. Genetic and epigenetic consequences of recent hybridization and polyploidy in *Spartina* (Poaceae). – *Mol. Ecol.* 14: 1163–1175.
- Sasaki, K. et al. 2009. Rapid evolution in the wild: changes in body size, life-history traits and behavior in hunted populations of the Japanese Mamushi snake. – *Conserv. Biol.* 23: 93–102.
- Sax, D. F. et al. 2007. Ecological and evolutionary insights from species invasions. – *Trends Ecol. Evol.* 22: 465–471.
- Scheffer, M. et al. 1993. Alternative equilibria in shallow lakes. – *Trends Ecol. Evol.* 8: 275–279.
- Schulte, D. M. et al. 2009. Unprecedented restoration of a native oyster metapopulation. – *Science* 325: 1124–1128.
- Seehausen, O. et al. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. – *Science* 277: 1808–1811.
- Siemann, E. et al. 2006. Rapid adaptation of insect herbivores to an invasive plant. – *Proc. R. Soc. B* 273: 2763–2769.
- Smith, S. et al. 2004. Cross-cordillera exchange mediated by the Panama Canal increased the species richness of local freshwater fish assemblages. – *Proc. R. Soc. B* 271: 1889–1896.
- Smith, V. H. et al. 2006. Eutrophication of freshwater and marine ecosystems. – *Limnol. Oceanogr.* 51: 351–355.
- Stevens, C. J. et al. 2004. Impact of nitrogen deposition on the species richness of grasslands. – *Science* 303: 1876–1879.
- Stinson, K. A. et al. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. – *PloS Biol.* 4: 727–731.
- Stoker, C. et al. 2003. Sex reversal effects on *Caiman latirostris* exposed to environmentally relevant doses of the xenoestrogen bisphenol A. – *Gen. Comp. Endocrinol.* 133: 287–296.
- Strauss, S. Y. et al. 2006a. Exotic taxa less related to native species are more invasive. – *Proc. Natl Acad. Sci. USA* 103: 5841–5845.
- Strauss, S. Y. et al. 2006b. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? – *Ecol. Lett.* 9: 354–371.
- Suding, K. N. et al. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. – *Proc. Natl Acad. Sci. USA* 102: 4387–4392.
- Templeton, A. et al. 2001. Disrupting evolutionary processes: the effect of habitat fragmentation on collared lizards in the Missouri Ozarks. – *Proc. Natl Acad. Sci. USA* 98: 5426–5432.
- Terborgh, J. et al. 2001. Ecological meltdown in predator-free forest fragments. – *Science* 294: 1923–1926.
- Thackeray, S. J. et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. – *Global Change Biol.* 16: 3304–3313.
- Tilman, D. et al. 2001. Forecasting agriculturally driven global environmental change. – *Science* 292: 281–284.
- Tingley, M. W. et al. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. – *Global Change Biol.* 18: 3279–3290.
- Torchin, M. et al. 2003. Introduced species and their missing parasites. – *Nature* 421: 628–630.
- Vie, J. C. et al. 2009. Wildlife in a changing world – an analysis of the 2008 IUCN red list of threatened species. – <www.iucnredlist.org>
- Vila, C. et al. 2003. Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. – *Proc. R. Soc. B* 270: 91–97.
- Visser, M. et al. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). – *Proc. R. Soc. B* 265: 1867–1870.
- Vitousek, P. and Walker, L. 1989. Biological invasion by *Myrica faya* in Hawaii – plant demography, nitrogen-fixation, ecosystem effects. – *Ecol. Monogr.* 59: 247–265.
- Vitousek, P. et al. 1997. Human domination of Earth's ecosystems. – *Science* 277: 494–499.
- Vonlanthen, P. et al. 2012. Eutrophication causes speciation reversal in whitefish adaptive radiations. – *Nature* 482: 357–362.
- Wake, D. B. and Vredenburg, V. T. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. – *Proc. Natl Acad. Sci. USA* 105: 11466–11473.
- Ward, J. L. et al. 2012. Discordant introgression in a rapidly expanding hybrid swarm. – *Evol. Appl.* 5: 380–392.
- Wassen, M. J. et al. 2005. Endangered plants persist under phosphorus limitation. – *Nature* 437: 547–550.
- Westemeier, R. et al. 1998. Tracking the long-term decline and recovery of an isolated population. – *Science* 282: 1695–1698.
- Whitham, T. G. et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. – *Nat. Rev. Genet.* 7: 510–523.
- Williams, J. W. and Jackson, S. T. 2007. Novel climates, no-analog communities, and ecological surprises. – *Front. Ecol. Environ.* 5: 475–482.
- Willis, C. G. et al. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. – *Proc. Natl Acad. Sci. USA* 105: 17029–17033.
- Winder, M. and Schindler, D. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. – *Ecology* 85: 2100–2106.
- Wu, J. et al. 2003. Three-Gorges dam – experiment in habitat fragmentation? – *Science* 300: 1239–1240.
- Yoshida, T. et al. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. – *Nature* 424: 303–306.
- Zangerl, A. R. and Berenbaum, M. R. 2005. Increase in toxicity of an invasive weed after reassociation with its coevolved herbivore. – *Proc. Natl Acad. Sci. USA* 102: 15529–15532.

Supplementary material (available online as Appendix oik-00698 at <www.oikosofficelu.se/appendix>). Appendix A1 and A2.