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Opportunity for some, extinction for others: the fate of tetrapods in the Anthropocene

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ABSTRACT

Question: Are there general traits that will foster the persistence of terrestrial vertebrates (Superclass Tetrapoda) through the challenges of the Anthropocene?

Methods: We identified five primary anthropogenic threats to terrestrial biodiversity: habitat change, direct interaction/exploitation, invasive species, climate change, and pollution. We summarized four attributes that are frequently assumed to promote species' persistence: ability to maintain high genetic diversity, phenotypic and behavioural plasticity, generalism, and fortuitous evolutionary history. We then reviewed the literature to assess their effectiveness in helping tetrapods to face anthropogenic threats.

Results and conclusion: Our literature review of hundreds of articles illustrates that all four attributes are indeed beneficial. However, only a species' evolutionary history promotes resilience to all five anthropogenic stressors. The most consistent trends across taxa are that plasticity buffers species against climate change and deleterious consequences from invasive species, while generalism benefits species threatened with habitat change. There is limited evidence demonstrating that high genetic diversity aids in species persistence and there appears to be few attributes that can help species avoid the negative impacts of pollutants.

Keywords: climate change, evolutionary history, exploitation, generalism, genetic diversity, habitat change, invasive species, plasticity, pollution.

INTRODUCTION

Human activities now directly or indirectly impact nearly all species on Earth. Current consumption patterns and a projected global population of 8–11 billion by 2050 (UNDESA, 2013) are resulting in an Earth with no haven absent of human impacts (Vitousek *et al.*, 2008).

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Indeed, human impacts now rival the 'natural' environmental forces that shaped the vast history of biodiversity on our planet, leading some to declare that we are living in a new geologic epoch: the Anthropocene (Crutzen, 2002).

The Anthropocene ushers in fundamentally new conditions for life on Earth – conditions that threaten to force thousands of species into extinction (Dow and Downing, 2007; Barnosky *et al.*, 2011; Ceballos *et al.*, 2015; McCauley *et al.*, 2015) while promoting survival and expansion of others. The success or failure of a species in responding to these conditions largely hinges on how well suited its current or potential phenotype is to new human-modified conditions. In this review, we build upon previous literature highlighting factors important to the successful response of organisms to different stressors of the Anthropocene (Purvis *et al.*, 2000b; Parmesan, 2006; Williams *et al.*, 2008; Hendry *et al.*, 2011; Sih *et al.*, 2011). We begin by outlining some of the challenges and opportunities of the Anthropocene and investigate characteristics of species that are generally thought to foster persistence. We then analyse a cross-section of examples of tetrapods that are responding positively or negatively to the Anthropocene. We use the examples to examine the overall ability of these characteristics to predict the persistence or extinction of species. We focus on terrestrial tetrapods (Superclass Tetrapoda, which includes mammals, reptiles, amphibians, and birds) because they represent a well-studied subset of animals of particular conservation concern.

CHALLENGES AND OPPORTUNITIES OF THE ANTHROPOCENE

To evaluate what characteristics promote species survival and persistence in the Anthropocene, we must (1) break down the Anthropocene into biologically relevant stressors, and (2) address how those stressors impact species. Following Barnosky *et al.* (2014), we focus on five categories of human impacts as representative stressors of the Anthropocene: habitat change, direct exploitation/interaction, invasive species, climate change, and pollution (Fig. 1).

Habitat change

Humans have physically altered more than 50% of the Earth's ice-free land (Hooke *et al.*, 2012). Most of this land has been converted into cropland and pastureland: 12% and 26% of Earth's ice-free land, respectively (Foley *et al.*, 2011; Hooke *et al.*, 2012). Habitat conversion is multi-faceted, and human-dominated habitats vary widely in their ability to support biodiversity (Karp *et al.*, 2012). Natural and human-dominated habitats may support roughly equivalent numbers of species when habitat conversion is subtle and the majority of abiotic and biotic conditions of the natural environment are conserved (e.g. converting natural forest to plantation forest) (Daily *et al.*, 2001; Mendenhall *et al.*, 2011; Frishkoff *et al.*, 2014). However, habitat conversion that drastically alters the environmental state (e.g. urbanization or complete deforestation) results in structural simplification of vegetation, loss of microhabitats, and the degradation of remaining habitat (McKinney, 2008). These radical changes reduce the number of species capable of persisting (McKinney, 2008; Newbold *et al.*, 2015). Additionally, habitat fragmentation that accompanies habitat loss increases edge effects and often reduces gene flow and species persistence (Fahrig, 2003; Ewers and Didham, 2006).

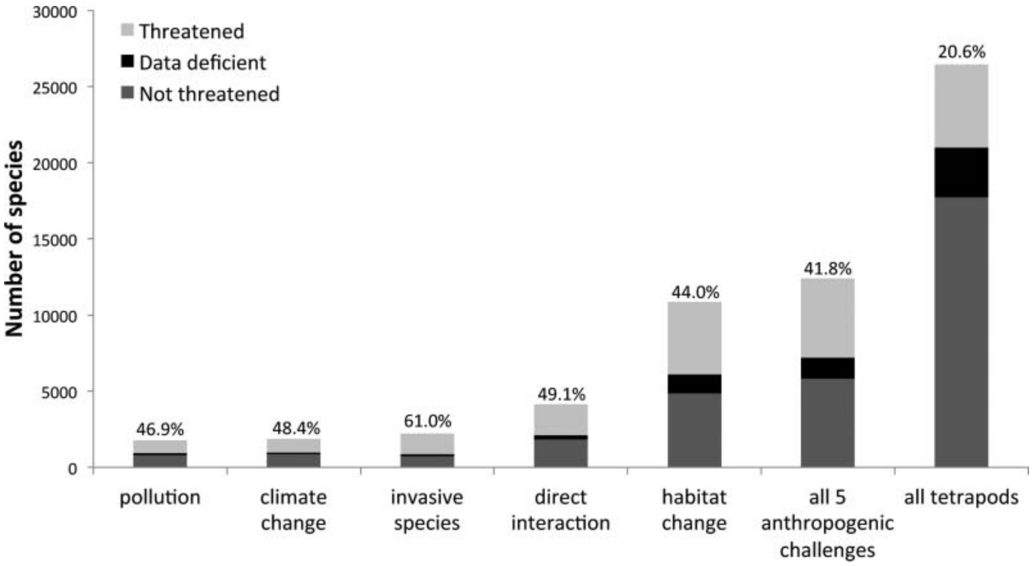

Fig. 1. Number of terrestrial tetrapods impacted by each anthropogenic challenge based on IUCN data (IUCN, 2015). The fraction of species threatened by extinction or data deficient are indicated (IUCN, 2015). The remainder are species impacted by each challenge that are not designated as threatened. Threatened species are those listed as critically endangered, endangered or vulnerable by the IUCN. The percentage of species that are threatened by extinction out of all the species impacted by each effect is also indicated. 'Invasive species' only includes the IUCN threat category of invasive non-native/alien species. 'Habitat change' includes species impacted by residential and commercial development, agriculture and aquaculture, energy production and mining, transportation and service corridors, gathering terrestrial plants, logging and wood harvesting, and natural system modification. 'Direct interaction' includes species negatively affected by hunting and trapping terrestrial animals, fishing and harvesting aquatic resources, human intrusion and disturbance, and transportation and service corridors. Transportation and service corridors include both indirect impacts as well as the direct impact that vehicles have on wildlife.

Direct exploitation/interaction

Direct interactions between humans and wildlife can come in the form of humans killing or disturbing animals while protecting property or resources, killing animals for food or trophies, removing animals from their natural habitat to be used as pets, or even hitting animals with vehicles. Road kill exceeds hunting as the leading direct human cause of terrestrial vertebrate mortality in some areas, with an estimated one million vertebrate individuals killed daily on United States roads (Forman and Alexander, 1998). In Southern Florida, road kill was once responsible for an annual mortality of 10% of the endangered Florida panther population and 17% of the Key deer population (Forman and Alexander, 1998).

Targeted killing of 'pest' wildlife has occurred on all inhabited continents and contributes to the threatened status of many species, including prairie dogs and wolves in parts of North America, lions and cheetahs in Asia, African wild dogs, as well as brown bears, lynx, and wolves in Western Europe (Woodroffe *et al.*, 2005). Lethal protection of crops and livestock has contributed to numerous extinctions, including the Falkland island wolf in 1876 (IUCN, 2008), the Guadalupe caracara raptor in 1900 (Greenway, 1967; Fuller, 2000), the Carolina parakeet in 1904 (Saikku, 1991), and the marsupial wolf in Tasmania in 1930 (Mooney and Rounsevell, 2008).

The killing and collection of animals for pets, trophies or skins can also have a significant impact on populations. Between 2000 and 2005, the Convention on International Trade in Endangered Species of Wild Fauna and Flora reported an average annual trade of more than 1.3 million live birds, over 1.6 million live reptiles, and 6 million reptile skins (Roe, 2008). In some cases, road construction has facilitated the deliberate poaching of the last of rare and endangered animals in the pursuit of high-priced body parts such as elephant ivory, rhino horn, tiger bones, bear paws, and whole pangolins (Bennett, 2011; Clements *et al.*, 2014). This illicit trade is almost certainly a greater threat to the persistence of many species than is environmental change (Courchamp *et al.*, 2006; Moyle, 2009).

Invasive species

Human activities such as transportation, agriculture, and recreation compromise the regional uniqueness of Earth's biodiversity by eroding ancient barriers to dispersal between continental landmasses by intentionally or inadvertently facilitating the spread of species beyond their natural range (Capinha *et al.*, 2015). The isolation of continents allowed the Earth to support over twice as many mammal species as would be expected from the species–area relationship (Vitousek *et al.*, 1997). The erosion of this isolation will homogenize ecosystems and is predicted to lead to the extinction of 47% of terrestrial vertebrate species and 49% of genera (Rosenzweig *et al.*, 2012, 2013). Indeed, invasive species are the primary threat to an estimated 42% of the species on the threatened or endangered list in the United States (Pimentel *et al.*, 2005). Feral cats alone are responsible for at least 14% (33 extinctions) of global bird, mammal, and reptile extinctions as well as the status of at least 8% (38 species) of critically endangered birds, mammals, and reptiles (Medina *et al.*, 2011).

Invasive species may directly interact with native species through competition, predation, parasitism or hybridization (Simberloff and Rejmánek, 2011). They can also indirectly impose selection on native species by altering the availability of resources to other species by physically changing the biotic and/or abiotic environment (Jones *et al.*, 1994; Ehrenfeld, 2010).

Climate change

Carbon dioxide concentrations in the atmosphere are 40% greater than in A.D. 1750 as a result of human activities, including the burning of fossil fuels and land-use change (deforestation and animal agriculture) (IPCC, 2013; Eshel *et al.*, 2014). This rise in atmospheric carbon dioxide is the main cause for an energy uptake by the climate system causing surface warming (IPCC, 2013). Current climate trends predict a 4°C jump in global mean temperature by 2100 (IPCC, 2014). Even a 1.5–2.5°C increase in global mean temperature will put 12,000 to 24,000 species at a greater risk of extinction (Dow and Downing, 2007). Climate change increases extinction risk by disrupting delicate balances in species' physiology, metabolism, phenology, reproductive strategies, competition, mutualism, and trophic interactions (Richardson *et al.*, 2011). Continued increases in global temperature will accelerate these increases in global extinction risk (Urban, 2015). Anthropogenic-induced climate change has also been linked to increases in the frequency, duration, and intensity of climate extremes and severe environmental disturbances, including fires, droughts, hurricanes, cyclones, landslides, and storms, all of which will further disrupt existing habitats (Meehl *et al.*, 2000; Dale *et al.*, 2001; Fischer and Knutti, 2015).

Pollution

Humans produce thousands of toxic compounds, many of which are long-lived endocrine disruptive chemicals. Wide-ranging biological impacts of these compounds include weakened immune function, decreased fertility, and demasculanization in birds and mammals (Colborn *et al.*, 1993), as well as impaired larval growth and development, altered metamorphosis time and size, a weakened immune response, and changes in sexual development in amphibians (Hayes *et al.*, 2002, 2006). In 1995, it was estimated that only 0.1% of pesticides were actually reaching their intended pest, with many airborne pesticides carried aloft, before being deposited in arctic snow, oceans, and mountain ranges far from the targeted agricultural areas (Pimentel, 1995). Oil spills threaten oceans and coasts with long-lived effects (Peterson *et al.*, 2003), and nuclear waste and mining activities release toxins into many terrestrial and marine ecosystems (Salomons, 1995; Mousseau and Møller, 2014). Even nitrogen fertilizers are atmospheric and aquatic pollutants that change soil chemistry, plant diversity, and nutrient cycling in lakes, streams, and coastal areas (Good and Beatty, 2011).

PROPOSED CHARACTERISTICS OF ANTHROPOCENE SURVIVORS

Humans are thus influencing the trajectories of populations, species, and ecosystems worldwide; however, not all species are affected equally. Indeed, human impacts may contribute to the ability of some species to persist or even thrive in the Anthropocene. It is thus important to evaluate the consequences on biodiversity of the four key characteristics most often associated with species persistence: (1) the ability to maintain high genetic diversity, (2) plasticity, (3) generalism, and (4) the unique features of a lineage's evolutionary history (Fig. 2) (Goerck, 1997; Purvis *et al.*, 2000a; Jones *et al.*, 2003; Devictor *et al.*, 2008; Chown *et al.*, 2010). Although these four characteristics are not independent, we attempt to disentangle them in order to evaluate the respective roles of each one in the success or failure of species in the Anthropocene.

High genetic diversity

The environmental challenges of the Anthropocene threaten to decrease the genetic diversity of populations in two ways: bottlenecks, in which a population dramatically decreases in size (Nei *et al.*, 1975); or isolation, in which gene flow is reduced or absent in separated populations (Garner *et al.*, 2005). Loss of genetic diversity increases the extinction risk of a species or population by reducing the probability that the genotypes necessary to persist in the new environment will be present (Fig. 2A), as standing genetic variation is necessary for rapid adaptation to new environments (Barrett and Schluter, 2008).

The unprecedented rate of environmental change observed in the Anthropocene highlights the importance of standing genetic variation. Species with high mutation rates and/or short generation times will often be capable of adapting rapidly enough to respond to anthropogenic challenges, facilitating species persistence in some circumstances (e.g. Gienapp *et al.*, 2008; de Bruyn *et al.*, 2014). However, the pace of anthropogenic change rules out new mutations as a solution for most tetrapods (Bradshaw and Holzapfel, 2006; Visser, 2008; Quintero and Wiens, 2013). For instance, in order for vertebrate species to keep up with climate projections for 2100, they would have to display rates of climatic niche evolution over 10,000 times faster than those currently observed (Quintero and Wiens, 2013).

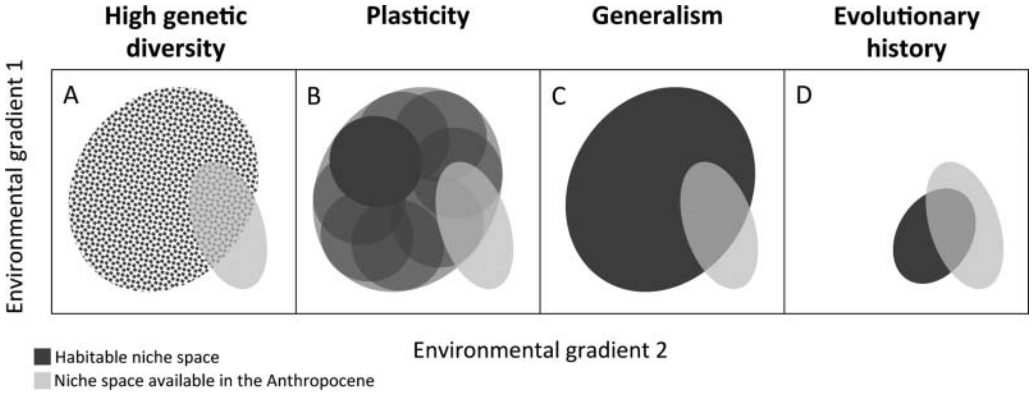

Fig. 2. Conceptual diagrams illustrating how four characteristics can improve a species' persistence in the Anthropocene. Overlap between habitable niche space and that available in the Anthropocene represents opportunities for persistence. (A) Each dot represents a unique genotype with a fixed niche space. Genotypes falling within the anthropogenic space will persist and reproduce in the Anthropocene. In this case, the greater the genetic diversity, the more likely it is that some individuals will fall within the anthropogenic niche space. (B) The current niche space occupied by a species (indicated by the most saturated space) may not overlap with the new anthropogenic niche space available; however, a plastic species is flexible and can move its niche space, potentially in numerous directions (lighter spaces), facilitating movement into the anthropogenic niche space. (C) Generalist species naturally occupy a large niche space, thus increasing the chances that the anthropogenic niche space will fall within its existing niche space. (D) A fortuitous evolutionary history will position some species' niches, regardless of niche breadth, to fall within the new anthropogenic environment due to chance pre-adaptations. Plasticity, generalism, and evolutionary history are different from high genetic diversity because these are characteristics that every individual in a species shares, such that every individual theoretically has equal capacity to move into the anthropogenic space.

Plasticity

Phenotypic and behavioural plasticity, or the ability of one genotype to generate multiple phenotypes or behaviours in response to the environment (Fig. 2B) (Scheiner, 1993), can buffer species against direct and indirect human impacts by allowing them to utilize or tolerate the new environmental conditions. Species are often able to display plasticity on short time scales, making it a mechanism capable of keeping pace with the rapid rate of change in the Anthropocene. Indeed, numerous reviews highlight the importance of plasticity over genetic change in species' responses to climate change (Hadly, 1997; Charmantier *et al.*, 2008; Hoffmann and Sgrò, 2011; Merilä, 2012; Merilä and Hendry, 2014).

Generalism

The broader a species' diet, climate or habitat niche, the more likely it is that the human-altered environment will contain the resources necessary to sustain that species (Fig. 2C). Generalist species capable of using a wide range of resources or tolerating a wide variety of abiotic conditions, should thus be more capable of surviving human impacts than more specialized species (Gallagher *et al.*, 2014).

Evolutionary history

The selection regime under which a species evolved and the environmental features to which it is adapted, its evolutionary history, can provide insight into the current and future responses of species to the Anthropocene. Particular species may be pre-adapted to novel human habitats or challenges through a fortuitously fitting evolutionary history. Environmental changes are perceived as minor by such species, and fall well within their niche even if by other measures they could be considered specialists (Fig. 2D). Ultimately, success (or failure) in human-altered environments is determined by the degree to which a species' genotypes, evolved over millions of years, predispose it to benefit (or suffer) from human environmental impacts (Gaston and Blackburn, 1997; McKinney and Lockwood, 1999; Purvis *et al.*, 2000a).

In this review, we focus on how the specific trajectory of a species' evolutionary history impacts its survival rather than the presence of evolutionary history, which all species have. This evolutionary inheritance is the same as 'historical contingency', or the unique accidents of history that have provided some species an advantage or a 'key innovation' over others (Blount *et al.*, 2008).

METHODS

We reviewed the literature to determine the quality of evidence for, and relative contribution of, each of the four characteristics in promoting either the survival or decline of species in the Anthropocene. In September 2015, we searched the Web of Science database that offers access to over 12,000 scientific and scholarly journals with articles dating from 1864. We searched the database combining key words to describe each of the five main stressors of the Anthropocene [pollution (pollut* OR toxin*), climate change ('climate change' OR 'global warming' OR 'climate warming'), invasive species ('invasive species' OR 'exotic species'), habitat loss ('habitat loss' OR 'habitat fragmentation' OR 'habitat change' OR 'land use change'), direct exploitation ('direct exploitation' OR hunt* OR 'poaching' OR 'road kill' OR 'direct interaction')] with proposed persistence characteristics [generalism ('generalist' OR 'generalism'), plasticity ('plasticity' OR 'plastic response'), genetic diversity ('genetic diversity'), and evolutionary history ('evolutionary history')] and our taxa of interest [mammals (mammal*), birds (bird* OR 'aves'), reptiles (reptile* OR reptilia*), and amphibians (amphibia*)]. We narrowed the search results by filtering for the terms extinction* OR persistence*. Our search yielded 541 articles with some falling into multiple categories (Fig. 3). We searched through these hundreds of articles for examples of the roles that maintaining high genetic diversity, plasticity, generalism, and fortuitous evolutionary history play in the successful or unsuccessful responses of tetrapods to anthropogenic stressors. Although our aim was to focus only on tetrapods, we also reference other taxa where tetrapod examples are lacking, or where we found specific non-tetrapod examples to be particularly informative (Table 1). Additionally, although invasive species themselves are a stressor facilitated by human activities of the Anthropocene, we use examples of invasive species succeeding in new environments to examine also the importance of these proposed characteristics to success in the Anthropocene. The characteristics that make an invader resilient to the challenges of a new habitat are often the same characteristics that make a native species resilient to the challenges of the Anthropocene.

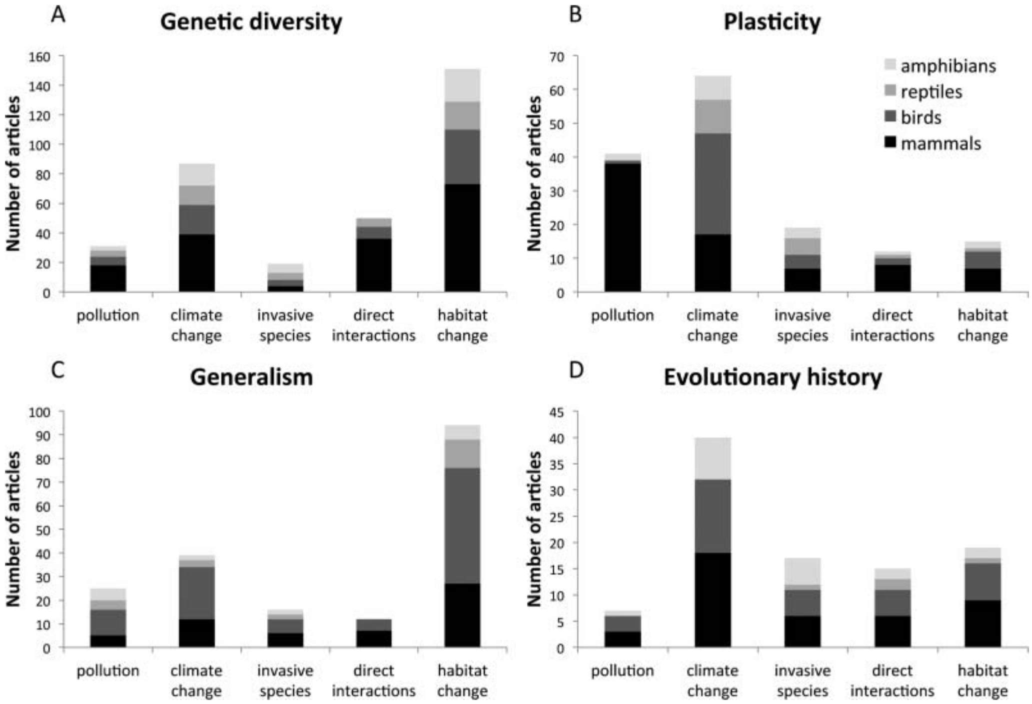

Fig. 3. Number of articles resulting from the Web of Science search that link four characteristics of Anthropocene survivors – (A) genetic diversity, (B) plasticity, (C) generalism, and (D) evolutionary history – with five anthropogenic challenges (pollution, climate change, invasive species, direct interactions, and habitat loss). Tetrapod groups are coded on a greyscale.

We read each title and abstract to identify 87 relevant articles (genetic diversity: 32, plasticity: 21, generalism: 20, and evolutionary history: 14) within these search results that we read more thoroughly for our review. We also used citations within the resultant literature and our existing knowledge to identify case studies that we use to exemplify how each characteristic can mediate tetrapod responses to the Anthropocene.

CASE STUDIES AND DISCUSSION

Maintaining genetic diversity

We found 268 articles connecting genetic diversity in tetrapods with anthropogenic challenges (Fig. 3). Most of these articles discuss how the genetic structure of species or populations has been impacted by human actions, and few studies link this explicitly to extinction risk in the near future. We suggest that there are two requirements to link the ability to maintain genetic diversity to success in the Anthropocene: (1) a demonstration that species undergoing population bottlenecks or increasing isolation due to the Anthropocene are sometimes capable of avoiding losses in genetic diversity; and (2) evidence that higher genetic diversity is connected with persistence in the Anthropocene.

Table 1. Examples shared in the text of species responding successfully to the challenges of the Anthropocene using one of the four characteristics presented in this review. Examples of invasive species succeeding with the help of these characteristics are also included and indicated as such in the 'Notes' column

Characteristic of survivor	Anthropogenic challenge	Mechanism	Taxon	Reference	Notes
Maintenance of genetic diversity	Direct exploitation – hunting	Dispersal and gene flow	Mammal – Northern fur seal	Pinsky *et al.* (2010)	
	Climate change				
	Habitat change	Gene flow	Mammal – tiger	Bay *et al.* (2014)	
	Direct exploitation – poaching				
	Invading new territory	Admixing	Reptile – anole lizard	Kolbe *et al.* (2007)	invasive
	Invading new territory	Rapid population growth	Mammal – reindeer	Lovatt and Hoelzel (2013)	invasive
	Invading new territory	High genotypic diversity	Plants and animals	Forsman (2014)	invasive
	Direct interaction – extermination	Standing genetic variation	Mammal – rodent	Pelz *et al.* (2005)	invasive
	Habitat change	Standing genetic variation	Insect – butterfly	Singer *et al.* (1993)	non-tetrapod
Plasticity	Climate change	Phenology plasticity	Mammal – yellow-bellied marmot	Ozgul *et al.* (2010)	
	Climate change	Developmental plasticity	Amphibian – tiger salamander	McMenamin and Hadly (2012)	
	Climate change	Phenotypic plasticity	Mammal – red deer	Moyes *et al.* (2011)	
	Climate change	Behavioural plasticity	Reptile – turtle	Refsnider and Janzen (2012)	
	Climate change	Phenotypic plasticity and behavioural plasticity	Bird – gentoo penguin	Juáres *et al.* (2013)	
	Habitat change	Behavioural plasticity	Insect – butterfly	Bonte and Van Dyck (2009)	non-tetrapod
	Habitat change	Life-history plasticity	Bird – Mauritius kestrel	Cartwright *et al.* (2014)	

Continued

Table 1—*continued*

Characteristic of survivor	Anthropogenic challenge	Mechanism	Taxon	Reference	Notes
	Invading new territory	Large brains – behavioural plasticity	Birds, mammals, amphibians, reptiles	Sol *et al.* (2005, 2008), Amiel *et al.* (2011)	invasive
	Invasive species	Behavioural plasticity	Reptile – anole lizard	Losos *et al.* (2006)	
	Invasive species	Behavioural plasticity	Reptile – gecko	Hoare *et al.* (2007)	
	Invasive species	Behavioural plasticity	Amphibian – frog	Greenlees *et al.* (2010)	
	Invasive species	Behavioural plasticity	Mammal – planigale	Webb *et al.* (2008)	
Generalism	Habitat change	Broad habitat and climate niche	Amphibian – frog	Botts *et al.* (2013)	
	Habitat change	Habitat generalist	Birds	Carrara *et al.* (2015)	
	Habitat change	Habitat generalist and dietary generalist	Birds	Morante-Filho *et al.* (2015)	
	Habitat change	Habitat generalist	Mammal – rodents and shrews	de la Pena *et al.* (2003)	
	Habitat change	Dietary generalist	Insect – bumblebee	Goulson *et al.* (2005)	non-tetrapod
	Invasive species	Habitat generalist	Insect – grasshopper	Yoshioka *et al.* (2010)	non-tetrapod
	Invading new territory	Habitat generalist	Mammal – American mink	Santulli *et al.* (2014)	invasive
	Invasive species	Dietary generalist	Mammal – rat	Gregory and MacDonald (2009)	
	Invading new territory	Wide native distribution – wide niche	Mammals	González-Suárez *et al.* (2015)	invasive
Evolutionary history	Habitat change	Heat-adapted	Amphibian – frog	Frishkoff *et al.* (2015)	
	Pollution – radiation	Chemical basis of feather coloration	Birds	Galván *et al.* (2011)	
	Pollution – pesticides	Phylogenetic signal of unknown origin	Amphibians	Chiari *et al.* (2015)	

	Climate change	Hypoxia-adaptation	Mammal – pikas	Solari and Hadly (n.d.)
	Invasive species	Physiological pre-adaptation	Reptile – snakes	Llewelyn *et al.* (2011)
	Invasive species	Physiological pre-adaptation	Reptile – skink	Price-Rees *et al.* (2012)
	Habitat change	Large bodies	Amphibians	Mendenhall *et al.* (2014)
	Direct exploitation	Small bodies	Mammals	Cardillo *et al.* (2005)
	Direct exploitation Invasive species	Small bodies	Birds	Owens and Bennett (2000)
	Habitat change	Granivorous diet	Birds	Karp *et al.* (2011), Newbold *et al.* (2013)
	Climate change	Granivorous diet	Mammal – rodents	Terry *et al.* (2011)
	Habitat change	More recently evolved	Birds	Frishkoff *et al.* (2014)
	Climate change	More basal clades	Amphibians	Loyola *et al.* (2014)

Gene flow can sometimes rescue bottlenecked populations by counteracting the expected decrease in genetic variability and subsequent increased chance for population extirpation or species extinction (Newman and Pilson, 1997; England *et al.*, 2003). A high rate of dispersal among northern fur seal (*Callorhinus ursinus*) colonies, and a genetically diverse refuge, facilitated the maintenance of genetic diversity even as the species faced range contractions and local extirpations caused by hunting and climate change (Pinsky *et al.*, 2010). The importance of gene flow to help maintain a species' genetic diversity is also highlighted in theoretical studies forecasting species persistence. Coalescence modelling of tiger (*Panthera tigris*) populations threatened by habitat loss and poaching predicts that, although tigers have a higher level of overall genetic diversity than expected based on census size, increased gene flow will be necessary for the species to maintain current levels of genetic diversity (Bay *et al.*, 2014).

The success of some invasive species demonstrates other mechanisms that can maintain high genetic diversity in the Anthropocene. New founder populations of invasive species face the same challenges of dealing with low genetic diversity, given that they usually experience a colonization bottleneck with only a few individuals in the fledgling population. Founder effects that reduce allelic richness in introduced species is at least partially reversed with multiple introductions (Dlugosch and Parker, 2008). In rare cases, genetic diversity in invasive ranges can even exceed that of single native ranges if multiple unique colonizing populations have subsequently admixed [demonstrated in anole lizard introductions of the Caribbean and Florida (Kolbe *et al.*, 2007)]. In fact, the prevention of gene flow among introduced populations has been recommended as a way to limit the success of unwanted invasive species (Dlugosch and Parker, 2008).

High population growth rates and increased monogamy (which increases the genetic contribution from males that could be excluded in polygynous systems) can also play important roles in maintaining genetic diversity after founder events. The genetic diversity of two reindeer (*Rangifer tarandus*) populations originating from small founder events was much higher than expected, consistent with rapid population growth and less polygny following the colonization (Lovatt and Hoelzel, 2013).

Benefits of high genetic diversity

A meta-analysis offering a link between high genetic diversity and success in the Anthropocene found that plant and animal founder groups with greater genotypic diversity had higher establishment and persistence success (Forsman, 2014). However, our search only yielded two concrete examples directly linking high standing genetic variation to successful responses to anthropogenic stressors. Brown rat (*Rattus norvegicus*) and mouse (*Mus musculus/domesticus*) populations survived extermination efforts due to variation in a single gene conferring resistance to anticoagulant compounds used to eradicate them (Pelz *et al.*, 2005). Genetic-based changes in host plant preference allowed populations of the butterfly *Euphydryas editha* to track shifting environments when logging or cattle grazing changed host plant community composition (Singer *et al.*, 1993). In these examples, the genotype necessary to withstand the anthropogenic stressor existed in the standing genetic variation of the population, enabling persistence.

Consequences of failing to maintain genetic diversity

There is also evidence of the consequences of the inability to maintain high genetic diversity. The last remaining population of timber rattlesnakes (*Crotalus horridus*) in New Hampshire, isolated by habitat loss and affected by climate change, has very low genetic diversity compared with six non-isolated New York populations. In 2006, the isolated New Hampshire population was afflicted with a skin infection causing mass mortality in this population while the more genetically diverse New York populations were unaffected (Clark *et al.*, 2011). The crested ibis (*Nipponia nippon*) of North-East Asia, critically endangered due to overhunting and habitat loss, has very low genetic diversity with many deleterious mutations resulting in genetic defects (Li *et al.*, 2014). These examples suggest that low genetic diversity may contribute to disease susceptibility, accumulation of deleterious genetic mutations, and ultimately local extirpation or extinction.

Plasticity in body size and phenology

Our literature search yielded 122 articles linking plasticity in tetrapods to anthropogenic challenges (Fig. 3). Many of these provide supporting evidence that plasticity increases a species' potential to persist in its new human-altered environment.

Some of the best documented responses to climate change concern a phenotypically plastic change in body size involving environmentally induced adjustments during development, as well as alterations in phenology (Menzel *et al.*, 2006). Average body size of endothermic animals usually decreases in response to climate warming (Hadly *et al.*, 1998; Ozgul *et al.*, 2009; Sheridan and Bickford, 2011), and may indicate that species are exposed to more stressful conditions during development. However, this response can vary greatly, with other examples of increases in body size with warming (Gardner *et al.*, 2011). Changes in body size are often an indirect result of climate change caused by changes in food or water availability (Hadly *et al.*, 1998; Yom-Tov *et al.*, 2008; Ozgul *et al.*, 2009; Sheridan and Bickford, 2011). Analyses of over 30 years of data on the yellow-bellied marmot (*Marmota flaviventris*) document shortened hibernation and earlier reproduction in response to environmental change. The increased growing season has resulted in an increase in body mass, a subsequent decrease in adult mortality, and increase in population size (Ozgul *et al.*, 2010). In this case, the yellow-bellied marmot is an example of how plasticity in phenology may allow some species to benefit from anthropogenic changes.

Developmentally plastic tiger salamanders (*Ambystoma tigrinum melanostictum*) remain in natal ponds through sexual maturity as paedomorphic adults when pond water levels are high, but rapidly metamorphose into terrestrial adults when ponds desiccate (McMenamin and Hadly, 2012). A 28-year study of the red deer in Scotland (*Cervus elaphus*) linked climate warming to the advancement of oestrus and birthing in females, and antler formation, antler falling, and rut start and end dates in males (Moyes *et al.*, 2011). There are also many well-documented examples of earlier migration, breeding, and egg-laying in birds correlated with climate change (Crick and Sparks, 1999; Miller-Rushing *et al.*, 2008; Fletcher *et al.*, 2013). However, such plasticity in phenology can lead to mismatches in the phenology of interacting species, profoundly disrupting food webs (Yang and Rudolf, 2010). Populations of the migratory pied flycatcher (*Ficedula hypoleuca*) declined by 90% in just 20 years because they were unable to synchronize their migration with the advance in peak population sizes of their primary caterpillar prey (Both *et al.*, 2006).

Plastic behaviour

Many animals are able to alter their activity patterns in order to avoid exposure to unfavourable temperatures (McFarland *et al.*, 2014). In North America, climate influences the amount of shade that female turtles (*Chrysemys picta*) choose for their nest site (Refsnider and Janzen, 2012). *Chrysemys picta* thus avoids a skew in sex ratio that climate change often creates in species that have temperature-dependent sex determination. The gentoo penguins (*Pygoscelis papua*) on King George Island in Antarctica display plasticity in both phenology and behaviour that buffers them against climate change. Adjustments in breeding phenology and selection of nesting sites maintains the population's mean reproductive success despite yearly differences in snow conditions instigated by climate change (Juáres *et al.*, 2013). Behavioural plasticity also helps species cope with habitat change. *Salamis parhassus*, a butterfly impacted by deforestation in Kenyan cloud forests, has altered its mate-location strategy from perching to patrolling because patrolling is more effective in deforested areas where there are no landmarks to aid mate searching (Bonte and Van Dyck, 2009). Female Mauritius kestrels (*Falco punctatus*) born in areas affected by anthropogenic habitat alterations invested more into early reproduction at the cost of lower survival later in life. This plasticity yields fitness equal to that of females born in intact habitat (Cartwright *et al.*, 2014). In these cases, we see that while the rapid pace of the changing environment hinders evolutionary adaptation, a wide variety of phenotypes and behaviours contribute to persistence.

Attributes that help organisms survive anthropogenic changes in their native habitat may also help invasive organisms succeed in new habitats. Invasive species of birds, mammals, amphibians, and reptiles with larger brains are more successful at establishing themselves in new environments than invasives with smaller brains (Sol *et al.*, 2005, 2008; Amiel *et al.*, 2011). Larger brains are thought to be associated with enhanced behavioural and social flexibility and thereby enable species to take advantage of opportunities in their invasive range (Sol *et al.*, 2005, 2008; Amiel *et al.*, 2011). Behavioural flexibility can also allow native species to respond successfully to invasive species. Increased perch height by the native Caribbean lizard, *Anolis sagrei*, reduced predation from introduced predatory lizards [*Leiocephalus carinatus* (Losos *et al.*, 2006)]. Similarly, on New Zealand islands, a change in behaviour by Duvaucel's geckos (*Hoplodactylus duvaucelii*) reduced predation from the introduced Pacific rat [*Rattus exulans* (Hoare *et al.*, 2007)]. The introduction of the poisonous cane toad (*Bufo marinus*) to Australia provides additional examples of how flexibility in foraging behaviour enables native species to mitigate the negative effects of invasive species. Rapid taste aversion learning in native Australian marbled frogs (*Limnodynastes convexiusculus*) has enabled them to avoid this poisonous prey (Greenlees *et al.*, 2010). And the common planigale (*Planigale maculate*), a small carnivorous marsupial, quickly learned to use scent and taste in order to avoid the potentially deadly cane toad (Webb *et al.*, 2008).

Pollutants and other toxins, however, can be difficult for organisms to detect and thus avoid through plastic behaviour. Eurasian otters (*Lutra lutra*) were exposed to hazardous levels of lead and arsenic when they recolonized the polluted Guadiamar River in Spain after a toxic spill (Delibes *et al.*, 2009). Similarly, waterfowl and shore birds that display no natural avoidance abilities often land in toxic tailing ponds created by the mining industry (Ronconi and St. Clair, 2006).

Generalism and habitat change

We found 117 articles connecting generalism in tetrapods to the challenges of the Anthropocene (Fig. 3). Generalization of diet and habitat is often credited with conferring resistance to habitat alterations (Swihart *et al.*, 2003; Travis, 2003; Lindenmayer *et al.*, 2008), which is the anthropogenic challenge most represented in the literature on generalism (Fig. 3). For example, frog species in South Africa that have narrower habitat or climate niches have experienced more severe range contractions due to land transformation over the last 100 years than species with a broader habitat or climate niche (Botts *et al.*, 2013). Similarly, in Lacadona rainforest, Mexico, the loss of forest cover has resulted in a decrease in forest specialist bird species at the local scale, and an increase in habitat generalist bird species (Carrara *et al.*, 2015). Bird communities threatened with habitat loss in the Brazilian Atlantic Forest display similar trends. Declines in forest cover have reduced the diversity of forest and dietary specialists, while increasing the species diversity of generalists (Morante-Filho *et al.*, 2015). Agricultural intensification has reduced the densities of habitat-specialist rodents and shrews in western France, while increasing the presence of habitat-generalist rodents and shrews (de la Pena *et al.*, 2003). Plentiful bumblebee species in the United Kingdom are dietary generalists, while long-tongued species specializing on pollen from the *Fabaceae* family are rare, likely due to the decline of grasslands rich in *Fabaceae* (Goulson *et al.*, 2005).

Generalism and invasive species

Invasive species can also disproportionately impact specialist species, such as the invasive weeping lovegrass in Japan, which caused declines in all of the habitat-specialist grasshopper species and only some of the habitat-generalist species (Yoshioka *et al.*, 2010). Niche breadth can also play an important role in competitive interactions between native and invasive species. In Spain, the habitat-specialized European mink (*Mustela lutreola*) is being outcompeted by the more habitat-generalist invasive American mink (*Neovison vison*), resulting in its extirpation where the American mink is present (Santulli *et al.*, 2014). A review of 511 different mammal introduction events found that species with a wider native distribution, presumably indicative of wider niches, were more successful invaders (González-Suárez *et al.*, 2015). When native species have wider diet breadths or more flexible diets, however, they are often able to outcompete invasive species or shift to using different resources. The native Galapagos rat (*Nesoryzomys swarthi*) is able to co-exist with the invasive black rat (*Rattus rattus*) owing to its greater diet breadth (Gregory and MacDonald, 2009).

Specialties of generalism

In some cases, generalism may be effective in helping species overcome one anthropogenic challenge but not another. A phylogenetic comparison using 95 bird families showed that extinction risk due to habitat loss was correlated with habitat specialization, while extinction risk due to introduced predators or direct interaction/exploitation was not (Owens and Bennett, 2000). Similarly, in mammal families, habitat specialists are more likely to be threatened by habitat loss or fragmentation, but not by invasive species or direct exploitation (González-Suárez *et al.*, 2013).

Evolutionary history and physiology

Of all four characteristics, the fewest articles (61) linked evolutionary history to anthropogenic challenges in tetrapods (Fig. 3); however, there are compelling examples connecting evolutionary history to all five challenges.

Many species possess physiologies that predispose them to succeed despite anthropogenic stressors. In the tropics, warm-adapted amphibians and reptiles (typically lowland species) fare better after deforestation than do their cool-adapted counterparts (Frishkoff *et al.*, 2015). In the aftermath of radiation exposure at Chernobyl, birds with eumelanin-based coloration (in contrast to pheomelanin-based coloration) persisted in the face of radiation exposure. Pheomelanin-based coloration led to greater population declines because creating pheomelanin pigments requires antioxidants that are depleted by radiation (Galván *et al.*, 2011). Sensitivity in amphibians to copper sulphate, a common pesticide, shows a strong phylogenetic signal, indicating that evolutionary history is playing a key role in this interaction (Chiari *et al.*, 2015).

Physiological adaptations may be particularly important in mountain ecosystems that are experiencing climate change at a rate higher than the global average (IPCC, 2007). Species' ranges often shift to higher altitudes in response to climate change (Chen *et al.*, 2011). However, at particularly high elevations, such as in the Himalayas, high elevation hypoxia may prevent species from moving higher. While plasticity is known to play a role in hypoxia tolerance (Cheviron *et al.*, 2008, 2014), genetic adaptations have been found in all Himalayan vertebrates studied to date (Solari and Hadly, n.d.; Yi *et al.*, 2010; Scott *et al.*, 2011; Qiu *et al.*, 2012; Cho *et al.*, 2013; Li *et al.*, 2013; Gou *et al.*, 2014; Guan *et al.*, 2014; Zhang *et al.*, 2014), indicating a specialization required to inhabit high-elevation environments. In pikas (genus *Ochotona*), only species occupying the highest elevations are adapted to use oxygen more efficiently; a lack of such adaptations may inhibit altitudinal range shifts in lower-elevation species (Solari and Hadly, n.d.). In mountain ecosystems, it is thus possible that only species whose evolutionary history exposed them to hypoxic conditions will persist.

Other species are incidentally pre-adapted physiologically to withstand invasives. In Australia, keelback snakes (*Tropidonophis mairii*) display a physiological tolerance to the toxin in the invasive cane toad, due to a co-evolutionary history with bufonids in Asia (Llewelyn *et al.*, 2011). Some populations of omnivorous bluetongue skink in Australia (*Tiliqua scincoides*) are also resistant to the cane toad toxin because they had previously evolved resistance to a similar toxin in an invasive Malagasy plant (*Bryophyllum* spp.) (Price-Rees *et al.*, 2012).

Fortuitous morphology

Chance pre-adaptations in the form of morphology can lead to better avoidance of 'inadvertent predators' such as automobiles: swallows (*Petrochelidon pyrrhonotaI*) with short manoeuvrable wings are less likely to be hit by cars than less manoeuvrable birds (Brown and Bomberger Brown, 2013). Other morphological traits, such as body size, show countervailing trends across organisms in terms of which morphologies are favoured in anthropogenic landscapes (Henle *et al.*, 2004). Large-bodied amphibians tend to do better in human-modified habitats, presumably because they are more resistant to desiccation than their smaller counterparts, which have larger surface area to volume ratios (Mendenhall *et al.*, 2014). Populations of large-bodied mammals are especially threatened because low population densities, slow population growth rates, and the need for large home ranges put them at greater risk from human exploitation (Cardillo *et al.*, 2005). Similarly, bird families with large body size and slow life history are more impacted by direct human exploitation and introduced predators (Owens and Bennett, 2000). Whatever constellation of traits allows species to survive anthropogenic impacts, many of these traits were laid down in deep evolutionary time.

Pre-adapted clades

Some avian feeding guilds often benefit from habitat conversion: granivorous species are pre-adapted to exploit much of human agriculture (Karp *et al.*, 2011; Newbold *et al.*, 2013), and in periods of warming and drying climates, granivorous rodent species persist because their seed food source is likely to last longer both aboveground and in their underground food caches (Terry *et al.*, 2011). In Costa Rica, more recently evolved bird species seem to be predisposed to do better in human-modified agricultural habitats while species on the oldest branches of the bird phylogeny are prone to fare particularly poorly. This may be because these younger species evolved during the last glacial period when the Neotropics were dominated by grasslands, a habitat that shares many characteristics with human-modified agriculture (Frishkoff *et al.*, 2014). Conversely, in Brazil, it is the more basal amphibian clades that are positively impacted by climate change and the younger clades that are negatively impacted (Loyola *et al.*, 2014). However, this is also an example of the benefits of generalism, as these older clades are believed to be favoured due to less specialized habitat requirements and reproductive modes than the younger clades (Loyola *et al.*, 2014).

The threatened status of the world's mammals displays a strong phylogenetic signal for species threatened by harvesting (direct exploitation), more so than habitat change or invasive species (Fritz and Purvis, 2010). The risk of harvesting is closely linked to traits with a strong phylogenetic signal such as body size or reproductive rate (Bodmer *et al.*, 1997; Owens and Bennett, 2000; Fritz and Purvis, 2010). Similarly, in amphibians, four families (Rheobatrachidae, Leptodactylidae, Bufonidae, and Ambystomatidae) show much stronger declines than the average (Stuart *et al.*, 2004). However, in this case, some families are more impacted by overexploitation while others are more impacted by habitat loss (Stuart *et al.*, 2004). These numerous examples of phylogenetic signal show that a shared evolutionary history can result in related taxa sharing the same degree of extinction risk.

Evolutionary history of a community

In other cases, how a species will weather the Anthropocene seems to depend not only on its (or its clade's) evolutionary history, but also on the evolutionary history of the larger community. Diverse co-evolved communities saturated with species are better at staving off invasions than communities with unoccupied niche space. The colonization of *Anolis* on Caribbean islands is especially high on isolated, small, species-depauperate islands where *in situ* diversification had not occurred (Losos and Schluter, 2000; Helmus *et al.*, 2014). In this case, invasive species flourished only where native communities were less rich, and ample ecological opportunity still remained.

Similar processes may account for the high rates of extinction of island endemic birds (Blackburn *et al.*, 2004). Rates are highest on remote islands where species evolved in the absence of predators or invasive species prior to human colonization (Blackburn *et al.*, 2004). Prey naiveté is evident in many terrestrial and aquatic systems where prey have not been exposed to a certain predator type in their evolutionary past (Cox and Lima, 2006). Additionally, a lack of predators in a community represents an ecological opportunity that an invasive species can exploit. The establishment of the brown tree snake (*Boiga irregularis*) on Guam in the 1950s was successful partly because other predators were absent; its presence led to a significant loss in bird, mammal, and reptile diversity such that only a few small, native lizards are found in the island's forested areas today (Fritts and Rodda, 1998). The presence of other invasives also has a profound effect on the establishment capabilities of later arrivals. On Guam, introduced prey species such as *Anolis carolinensis* served as an additional food source for the brown tree snake, which likely would have gone extinct after devastating populations of native species. In many cases, introduced species have co-evolutionary histories with introduced predators and are thus able to live in higher abundances than their native counterparts. The presence of more resistant introduced prey can in turn facilitate the persistence of the invasive predator (Pimm, 1987; Fritts and Rodda, 1998). Prey naiveté can also facilitate the persistence of an invasive predator. In Spain, amphibian tadpoles are able to recognize and respond to chemical cues from native endangered predatory freshwater turtles (the European pond turtle, *Emys orbicularis*, and the Spanish terrapin, *Mauremys leprosa*) but not the invasive red-eared slider (*Trachemys scripta elegans*). In this case, prey naiveté may facilitate the success of the invasive turtle and ultimate decline of the native species (Polo-Cavia *et al.*, 2010).

CONCLUSION

Our review identifies several areas that will benefit from further empirical research and theoretical investigation. We were unable to find case studies demonstrating that plasticity or generalism help organisms resist the impacts of direct interactions/exploitation, or that maintaining high genetic diversity helps to avoid the negative effects of invasive species (Fig. 4). These trends may be a side effect of a lack of research effort in these specific areas (Fig. 3). We were also unable to link resistance to pollution to most of the characteristics (Fig. 4). Pollution may represent a unique challenge that is particularly hard for organisms to tolerate or avoid. Additionally, some characteristics lack evidence from certain

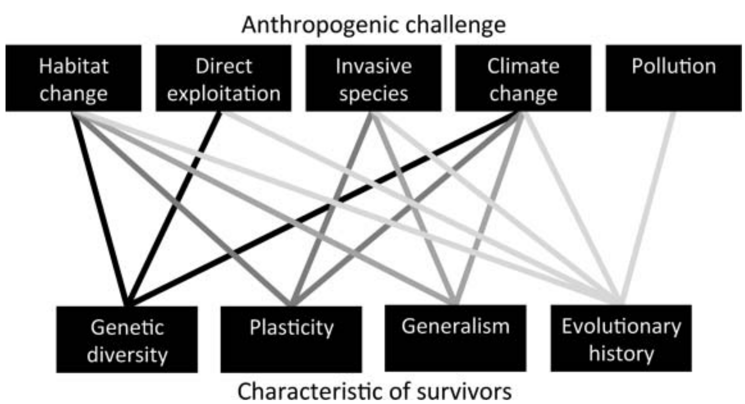

Fig. 4. Characteristics of survivors and the anthropogenic challenges that those characteristics help overcome. Lines joining characteristics and challenges indicate connections for which examples are given in the text.

tetrapod groups, perhaps again indicating areas of limited research effort. We found no relevant examples of genetic diversity improving persistence in birds or generalism reducing extinction risk in reptiles.

The Anthropocene presents an array of novel and abrupt challenges for species on Earth. Qualities that offer species a larger toolkit with which to meet the challenges of human impacts, such as the ability to maintain high levels of genetic diversity, phenotypic and behavioural plasticity, and broad ecological niches may confer survival advantages. Similarly, qualities that pre-adapt species through a serendipitous evolutionary history also confer survival advantages. Based on our literature review: (1) the trends most consistent across taxa are plasticity, which buffers the otherwise negative impacts of climate change and invasive species, and generalism, which benefits species threatened with habitat change (Table 1); (2) evolutionary history may be particularly valuable in evaluating species risk, as this characteristic can be linked to resistance to every challenge considered (Fig. 4); (3) genetic diversity is positively associated with species persistence in some cases, but the evidence for this is weak; and (4) few attributes arm tetrapods to withstand pollutants in the environment.

While it may be impossible to predict exactly which populations, species, clades or communities will survive in the Anthropocene, we can use insights from existing 'winners' to formulate predictions of how a species will respond to humanity's influence on the Earth. Such information will be increasingly vital to the design of effective conservation strategies as we endeavour to sustain biodiversity and its ecological dynamics in this new, human-dominated era.

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