



ELSEVIER

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Perspective

Scientists' warning to humanity on insect extinctions

Pedro Cardoso^{a,*}, Philip S. Barton^b, Klaus Birkhofer^c, Filipe Chichorro^a, Charl Deacon^d, Thomas Fartmann^e, Caroline S. Fukushima^a, René Gaigher^d, Jan C. Habel^f, Caspar A. Hallmann^g, Matthew J. Hill^h, Axel Hochkirch^{i,j}, Mackenzie L. Kwak^k, Stefano Mammola^{a,l}, Jorge Ari Noriega^m, Alexander B. Orfinger^{n,o}, Fernando Pedraza^p, James S. Pryke^d, Fabio O. Roque^{q,r}, Josef Settele^{s,t,u}, John P. Simaika^{v,w}, Nigel E. Stork^x, Frank Suhling^y, Carlien Vorster^d, Michael J. Samways^d

^a Laboratory for Integrative Biodiversity Research (LIBRe), Finnish Museum of Natural History (LUOMUS), PO17 (Pohjoinen Rautatiekatu 13), 00014, University of Helsinki, Finland

^b Fenner School of Environment & Society, Australian National University, Canberra, ACT 2601, Australia

^c Department of Ecology, Brandenburg University of Technology Cottbus-Senftenberg, Cottbus, Germany

^d Department of Conservation Ecology and Entomology, Stellenbosch University, South Africa

^e Department of Biodiversity and Landscape Ecology, Osnabrück University, Barbarastrasse 11, D-49076 Osnabrück, Germany

^f Evolutionary Zoology, Department of Biosciences, University of Salzburg, Salzburg, Austria

^g Institute for Water and Wetland Research, Radboud University, Heijendaalseweg, 135-6525 AJ Nijmegen, the Netherlands

^h School of Applied Sciences, University of Huddersfield, Huddersfield HD1 3DH, UK

ⁱ Trier Centre for Biodiversity Conservation, Department of Biogeography, Trier University, Universitätsring 15, D-54296 Trier, Germany

^j IUCN SSC Invertebrate Conservation Committee, Universitätsring 15, D-54296 Trier, Germany

^k Department of Biological Science, National University of Singapore, 16 Science Drive 4, 117558, Singapore

^l IRSA-Water Research Institute, National Research Council, Verbania, Italy

^m Laboratorio de Zoología y Ecología Acuática (LAZOE), Universidad de los Andes, Bogotá, Colombia

ⁿ Center for Water Resources, Florida A&M University, Tallahassee, FL 32307, USA

^o Department of Entomology and Nematology, University of Florida, Gainesville, FL 32611, USA

^p Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

^q Bioscience Institute, Federal University of Mato Grosso do Sul, Cidade Universitária, s/n, 79060-300 Campo Grande, MS, Brazil

^r Centre for Tropical Environmental and Sustainability Science (TESS), James Cook University, Cairns, QLD 4878, Australia

^s Helmholtz Centre for Environmental Research, UFZ, Department of Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany

^t German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

^u Institute of Biological Sciences, University of the Philippines Los Baños, College, 4031, Laguna, Philippines

^v Department of Water Science and Engineering, IHE Delft, 2611 AX, the Netherlands

^w Department of Soil Science, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa

^x Environmental Futures Research Institute, School of Environment and Science, Griffith University, Nathan, QLD 4111, Australia

^y Institute of Geocology, Department Landscape Ecology and Environmental Systems Analysis, Langer Kamp 19c, D-38106 Braunschweig, Germany



ARTICLE INFO

Keywords:

Arthropods
Biodiversity loss
Centinelan extinctions
Drivers of extinction
Ecosystem services
Threatened species

ABSTRACT

Here we build on the manifesto 'World Scientists' Warning to Humanity, issued by the Alliance of World Scientists. As a group of conservation biologists deeply concerned about the decline of insect populations, we here review what we know about the drivers of insect extinctions, their consequences, and how extinctions can negatively impact humanity.

We are causing insect extinctions by driving habitat loss, degradation, and fragmentation, use of polluting and harmful substances, the spread of invasive species, global climate change, direct overexploitation, and co-extinction of species dependent on other species.

With insect extinctions, we lose much more than species. We lose abundance and biomass of insects, diversity across space and time with consequent homogenization, large parts of the tree of life, unique ecological functions and traits, and fundamental parts of extensive networks of biotic interactions. Such losses lead to the decline of key ecosystem services on which humanity depends. From pollination and decomposition, to being resources for new medicines, habitat quality indication and many others, insects provide essential and irreplaceable services. We appeal for urgent action to close key knowledge gaps and curb insect extinctions. An investment in research

* Corresponding author at: Finnish Museum of Natural History (LUOMUS), PO17 (Pohjoinen Rautatiekatu 13), 00014, University of Helsinki, Finland.

E-mail address: pedro.cardoso@helsinki.fi (P. Cardoso).

<https://doi.org/10.1016/j.biocon.2020.108426>

Received 15 November 2019; Received in revised form 27 December 2019; Accepted 19 January 2020

Available online 09 February 2020

0006-3207/ © 2020 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license

(<http://creativecommons.org/licenses/by/4.0/>).

programs that generate local, regional and global strategies that counter this trend is essential. Solutions are available and implementable, but urgent action is needed now to match our intentions.

1. Introduction

Insect extinctions, their drivers, and consequences have received increasing public attention in recent years. Media releases have caught the interest of the general public, and until recently, we were largely unaware that insects could be imperilled to such an extent, and that their loss would have consequences for our own well-being. Fuelled by declining numbers from specific regions (Hallmann et al., 2017, 2020; Lister and Garcia, 2018; Powney et al., 2019; Seibold et al., 2019; and many other studies), concern over the fate of insects has gained traction in the non-scientific realm.

Current estimates suggest that insects may number 5.5 million species, with only one fifth of these named (Stork, 2018). The number of threatened and extinct insect species is woefully underestimated because of so many species being rare or undescribed. For example, the IUCN Red List (version 2019-2) only includes ca. 8400 species out of one million described, representing a possible 0.2% of all extant species (IUCN, 2019). However, it is likely that insect extinctions since the industrial era are around 5 to 10%, i.e. 250,000 to 500,000 species, based on estimates of 7% extinctions for land snails (Régnier et al.,

2015). In total at least one million species are facing extinction in the coming decades, half of them being insects (IPBES, 2019).

It is not only their vast numbers, but the dependency of ecosystems and humanity on them, that makes the conservation of insect diversity critical for future generations. A major challenge now and in the coming years is to maintain and enhance the beneficial contributions of nature to all people. Insects are irreplaceable components in this challenge, as are other invertebrates and biodiversity in general.

Here we build on the manifesto World Scientists' Warning to Humanity, issued by the Union of Concerned Scientists (1992) and re-issued 25 years later by the Alliance of World Scientists (Ripple et al., 2017). The latter warning was signed by over 15,000 scientists and claims that humans are "pushing Earth's ecosystems beyond their capacities to support the web of life." (<https://www.scientistswarning.org/the-warning/>). As a group of conservation biologists deeply concerned about the decline of insect populations worldwide, we here review what we know about the drivers of insect extinctions, their consequences, and how extinctions can negatively impact humanity. We end with an appeal for urgent action to decrease our knowledge deficits and curb insect extinctions.

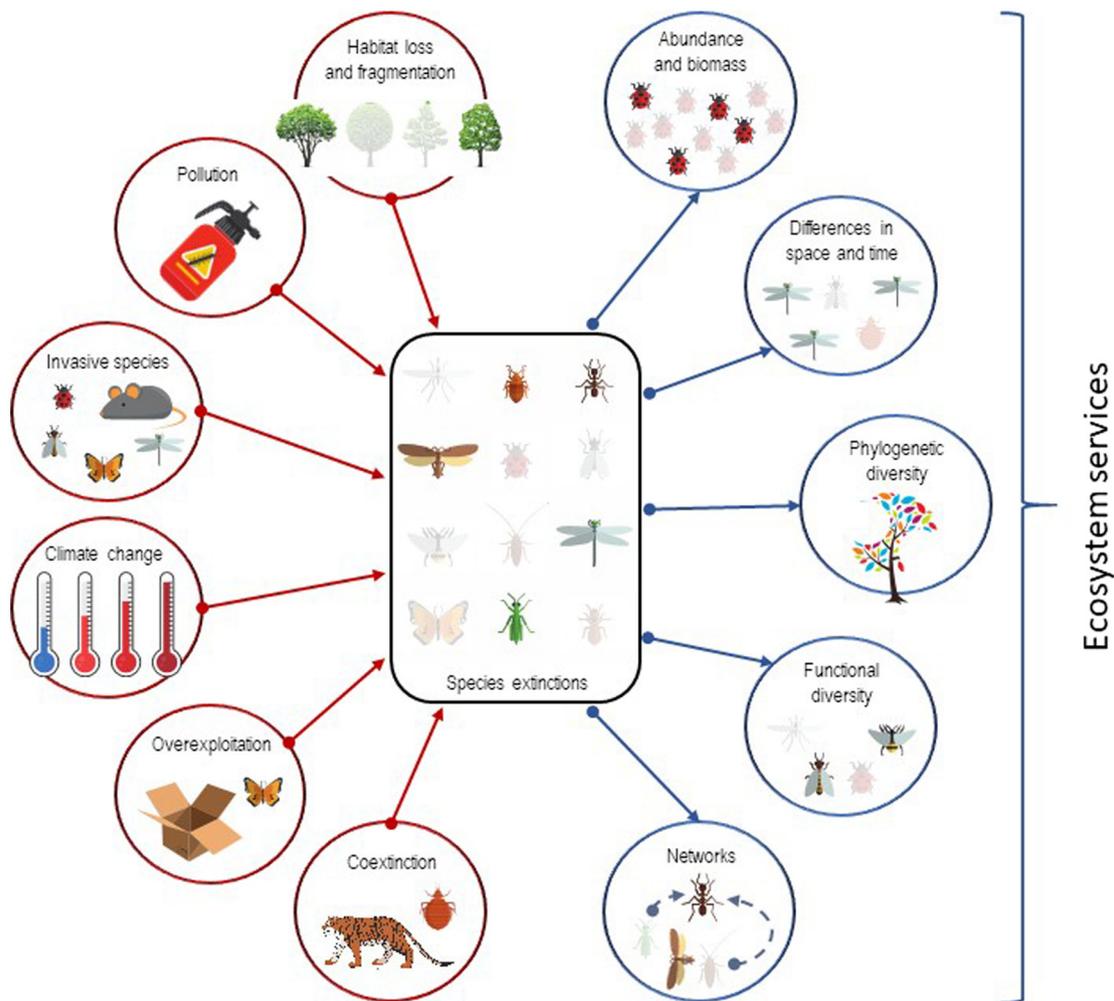


Fig. 1. Drivers (in red) and consequences (in blue) of insect extinctions. Note that drivers often act synergistically or through indirect effects (e.g., climate change favours many invasive species and the loss of habitat). All these consequences contribute to the loss of ecosystem services essential for humans (see Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. We are causing insect extinctions

Irrespective of the precise trends and their spatial distribution, human activity is responsible for almost all current insect population declines and extinctions. Yet, in order to act, we first need to identify and quantify the different ways we are acting upon them, recognizing that much is still to be understood, and more often than not, several factors contribute synergistically to decline or extinction (Fig. 1).

2.1. Habitat loss and fragmentation

Habitat loss, degradation, and fragmentation are probably the most relevant threats to biodiversity (Foley et al., 2005; Dirzo et al., 2014; Habel et al., 2019a). Globally, 50% of endemic species of plants and vertebrates are restricted to some 36 biodiversity hotspots covering just 2.5% of the Earth's surface (Mittermeier et al., 2004) and arguably, these hotspots likely harbour similar percentages of endemic insect species (Stork and Habel, 2014). Recent modelling suggests that agro-economic pressure for land will reduce the currently very restricted natural intact vegetation by a further 50% by 2050 in one third of the world's hotspots (Habel et al., 2019b). Processes associated with deforestation, agricultural expansion, and urbanization are the proximate drivers of loss of natural or semi-natural habitats and their insect assemblages across the world (Brook et al., 2003; Basset and Lamarre, 2019; Habel et al., 2019c). Mining is particularly relevant for subterranean species, which are often spatially restricted (Mammola et al., 2019a). Freshwater habitats additionally suffer from river flow regulation and damming (Dudgeon et al., 2006). Increased siltation in rivers and streams from agricultural runoff (Wood and Armitage, 1997; and references therein), as well as flow regulation, degrade habitats of typical stream dwelling insect larvae (Jones et al., 2012). There is also a significant loss of pond ecosystems largely due to agricultural land drainage and urban development (e.g., Boothby and Hull, 1997; Wood et al., 2003).

Habitat loss is often accompanied by habitat fragmentation, and both lead to decreasing connectivity (Fischer and Lindenmayer, 2007; Fletcher Jr. et al., 2018). However, depending on the mobility of the insect species and the degree of habitat fragmentation their relative importance varies. Insects with low mobility may survive in isolated populations (e.g., many flightless Orthoptera; Poniatowski and Fartmann, 2010; Poniatowski et al., 2018). In contrast, many species with a higher mobility – such as butterflies – usually form metapopulations (Hanski, 1999). They depend on a network of suitable habitat patches of sufficient size and in spatial proximity (Eichel and Fartmann, 2008; Stuhldreher and Fartmann, 2014). However, in less fragmented landscapes – even among metapopulation species – habitat connectivity usually plays a minor role for patch occupancy. Here habitat quality is the main driver of insect species occurrence (Krämer et al., 2012; Poniatowski et al., 2018; Münsch et al., 2019). In these times of global warming, habitat connectivity becomes increasingly important for all insect survival. This is because insect range shifts in response to climate change are often constrained by insufficient habitat connectivity in fragmented landscapes (Platts et al., 2019), and so lag behind the increase in temperature, even for mobile species (Devictor et al., 2012; Termaat et al., 2019).

2.2. Pollution

Pesticides are key drivers of insect declines due to their intensive use, as well as inappropriate risk assessment regulations (Brühl and Zaller, 2019). Pesticides impact insect populations via direct toxicity and sub-lethal effects (mainly insecticides), and indirectly through habitat alteration (mainly herbicides). Bioaccumulation, due to chronic exposure and biomagnification along food chains, pose significant additional threats for insect populations (Hayes and Hansen, 2017) that can have undetected harmful effects on insect physiology and

behaviour (Desneux et al., 2007).

Many fertilizers (including organic and mineral fertilizers) widely used in agriculture, can affect insect populations indirectly, via impacts on the composition or quality of plant resources, on structural habitat properties or causing soil acidification, and through eutrophication (Fox, 2013; Villalobos-Jiménez et al., 2016). Effects of high-levels of fertilizer use can be positive for a few herbivorous insects in agroecosystems (e.g., aphids; Kytö et al., 1996), but have negative effects on most insects (Kurze et al., 2018; Habel et al., 2019a). Also, the use of anthelmintic substances (e.g. Ivermectin) in livestock systems has a negative impact on the abundance and richness of insects associated with dung decomposition (Verdú et al., 2018).

Industrial pollution (including air pollution, chemicals from factories or mining operations, and heavy metals) also causes insect population declines (Zvereva and Kozlov, 2010). Similar to pesticides, sub-lethal negative effects on individuals, and biomagnification along food chains, add further threats to insect populations (Gall et al., 2015). Several economically important insect species (such as pollinators or natural enemies of pests) may be threatened by chronic exposure to pollutants (e.g., heavy metals), but community-wide effects are often not well understood (Skaldina and Sorvari, 2019). Freshwater invertebrates (including several insect taxa) are disproportionately affected by pollution, with over 41% of species on the IUCN Red List threatened by water pollution (Darwall et al., 2012). Industrial discharge, sewage, and agricultural and urban run-off as well as increased sediment deposition, all reduce freshwater habitat quality (Jones et al., 2012).

Light and noise pollution are becoming increasingly pervasive globally (Morley et al., 2014; Gaston, 2018; Owens and Lewis, 2018), and gaining a better understanding of these novel impacts is critical. Nocturnal insects are especially vulnerable to changes in natural light/dark cycles. Light pollution interferes with insects that use natural light (from the moon or stars) as orientation cues for navigation and with communication of insects that use bioluminescent signals, such as fireflies. It desynchronizes activities triggered by natural light cycles, such as feeding and egg-laying, and causes temporal mismatches in mutualistic interactions (Owens and Lewis, 2018). Noise pollution greatly changes the acoustic landscape and interferes with acoustic communication of insects and their auditory surveillance of the environment, having significant fitness costs (Morley et al., 2014). Finally, the effects of electromagnetic pollution on insects and other life-forms, including humans, are still very badly understood and deserve further exploration (Thielens et al., 2018).

2.3. Invasive species

Invasive alien species (IAS) are anthropogenically introduced species to locations outside of their natural geographical range, which have a demonstrable environmental, ecological, or socio-economic effect (Turbelin et al., 2017). Impacts may be direct (e.g., through predation, competition, or disease vectoring) and/or indirect (e.g., through trophic cascades, co-extinction of herbivore or parasitoid hosts). Species introductions may ultimately lead to local loss of native insects, with those exhibiting narrow geographic distributions or specialist feeding habits being most vulnerable (Wagner and Van Driesche, 2010).

Direct competition by non-native species can drive local populations towards extinction (Williamson and Griffiths, 1996; Sala et al., 2000; Havel et al., 2015). The degree of ecological overlap with the invasive ladybird, *Harmonia axyridis* Pallas, 1773, was a main predictor for local extinctions of endemic ladybird fauna in Britain (Comont et al., 2014). Invasive ants (e.g. the Argentine ant, *Linepithema humile* Mayr, 1868) are perhaps the best example of IAS that challenge native insect fauna. Due to their large numbers and generalist predatory behaviour, many invasive ant species are primary threats to native insects (see Wagner and Van Driesche, 2010). The invasive amphipod *Dikerogammarus villosus* (Sowinsky, 1894) kills significantly greater numbers of aquatic

invertebrates than native amphipods, reducing invertebrate diversity and displacing native amphipod species (Dick et al., 2002; Rewicz et al., 2014).

The high biomass and dense structure of invasive plants often has a major impact on insect communities (Strayer, 2010). The monotypic nature of invasive plants reduces the quantity and/or quality of food, and leads to declines in essential resources for many insects (Severns and Warren, 2008; Preston et al., 2012; Havel et al., 2015). Additionally, invasive plants can change matrix composition, adversely affecting insect host-parasitoid relationships (Cronin and Haynes, 2004). Invasive plants may also provide eco-evolutionary traps for native insects. Once an invader has outcompeted and displaced native hosts, it may act as a host that results in poor larval development, or increased larval mortality (Sunny et al., 2015), leading to insect population decline.

Invasive pathogens can also lead to native insect extinctions. European strains of the fungal pathogen, *Nosema bombi*, are thought to have resulted in the widespread collapse of North American bumblebees (Cameron and Sadd, 2020). Furthermore, the introduced bumblebee *Bombus terrestris* L., 1758 has caused the disappearance of the Patagonian bumblebee, *B. dahlbomii* Guérin-Méneville, 1835, across much of its native range, either due to direct competition or the introduction of pathogens to which the native species have no defences (Cameron and Sadd, 2020).

2.4. Climate change

Climate change poses threats to insects and the ecosystems they depend on, whether terrestrial (Burrows et al., 2011), freshwater (Woodward et al., 2010) or subterranean (Mammola et al., 2019b). The complexity of global climate change goes far beyond simply global temperature increase (Walther et al., 2002; Ripple et al., 2019). It also leads to a variety of multifaceted ecological responses to environmental changes, including shifts in species distribution ranges (Chen et al., 2011), phenological displacements (Forrest, 2016), novel interactions among previously isolated species (Krosby et al., 2015), extinctions (Dirzo et al., 2014), and other unpredictable cascading effects at different levels of ecosystem organisation (Peñuelas et al., 2013). Changes in species phenology, distributions, reduction in body size, assemblage structure, and desynchronization of species-specific interactions are all linked to climate change (Scheffers et al., 2016). For example, some British butterflies are emerging earlier than previously recorded, and in some cases, before their nectar plants have flowered (Roy and Sparks, 2000). In addition, changes in functional feeding group diversity can be associated with changes in trophic interactions in food webs (Jourdan et al., 2018).

Aquatic insects are disproportionately affected by climate change, due to the synergistic negative effects on freshwater ecosystems overall (Reid et al., 2019), and these insects having limited dispersal capacity, as well as them confronting barriers to their dispersal, particularly at higher elevations (Bush et al., 2013). There is a need for the development and implementation of bioindicators, and dragonflies are emerging as taxonomic champions for aquatic ecosystems (Chovanec et al., 2015; Dutra and De Marco, 2015; Valente-Neto et al., 2016; Vorster et al., 2020). Bush et al. (2013) dubbed dragonflies as 'climate canaries', with dragonfly species assemblages being three times more sensitive to climate variables than macroinvertebrate assemblages at family level. While there is evidence that water quality improvements have offset recent climatic debt for stream macroinvertebrates (Vaughan and Gotelli, 2019), this continued mitigation is not likely to reverse or even halt trends in aquatic insect species declines.

2.5. Overexploitation

Though rarely considered, overexploitation may play a role in insect decline for many groups. It primarily threatens free-living insects and

includes unsustainable harvesting for use as pets and decoration (as souvenirs and jewels), or as food resources and traditional medicine. Various insects are kept as pets, but they are especially popular in Japan, where there are many illegally traded insects (Actman, 2019). Ants maintained in commercial farms are probably the most common pet insect in USA, but field crickets, praying mantids, antlions, caterpillars, and mealworms are also reported worldwide as household pets (Smithsonian, 2019).

Ornamental insects as preserved decorations are also numerous, particularly regarding Lepidoptera and Coleoptera. Coloured wings and elytra are used in jewellery, embroidery, and pottery (Prasad, 2007; Lokeshwari and Shantibala, 2010). In regions where market demand is high, ornamental insects are frequently imported in large numbers (Kameoka and Kiyono, 2003), which fuels an illegal export industry in areas where high-demand insects occur naturally (Kameoka and Kiyono, 2003; New, 2005). Unsurprisingly, this demand for ornamental insects has driven declines of sought-after species (Tournant et al., 2012; Huang, 2014).

Entomophagy is another driver of overexploitation (Morris, 2004; Schabel, 2006). A worldwide inventory listed 2111 edible insect species (Jongema, 2017), with number of collected individuals often exceeding regeneration capacity (Cerritos, 2009). Wild populations are threatened because collection practices became less selective and sustainable (Illgner and Nel, 2000; Latham, 2003; Ramos-Elorduy, 2006), due to the dissipation of indigenous knowledge, which often includes the sustainable use of edible insects and their habitat (Kenis et al., 2006). In many subsistence societies, insects provide protein supplements and can constitute nearly a third of total protein intake during periods of meat protein shortage (Dufour, 1987).

The overexploitation of insects as alternative medicine also poses a risk. Demand for the hundreds of insect species that are used in such practices is reportedly threatening insect biodiversity (Feng et al., 2009). The commercial value of products based on medicinal insects comprises about US\$100 million per year (Themis, 1997).

2.6. Co-extinction

Specialisation has led to many insects becoming co-dependent, and therefore, vulnerable to co-extinction (Dunn, 2005; Dunn et al., 2009). Among these, numerous insect lineages have diversified with vertebrates, either as parasites, epizoic mutualists, or commensal coprophages. At least 5000 louse (Phthiraptera) species have been described, of which most (~4000) use avian hosts (Price et al., 2003; Smith et al., 2011). About 2500 flea species are recognised (Whiting et al., 2008) and > 6000 species of dung beetles are named (Schoolmeesters, 2019). Numerous insect lineages have also diversified with invertebrate hosts. Insects of the order Strepsiptera (twisted-wing insects) are obligate parasites of other insects, and > 600 species have been described, though they are dwarfed by the parasitic wasps, which are estimated to include as many as 350,000 species (Gaston, 1991). Insects co-dependent on plants are also extremely species rich, with gall-inducing insects alone comprising as many as 211,000 species (Espírito-Santo and Fernandes, 2007). Similarly, mycophagous insects are extremely diverse and often co-dependent on a few fungal hosts (Wertheim et al., 2000).

Co-dependent insects are greatly at risk of extinction through their specialised ecologies (Dunn, 2005; Dunn et al., 2009), even though examples of co-extinctions are rare (Colwell et al., 2012). Models suggest that co-extinction events should be far more common (especially among plant-dependent beetles and bird lice) than present records suggest (Koh et al., 2004a). This is either because of co-extinction events are poorly recorded, or due to unrecognised network resilience owing to the ability of co-dependent insects being able to use many more species than previously assumed (Colwell et al., 2012).

In the case of co-dependent insects, trophic cascades can be particularly relevant (Strona and Bradshaw, 2018). Host species are lost due

to habitat loss, as has been shown in Lepidoptera-host plant systems (Pearse and Altermatt, 2013). A historical example of indirect effects of invasive species is the co-extinction of Christmas Island flea (*Xenopsylla nesiotus* Jordan & Rothschild, 1909), resulting from loss of the Christmas Island rat (*Rattus macleari* Thomas, 1887) due to the introduced black rat (*Rattus rattus* L., 1758) (Kwak, 2018). There is evidence that decline of mammals due to synergistic causes (climate change, habitat destruction, hunting, etc.) lead to a pervasive co-decline of dung beetles at continental scales (Bogoni et al., 2019). The overexploitation of birds by the pet trade also threatens their dependent insects (Eaton et al., 2015).

3. We lose much more than species

All species, including insects, are valuable as unique combinations of evolutionary events, have innate value, and so require care and conservation. Yet, as George Orwell put it in *Animal Farm*, “All animals are equal, but some animals are more equal than others.”, with invertebrates being largely neglected in conservation efforts worldwide (Cardoso et al., 2011), the so-called “institutional vertebratism” (Leather, 2013). There is no reason why an insect species deserves much less attention than a bird or mammal species. However, the importance of insect population declines and consequent extinctions goes way beyond loss of species and their intrinsic value.

Each species represents individuals, biomass, and functions being lost, and therefore not available for other living beings. Each species contributes a unique piece to a complex living tapestry that changes in space and time. Each species represents an unrepeatably part of the history of life. In turn, each species also interacts with others and their environment in distinctive ways, weaving a complex network that sustains other species, including us (Fig. 1).

3.1. Abundance and biomass

Hallmann et al. (2017) documented a loss of biomass of flying insects of about 75% over 30 years. This negative trend occurred in nature reserves in Germany. These results are a warning and stimulated an intense debate on the insect crisis. Also, in other parts of Germany, declining abundances and biomass for a broader set of arthropods have been recorded (Seibold et al., 2019). Similar trends have been recorded for other parts of Europe. Large declines in abundance have also occurred among UK butterflies and moths (Conrad et al., 2004, 2006; Thomas et al., 2004; Shortall et al., 2009; Fox, 2013; Knowler et al., 2016; Storkey et al., 2016), dragonflies (Clausnitzer et al., 2009) and carabid beetles (Brooks et al., 2012) in recent years. Negative trends are not restricted to Europe, but also occur in other parts of the world (Wagner, 2019). A global meta-analysis of insect abundances revealed a 45% decline across two-thirds of the taxa evaluated (Dirzo et al., 2014). Yet, the specific trend and strength of the decline or eventual increase is not universal and changes according to taxon and region (Macgregor et al., 2019).

Declines in insect abundance and biomass always precede species extinctions, as this is a continuous, not binary, process. Although critically dependent on the ecological role of the species, numerical loss in abundance, and by extension, biomass, reflect impairment of ecological function and provisioning of ecosystem services. For example, biomass is a measurement of the amount of energy flowing through trophic levels that insects represent. In turn, reduced abundance and biomass affects ecosystem functionality and resilience, food web structure, and species interactions, such as plant-pollinators, population persistence, and many ecosystem services (Biesmeijer et al., 2006; Losey and Vaughan, 2006).

These studies highlight numerical declines in abundance and biomass at the landscape level, but also inform us that declines are not restricted to rare and endangered species only, but are also present for more abundant species (Habel and Schmitt, 2018; Hallmann et al.,

2020). While insect conservation often target charismatic, rare, or threatened species, the temporal and spatial trends of common and widespread species are often overlooked (Gaston, 2011). Numerical declines of common and widespread species impact the functioning of ecosystems more severely. As such, safeguarding ecosystem function may be suffering un-noticed, highlighting the need for insect monitoring and conservation beyond rare and threatened species.

3.2. Differences in space and time

Insects and most arthropods are relatively small organisms that often occupy small microhabitats. As we move horizontally across a seemingly homogenous patch, small features, such as dead wood, rocks, or even a single tree can alter conditions, leading to replacement of species and allowing higher richness to persist within the larger patch (Barton et al., 2009; Stagoll et al., 2012; Crous et al., 2013). Insects also partition themselves vertically, i.e. in a forest, we find soil, ground active, undergrowth, sub-canopy, and canopy species, all of which contribute to the hyper-diversity found in, for example, tropical rainforests (Stork et al., 2016). This way, insect assemblages tend to be composed of few very common and many rare species (Pachepsky et al., 2001; McGill et al., 2007), leading to high levels of beta-diversity. Such high levels of species turnover can be difficult to monitor, as research tends to describe overall arthropod richness and compositional changes driven by the common species. Given their nature, it is much harder to quantify how rare species are responding to anthropogenic pressures (van Schalkwyk et al., 2019).

Processes that homogenise natural systems decrease beta-diversity by removing rare species from the system. These pressures not only remove native species, but also simplify the system, reducing the diversity of resources and biological interactions. Furthermore, they allow secondary invasions from ecologically dominant alien invasive insects that outcompete or simply feed on the native fauna (Silverman and Brightwell, 2008; Roy et al., 2016; see section on invasive species). The edges of transformed areas, including linear structures such as roads, show large edge effects on beta-diversity. This suggests that the presence of dominant species, either native or alien, reduce niche space by outcompeting and effectively replacing rare species (Swart et al., 2019).

Insects do not just partition themselves across space, but also time. Tropical rainforest cicadas and bush-crickets call during different times of the day and night or at different frequencies to avoid overlap (Schmidt and Balakrishnan, 2015). At the other extreme are the periodic cicadas, which only emerge as adults every 13 or 17 years (prime numbers to avoid frequent overlap). One of the major concerns with global climate change is how warmer temperatures might be interfering with arthropod phenology. For example, a population of the 17-year cicada emerged after just 13 years in 2017 (Sheikh, 2017), which is most likely due to the alteration of host tree cycles (Karban et al., 2000).

3.3. Phylogenetic diversity

Phylogenetic diversity takes the evolutionary relationships between taxa into account and reflects the evolutionary history of each species. Communities with identical taxonomic diversity may differ widely with respect to their evolutionary past, depending on the time of divergence of species from their nearest common ancestor (Webb et al., 2002; Graham and Fine, 2008). Studying the effects of species extinction on the phylogenetic tree of life is therefore imperative and provides a complementary view to the loss of taxon diversity.

Insects constitute a major branch of the tree of life, representing ca. 480 million years of evolution (Misof et al., 2014). Preserving this phylogenetic diversity is crucial to protect the evolutionary trajectories of the most successful taxonomic group on our planet. Understanding the phylogenetic relationships among and within species is crucial to

avoid detrimental decisions in conservation management, such as neglecting populations with unique evolutionary histories (e.g., Price et al., 2007), (re-)introducing non-native species or mis-adapted evolutionary lineages (Moritz, 1999), or outbreeding depression in captive breeding projects (Witzemberger and Hochkirch, 2011).

Insects comprise many unique evolutionary lineages with some old relict groups, such as the Zoraptera, Mantophasmatodea, Mecoptera, or Grylloblattodea. Among the latter, the Kosu Rock Crawler (*Galloisiana kosuensis* Namkung, 1974) is listed as Critically Endangered on the IUCN Red List of Threatened Species (Chung et al., 2018). This species is only known from a single cave, whose temperature has risen by > 3 °C from increased tourism, reaching 1400 visitors per day. Another example is the Mauritian endemic grasshopper species *Pyrgacris relictus* Descamps, 1968, which belongs to a distinct family (Pyrgacrididae) with only two species. This species, which only feeds on an endemic palm species is Critically Endangered, and only known from a single locality, imperilled by construction of a golf course (Hugel, 2014). Loss of such distinct evolutionary branches of the tree of life is irreversible and leads to the loss of unique genetic diversity.

3.4. Functional diversity

Functional diversity quantifies the components of biodiversity that influence how an ecosystem operates or functions (Tilman et al., 2001) and reflects the amount of biological functions or traits displayed by species in given communities. Communities with completely different species composition may be characterized by low variation in functional traits, with phylogenetically unrelated species replacing others with similar functional roles (Villéger et al., 2012). The functional diversity and role of insects in maintaining ecological processes are issues of immense interest, and are particularly relevant to landscapes undergoing anthropogenic change and biodiversity loss (Ng et al., 2018). This is because functional diversity provides a direct link between biodiversity and ecosystem processes. Moreover, loss of particular traits can result in changes to key ecological processes promoted by insects, such as pollination (Saunders, 2018) and decomposition (Barton and Evans, 2017).

Table 1

Ecosystem services provided by insects.
(Adapted from Samways, 2019)

Type of service	Area	Provision		
Commercial	Provisioning services	Medicine	New treatments	
		Engineering	Biomimetics	
		Monitoring	Monitoring of habitat quality	
		Genetic resources	New chemicals	
		Ornaments	Insect houses and deadstock	
		Biocontrol	Biocontrol agents	
		Production	Food and fibre	
Non-commercial	Regulating services	Climate	Climate regulation	
		Disease control	Burial of dung or carcasses	
		Erosion	Limiting erosion	
		Invasion resistance	Controlling invasive species	
		Herbivory	Nutrient cycling	
		Natural hazards	Protection from hazards	
		Pollination	Reproduction of flowering plants	
	Supporting services	Plant dispersal	Seed dispersal of plants	
		Water flow	Regulating water movement	
		Water treatment	Purification by larvae	
		Nutrient cycling	Through saprophagy/coprophagy	
		Oxygen production	Through interaction with plants	
		Habitat creation	Building mounts, nests, and others	
		Soil formation	Breakdown of plants, dung and carcasses	
		Cultural services	Cultural heritage	Arts, myths, and stories
			Education	Connecting with nature
			Knowledge systems	Models for scientific research
	Recreation	Nature tourism		
	Sense of place	Endemic species		
	Spiritual values	Views on nature		

Threatened species are not a random subset of all the species. Threatened species tend to share biological traits that influence their extinction risk (Chichorro et al., 2019). In general, specialists in either habitat type or feeding regime, very small or very large species, and poor dispersers, are at highest risk. The decline of both habitat and resource specialist species has been documented for bees, beetles, butterflies, dragonflies, and moths (e.g., Kotze and O'Hara, 2003; Koh et al., 2004b; Bartomeus et al., 2013). Species with narrower habitat requirements have less ability to escape from multiple pressures. The resource specialists depend not only on their effective population size, but also on the availability of their resources. When organisms are dependent on only one resource type, co-extinctions might also be more likely to occur.

Demise of both large and the very small species occurs among vertebrates (e.g., Ripple et al., 2017). There are two main reasons explaining the demise of large species: 1) they usually require more resources and therefore exist at lower population densities than smaller species, which in turn increases the risk of local extinction due to unpredictable events; 2) they usually have traits related to slower life cycles and therefore respond slower to environmental change. On the other hand, smaller species often decline in greater proportions than larger ones, due to their lower competitive ability (Powney et al., 2015). However, small insects can be sensitive to fragmentation (Basset et al., 2015) and habitat loss (Jauker et al., 2013) due to poor dispersal ability.

3.5. Ecological networks

Insects are crucial in structuring and maintaining communities, forming intricate networks that can influence species' coevolution (Guimarães Jr. et al., 2017), coexistence (Bastolla et al., 2009), and community stability (Thébault and Fontaine, 2010; Rohr et al., 2014). Insect extinctions not only reduce species diversity, but also simplify networks, and we may be losing interactions at a higher rate than species (Tylianakis et al., 2008; Valiente-Banuet et al., 2015). The implications of these changes will depend on the role a species plays in the network (Bascompte and Stouffer, 2009; Tylianakis et al., 2010). The

more a species shapes a network, the more the architecture will change if it goes extinct. Furthermore, species conferring network structure are most at risk of going extinct (Saavedra et al., 2011). Thus, we should aim to preserve both species and their interactions (Tylianakis et al., 2010).

In mutualistic networks, plants and insects weave nested relations (Bascompte et al., 2003). This leads to specialists interacting with subsets of generalist interaction partners. Nested networks tend to mitigate random extinctions or the loss of specialists (Memmott et al., 2004). In this case, when species are lost, the structure remains. In contrast, the extinction of generalists erodes the nested architecture. In this case, the loss of focal species makes the system more prone to co-extinction cascades (Dunne et al., 2002).

In antagonistic networks, species form intertwined subgroups, where inter-module interactions are rare (Olesen et al., 2007). Connectors and network hubs are important contributors to the modular structure, with beetles, flies, and small bees being the most common connectors (Olesen et al., 2007). Alarming, some of these hub species are currently at risk of extinction (Sirois-Delisle and Kerr, 2018). They not only benefit interaction partners, but also give cohesion to the entire community. Their disappearance may result in the fragmentation of networks into isolated modules (Bascompte and Stouffer, 2009; Tylianakis et al., 2010). This endangers communities by making them more susceptible to perturbations (Olesen et al., 2007).

Interactions drive the coevolution of plants and insects (Bronstein et al., 2006). They can result in remarkable trait complementarity, as in the case of pollination or ant protection of plants (Bronstein et al., 2006). Yet, in complex networks, indirect effects steer the evolution of traits (Guimarães Jr. et al., 2017). In species-rich networks, all members influence how traits evolve in the community. This means that extinctions will affect direct partners, and can reduce community-wide trait integration. This could incapacitate entire communities from responding to environmental change.

4. We depend on insects

Insects contribute to the four main types of ecosystem services defined by the Millennium Ecosystem Assessment (2003): i) provisioning services, ii) supporting services, iii) regulating services, and iv) cultural services (Noriega et al., 2018; Table 1). This animal group contributes to the structure, fertility, and spatial dynamics of soil, and they are a crucial element for maintaining biodiversity and food webs (Schowalter et al., 2018). A large number of insects provide medical or industrial products (Ratcliffe et al., 2011), and globally, > 2000 insect species are consumed as food. Also, in agroecosystems, insects perform many different functions, such as pollination, nutrient and energy cycling, pest suppression, seed dispersal, and decomposition of organic matter, feces, and carrion (Schowalter et al., 2018). Today, the agricultural sector already actively uses insect antagonists of pests (classical and augmentative biological control) or establishes habitat management practices to promote insects as natural enemies of pests. In this context, as a clear consequence, insect declines can negatively affect the maintenance of food supply and put at risk human well-being.

All described services translate to monetary value. In an initial approach, Costanza et al. (1997) estimated a global value of ecosystem services at US\$33 trillion annually. Later, ecosystem services provided by insects were estimated to have a value of \$57 billion per year in the United States alone (Losey and Vaughan, 2006), and insect pollination may have an economic value of \$235–577 billion per year worldwide (IPBES, 2016). Additionally, the annual contribution of ecosystem services provided by dung beetles to the cattle industry can reach \$380 million in the USA (Losey and Vaughan, 2006) and £367 million in the UK (Beynon et al., 2015).

However, there is little knowledge on the functional roles that insects play in many ecosystems, with their values likely greatly underestimated. Absence of detailed information is related to lack of

manipulative controlled experiments for several services (Noriega et al., 2018). Also, the few comprehensive studies available are focused on a few iconic groups or functions, such as bees and pollination (e.g., Brittain et al., 2010), ground beetles and pest control (e.g., Roubinet et al., 2017), dung beetles and decomposition (e.g., Griffiths et al., 2016), or aquatic insects and energy flow (e.g., Macadam and Stockan, 2015). This critical shortfall must be addressed to conserve insect diversity for our own survival.

5. We need immediate action

The current extinction crisis is deeply worrisome. Yet, what we know is only the tip of the iceberg. We provide here numerous examples of the loss of species diversity and abundance, and their consequences, but these are some of the few well-documented examples. Most insect species are undescribed (possibly as many as 80%; Stork, 2018), and even for most of those with names we have no distributional or population trend data to record ongoing extinctions. Edward O. Wilson (1992) called for a Linnean Renaissance to fully document and appreciate what is out there, and where, especially as many insect species are going extinct even before being described (Centinela extinctions).

Despite the known threats and consequences of insect extinction, decision-makers and civil society are only now becoming aware of the scale of the problem. Conservation efforts have largely been focused on charismatic megafauna, especially birds and mammals, with little thought on ecosystem connectivity (Cardoso et al., 2011; Donaldson et al., 2016; Mammides, 2019). Even within insects, some taxa have been favoured, such as butterflies and, more recently, pollinators. Legislation and agreements in the US (Endangered Species Act) and Europe (Habitats Directive) clearly reflect such biases (Cardoso, 2012; Leandro et al., 2017). Partly to blame for these biases is a lack of capacity and data, which, in the view of policymakers, leads to a lack of funding, which in turn, feeds back into lack of capacity and data, in a continuous cycle.

Existing data on insect population trends and drivers have several problems (Cardoso and Leather, 2019), yet it is possible to minimize them by taking advantage of multiple datasets. Published data from scientific papers or grey literature, online sources, such as the Predicts or Biotime databases, primary data from museum collections, as well as multiple citizen science projects could be collated to better understand richness, abundance, and composition data on insects across space and time. Knowledge gaps in space, habitat types, phylogeny, function, and time could then be identified, and additional efforts made to embrace them. Finally, any changes can really only be fully understood when possible drivers are considered. Given the heterogeneity of data sources, available predictor variables may vary across regions. Nevertheless, data on predictor values for the six main extinction drivers are often available at global (e.g., Forest Watch; Hansen et al., 2013) or at least regional levels.

Given the multiple dimensions of insect diversity loss, any research, monitoring and conservation initiative must minimize the phylogenetic, functional, habitat, spatial, and temporal biases. Recently, Cardoso and Leather (2019) proposed the development and global adoption of a standardized and optimized scheme that would allow comparisons across space and time with minimum investment per gain unit (Cardoso et al., 2016). However, while a monitoring scheme is running, we know enough to act immediately (Harvey et al., 2020).

Solutions include the removal of the root causes of the problem, the indirect drivers, as essential components of a transformative change of our economy and society (IPBES, 2019). Many solutions are now available to support insect populations at sustainable levels, especially through preserving and recovering natural habitats, eliminating deleterious agricultural practices including harmful pesticides, implementing measures for avoiding or eliminating the negative impacts of invasive species, taking aggressive steps to reduce greenhouse gas emissions, and curbing the deleterious effects of overexploitation of

many taxa. Multiple countries are already adopting concrete measures for averting further insect population depletions. As an example, many European countries are banning or phasing-out glyphosate-based weed killers. Solutions are now available – we must act upon them (Samways et al., 2020).

CRedit authorship contribution statement

Pedro Cardoso: Conceptualization, Writing - original draft, Writing - review & editing. **Philip S. Barton:** Writing - original draft, Writing - review & editing. **Klaus Birkhofer:** Writing - original draft, Writing - review & editing. **Filipe Chichorro:** Writing - original draft, Writing - review & editing. **Charl Deacon:** Writing - original draft, Writing - review & editing. **Thomas Fartmann:** Writing - original draft, Writing - review & editing. **Caroline S. Fukushima:** Writing - original draft, Writing - review & editing. **René Gaigher:** Writing - original draft, Writing - review & editing. **Jan C. Habel:** Writing - original draft, Writing - review & editing. **Caspar A. Hallmann:** Writing - original draft, Writing - review & editing. **Matthew J. Hill:** Writing - original draft, Writing - review & editing. **Axel Hochkirch:** Writing - original draft, Writing - review & editing. **Mackenzie L. Kwak:** Writing - original draft, Writing - review & editing. **Stefano Mammola:** Writing - original draft, Writing - review & editing. **Jorge A. Noriega:** Writing - original draft, Writing - review & editing. **Alexander B. Orfinger:** Writing - original draft, Writing - review & editing. **Fernando Pedraza:** Writing - original draft, Writing - review & editing. **James S. Pryke:** Writing - original draft, Writing - review & editing. **Fabio O. Roque:** Writing - original draft, Writing - review & editing. **Josef Settele:** Writing - original draft, Writing - review & editing. **John P. Simateika:** Writing - original draft, Writing - review & editing. **Nigel E. Stork:** Writing - original draft, Writing - review & editing. **Frank Suhling:** Writing - original draft, Writing - review & editing. **Carlien Vorster:** Writing - original draft, Writing - review & editing. **Michael J. Samways:** Conceptualization, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Special thanks are due to William J. Ripple for leading the Alliance of World Scientists, stimulating multiple “Scientists’ Warnings to Humanity” and encouraging the writing of the manuscript. Matthew P. Hill and Vincent Devictor provided valuable comments on the manuscript.

Role of the funding source

Pedro Cardoso, Filipe Chichorro, and Caroline Fukushima are supported by Koneen Säätiö. Alexander B. Orfinger is supported by the McIntire-Stennis Program from the USDA National Institute of Food and Agriculture. Fernando Pedraza is supported by the University of Zurich Research Priority Program on ‘Global Change and Biodiversity’. Charl Deacon, René Gaigher, James Pryke, Carlien Vorster and Michael Samways are supported by Mondi Group. Study sponsors had no role or influence in the study design; in the collection, analysis, and interpretation of data; in the writing of the report; and in the decision to submit the paper for publication.

References

Actman, J., 2019. Bug smuggling is a big business. <https://nationalgeographic.com/>

- animals/2019/09/bug-smuggling-big-business/, Accessed date: 5 September 2019.
- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., Winfree, R., 2013. Historical changes in northeastern U.S. bee pollinators related to shared ecological traits. *PNAS* 110, 4656–4660. <https://doi.org/10.1073/pnas.1218503110>.
- Barton, P.S., Evans, M.J., 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. *Ecol. Entomol.* 42, 364–374. <https://doi.org/10.1111/een.12395>.
- Barton, P.S., Manning, A.D., Gibb, H., Lindenmayer, D.B., Cunningham, S.A., 2009. Conserving ground-dwelling beetles in an endangered woodland community: multi-scale habitat effects on assemblage diversity. *Biol. Conserv.* 142, 1701–1709. <https://doi.org/10.1016/j.biocon.2009.03.005>.
- Bascompte, J., Stouffer, D.B., 2009. The assembly and disassembly of ecological networks. *Philos. Trans. Royal Soc. B* 364, 1781–1787. <https://doi.org/10.1098/rstb.2008.0226>.
- Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant-animal mutualistic networks. *PNAS* 100, 9383–9387. <https://doi.org/10.1073/pnas.1633576100>.
- Basset, Y., Lamarre, G.P.A., 2019. Toward a world that values insects. *Science* 364, 1230–1231. <https://doi.org/10.1126/science.aaw7071>.
- Basset, Y., Barrios, H., Segar, S., Srygley, R.B., Aiello, A., Warren, A.D., et al., 2015. The butterflies of Barro Colorado Island, Panama: local extinction since the 1930s. *PLoS One* 10 (8), e0136623. <https://doi.org/10.1371/journal.pone.0136623>.
- Bastolla, U., Fortuna, M.A., Pascual-García, A., Ferrera, A., Luque, B., Bascompte, J., 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1020. <https://doi.org/10.1038/nature07950>.
- Beynon, S.A., Wainwright, W.A., Christie, M., 2015. The application of an ecosystem services framework to estimate the economic value of dung beetles to the U.K. cattle industry. *Ecol. Entomol.* 40, 124–135. <https://doi.org/10.1111/een.12240>.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., et al., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>.
- Bogoni, J.A., da Silva, P.G., Peres, C.A., 2019. Co-declining mammal–dung beetle faunas throughout the Atlantic Forest biome of South America. *Ecography* 42, 1803–1818. <https://doi.org/10.1111/ecog.04670>.
- Boothby, J., Hull, A.P., 1997. A census of ponds in Cheshire, North West England. *Aquat. Conserv.: Mar. Freshw. Ecosyst.* 7, 75–79. [https://doi.org/10.1002/\(SICI\)1099-0755\(199703\)7:1<75::AID-AQC215>3.0.CO;2-7](https://doi.org/10.1002/(SICI)1099-0755(199703)7:1<75::AID-AQC215>3.0.CO;2-7).
- Brittain, C., Bommarco, R., Vighi, M., Settele, J., Potts, S.G., 2010. Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biol. Conserv.* 143, 1860–1867. <https://doi.org/10.1016/j.biocon.2010.04.029>.
- Bronstein, J.L., Alarcón, R., Geber, M., 2006. The evolution of plant-insect mutualisms. *New Phytol.* 172, 412–428. <https://doi.org/10.1111/j.1469-8137.2006.01864.x>.
- Brook, B.W., Sodhi, N.S., Ng, P.K.L., 2003. Catastrophic extinctions follow deforestation in Singapore. *Nature* 424, 420–423. <https://doi.org/10.1038/nature01795>.
- Brooks, D.R., Bater, J.E., Clark, S.J., Monteith, D.J., Andrews, C., Corbett, S.J., et al., 2012. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *J. Appl. Ecol.* 49, 1009–1019. <https://doi.org/10.1111/j.1365-2664.2012.02194.x>.
- Brühl, C.A., Zaller, J.G., 2019. Biodiversity decline as a consequence of an inappropriate environmental risk assessment of pesticides. *Front. Environ. Sci.* 7, 177. <https://doi.org/10.3389/fenvs.2019.00177>.
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., et al., 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* 334, 652–655. <https://doi.org/10.1126/science.1210288>.
- Bush, A., Theischinger, G., Nipperess, D., Turak, E., Hughes, L., 2013. Dragonflies: climate canaries for river management. *Divers. Distrib.* 19, 86–97. <https://doi.org/10.1111/ddi.12007>.
- Cameron, S.A., Sadd, B.M., 2020. Global trends in bumble bee health. *Annu. Rev. Entomol.* 65. <https://doi.org/10.1146/annurev-ento-011118-111847>.
- Cardoso, P., 2012. Habitats directive species list: urgent need of revision. *Insect Conserv. Diver.* 5, 169–174. <https://doi.org/10.1111/j.1752-4598.2011.00140.x>.
- Cardoso, P., Leather, S.R., 2019. Predicting a global insect apocalypse. *Insect Conserv. Diver.* 12, 263–267. <https://doi.org/10.1111/icad.12367>.
- Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R., 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biol. Conserv.* 144, 2647–2655. <https://doi.org/10.1016/j.biocon.2011.07.024>.
- Cardoso, P., Carvalho, J.C., Crespo, L.C., Arnedo, M.A., 2016. Optimal Inventorying and Monitoring of Taxon, Phylogenetic and Functional Diversity. *bioRxiv*, 060400. <https://doi.org/10.1101/060400>.
- Cerritos, R., 2009. Insects as food: an ecological, social and economical approach. *CAB Rev.: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 4, 1–10. <https://doi.org/10.1079/PAVSNNR20094027>.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333, 1024–1026. <https://doi.org/10.1126/science.1206432>.
- Chichorro, F., Juslén, A., Cardoso, P., 2019. A review of the relation between species traits and extinction risk. *Biol. Conserv.* 237, 220–229. <https://doi.org/10.1016/j.biocon.2019.07.001>.
- Chovanec, A., Schindler, M., Waringer, J., Wimmer, R., 2015. The Dragonfly Association Index (Insecta: Odonata) - a tool for the type-specific assessment of lowland rivers. *River Res. Appl.* 31, 627–638. <https://doi.org/10.1002/rra.2760>.
- Chung, H.-Y., Lee, Y.-W., Park, S.-H., Lim, C., Park, S.-H., Hong, M.-H., et al., 2018. Galloisiana kosuensis. In: The IUCN Red List of Threatened Species 2018, <https://doi.org/10.2305/IUCN.UK.2018-1.RLTS.T113551876A113555352.en>. T113551876A113555352. (accessed 21 October 2019).
- Clausnitzer, V., Kalkman, V.J., Ram, M., Collen, B., Baillie, J.E.M., Bedjnani, M., et al.,

2009. Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. *Biol. Conserv.* 142, 1864–1869. <https://doi.org/10.1016/j.biocon.2009.03.028>.
- Colwell, R.K., Dunn, R.R., Harris, N.C., 2012. Coextinction and persistence of dependent species in a changing world. *Ann. Rev. Ecol. Syst.* 43, 183–203. <https://doi.org/10.1146/annurev-ecolsys-110411-160304>.
- Comont, R.F., Roy, H.E., Harrington, R., Shortall, C.R., Purse, B.V., 2014. Ecological correlates of local extinction and colonisation in the British ladybird beetles (Coleoptera: Coccinellidae). *Biol. Invasions* 16, 1805–1817. <https://doi.org/10.1007/s10530-013-0628-3>.
- Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R., Warren, M.S., 2004. Long-term population trends in widespread British moths. *J. Insect Conserv.* 8, 119–136. <https://doi.org/10.1023/B:JICO.0000045810.36433.c6>.
- Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* 132, 279–291. <https://doi.org/10.1016/j.biocon.2006.04.020>.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., et al., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260. <https://doi.org/10.1038/387253a0>.
- Cronin, J.T., Haynes, K.J., 2004. An invasive plant promotes unstable host-parasitoid patch dynamics. *Ecology* 85, 2772–2782. <https://doi.org/10.1890/04-0303>.
- Crous, C.J., Samways, M.J., Pryke, J.S., 2013. Exploring the mesofilter as a novel operational scale in conservation planning. *J. Appl. Ecol.* 50, 205–214. <https://doi.org/10.1111/1365-2664.12012>.
- Darwall, W., Seddon, M., Clausnitzer, V., Cumberlidge, N., 2012. Freshwater invertebrate life. In: Collen, B., Böhm, M., Kemp, R., Baillie, J.E.M. (Eds.), *Spineless: Status and Trends of the World's Invertebrates*. Zoological Society of London, UK, pp. 26–33.
- Desneux, N., Decourtye, A., Delpuech, J.-M., 2007. The sublethal effects of pesticides on beneficial arthropods. *Annu. Rev. Entomol.* 52, 81–106. <https://doi.org/10.1146/annurev.ento.52.110405.091440>.
- Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., et al., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Chang.* 2, 121–124. <https://doi.org/10.1038/nclimate1347>.
- Dick, J.T.A., Platvoet, D., Kelly, D.W., 2002. Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). *Can. J. Fish. Aquat. Sci.* 59, 1078–1084. <https://doi.org/10.1139/f02-074>.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406. <https://doi.org/10.1126/science.1251817>.
- Donaldson, M.R., Burnett, N.J., Braun, D.C., Suski, C.D., Hinch, S.G., Cooke, S.J., Kerr, J.T., 2016. Taxonomic bias and international biodiversity conservation research. *Facets* 1, 105–113. <https://doi.org/10.1139/facets-2016-0011>.
- Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., et al., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* 81, 163–182. <https://doi.org/10.1017/S1464793105006950>.
- Dufour, D.L., 1987. Insects as food: a case study from the Northwest Amazon. *Am. Anthropol.* 89, 383–397. <https://doi.org/10.1525/aa.1987.89.2.02a00070>.
- Dunn, R.R., 2005. Modern insect extinctions, the neglected majority. *Conserv. Biol.* 19, 1030–1036. <https://doi.org/10.1111/j.1523-1739.2005.00078.x>.
- Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P., Sodhi, N.S., 2009. The sixth mass extinction: are most endangered species parasites and mutualists? *Proc. Royal Soc. B* 276, 3037–3045. <https://doi.org/10.1098/rspb.2009.0413>.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567. <https://doi.org/10.1046/j.1461-0248.2002.00354.x>.
- Dutra, S., De Marco, P., 2015. Bionomic differences in odonates and their influence on the efficiency of indicator species of environmental quality. *Ecol. Indic.* 49, 132–142. <https://doi.org/10.1016/j.ecolind.2014.09.016>.
- Eaton, J.A., Shepherd, C.R., Rheindt, F.E., Harris, J.B.C., Van Balen, S., Wilcove, D.S., Collar, N.J., 2015. Trade-driven extinctions and near-extinctions of avian taxa in Sundaic Indonesia. *Forktail* 31, 1–12.
- Eichel, S., Fartmann, T., 2008. Management of calcareous grasslands for Nickerl's fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation, and patch area. *J. Insect Conserv.* 12, 677–688. <https://doi.org/10.1007/s10841-007-9110-9>.
- Espírito-Santo, M.M., Fernandes, G.W., 2007. How many species of gall-inducing insects are there on earth, and where are they? *Ann. Entomol. Soc. Am.* 100, 95–99. [https://doi.org/10.1603/0013-8746\(2007\)100\[95:HMSOGI\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2007)100[95:HMSOGI]2.0.CO;2).
- Feng, Y., Zhao, M., He, Z., Chen, Z., Sun, L., 2009. Research and utilization of medicinal insects in China. *Entomol. Res.* 39, 313–316. <https://doi.org/10.1111/j.1748-5967.2009.00236.x>.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* 16, 265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>.
- Fletcher Jr., R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., et al., 2018. Is habitat fragmentation good for biodiversity? *Biol. Conserv.* 226, 9–15. <https://doi.org/10.1016/j.biocon.2018.07.022>.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., et al., 2005. Global consequences of land use. *Science* 309, 570–574. <https://doi.org/10.1126/science.1111772>.
- Forrest, J.R., 2016. Complex responses of insect phenology to climate change. *Curr Opin Insect Sci* 17, 49–54. <https://doi.org/10.1016/j.cois.2016.07.002>.
- Fox, R., 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conserv. Diver.* 6, 5–19. <https://doi.org/10.1111/j.1752-4598.2012.00186.x>.
- Gall, J.E., Boyd, R.S., Rajakaruna, N., 2015. Transfer of heavy metals through terrestrial food webs: a review. *Environ. Monit. Assess.* 187, 201. <https://doi.org/10.1007/s10661-015-4436-3>.
- Gaston, K.J., 1991. The magnitude of global insect species richness. *Conserv. Biol.* 5, 283–296. <https://doi.org/10.1111/j.1523-1739.1991.tb00140.x>.
- Gaston, K.J., 2011. Common ecology. *BioScience* 61, 354–362. <https://doi.org/10.1525/bio.2011.61.5.4>.
- Gaston, K.J., 2018. Lighting up the nighttime. *Science* 362 (6416), 744–746. <https://doi.org/10.1126/science.aau8226>.
- Graham, C.H., Fine, P.V.A., 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space in time. *Ecol. Lett.* 11, 1265–1277. <https://doi.org/10.1111/j.1461-0248.2008.01256.x>.
- Griffiths, H.M., Bardgett, R.D., Louzada, J., Barlow, J., 2016. The value of trophic interactions for ecosystem function: dung beetle communities influence seed burial and seedling recruitment in tropical forests. *Proc. Royal Soc. B* 283, 20161634. <https://doi.org/10.1098/rspb.2016.1634>.
- Guimarães Jr., P.R., Pires, M.M., Jordano, P., Bascompte, J., Thompson, J.N., 2017. Indirect effects drive coevolution in mutualistic networks. *Nature* 550, 511–514. <https://doi.org/10.1038/nature24273>.
- Habel, J.C., Schmitt, T., 2018. Vanishing of the common species: empty habitats and the role of genetic diversity. *Biol. Conserv.* 218, 211–216. <https://doi.org/10.1016/j.biocon.2017.12.018>.
- Habel, J.C., Samways, M.J., Schmitt, T., 2019a. Mitigating the precipitous decline of terrestrial European insects: requirements for a new strategy. *Biodivers. Conserv.* 28, 1343–1360. <https://doi.org/10.1007/s10531-019-01741-8>.
- Habel, J.C., Rasche, L., Schneider, U.A., Engler, J.O., Schmid, E., Rödder, D., Meyer, S.T., Trapp, N., del Diego, R.S., Eggermont, H., Lens, L., Stork, N.E., 2019b. Final countdown for biodiversity hotspots. *Conserv. Lett.* <https://doi.org/10.1111/conl.12668>. in press.
- Habel, J.C., Trusch, R., Schmitt, T., Ochse, M., Ulrich, W., 2019c. Long-term large-scale decline in relative abundances of butterfly and burnet moth species across southwestern Germany. *Sci. Rep.* 9, 14921. <https://doi.org/10.1038/s41598-019-51424-1>.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., et al., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 12 (10), e0185809. <https://doi.org/10.1371/journal.pone.0185809>.
- Hallmann, C.A., Zeegers, T., van Klink, R., Vermeulen, R., van Wielink, P., Spijkers, H., et al., 2020. Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conserv. Diver.* <https://doi.org/10.1111/icad.12377>.
- Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., et al., 2013. High-resolution global maps of 21st-century forest cover change. *Science* 342, 850–853. <https://doi.org/10.1126/science.1244693>.
- Hanski, I., 1999. *Metapopulation Ecology*. Oxford University Press Inc., New York.
- Harvey, J.A., Heinen, R., Armbrrecht, I., Basset, Y., Baxter-Gilbert, J.H., Bezemer, T.M., et al., 2020. International scientists formulate a roadmap for insect conservation and recovery. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-019-1079-8>.
- Havel, J.E., Kovalenko, K.E., Thomaz, S.M., Amalfitano, S., Kats, L.B., 2015. Aquatic invasive species: challenges for the future. *Hydrobiologia* 750, 147–170. <https://doi.org/10.1007/s10750-014-2166-0>.
- Hayes, T.B., Hansen, M., 2017. From silent spring to silent night: agrochemicals and the anthropocene. *Elem. Sci. Anth.* 5, 57. <https://doi.org/10.1525/elementa.246>.
- Huang, J.-P., 2014. Modeling the effects of anthropogenic exploitation and climate change on an endemic stag beetle, *Lucanus miwai* (Lucanidae), of Taiwan. *J. Asia Pac. Entomol.* 17, 423–429. <https://doi.org/10.1016/j.aspen.2014.03.009>.
- Hugel, S., 2014. *Pyrgacris relictus*. The IUCN Red List of Threatened Species 2014. e.T55929685A56790127. <https://doi.org/10.2305/IUCN.UK.2014-3.RLTS.T55929685A56790127.en>. (accessed 21 October 2019).
- Illgner, P., Nel, E., 2000. The geography of edible insects in Sub-Saharan Africa: a study of the mopane caterpillar. *Geogr. J.* 166, 336–351. <https://doi.org/10.1111/j.1475-4959.2000.tb00035.x>.
- IPBES, 2016. The assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production. In: Potts, S.G., Imperatriz-Fonseca, V.L., Ngo, H.T. (Eds.), *Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, (Bonn, Germany).
- IPBES, 2019. In: Díaz, S., Settele, J., Brondizio, E.S., Ngo, H.T., Guèze, M., Agard, J. (Eds.), *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat, Bonn, Germany.
- IUCN, 2019. The IUCN red list of threatened species. Version 2019-2. <https://www.iucnredlist.org>.
- Jauker, B., Krauss, J., Jauker, F., Steffan-Dewenter, I., 2013. Linking life history traits to pollinator loss in fragmented calcareous grasslands. *Landsc. Ecol.* 28, 107–120. <https://doi.org/10.1007/s10980-012-9820-6>.
- Jones, J.I., Murphy, J.F., Collins, A.L., Sear, D.A., Naden, P.S., Armitage, P.D., 2012. The impact of fine sediment on macro-invertebrates. *River Res. Appl.* 28, 1055–1071. <https://doi.org/10.1002/rra.1516>.
- Jongema, Y., 2017. List of edible insect species of the world. <https://www.wur.nl/en/Research-Results/Chair-groups/Plant-Sciences/Laboratory-of-Entomology/Edible-insects/Worldwide-species-list.htm>.
- Jourdan, J., O'Hara, R.B., Bottarin, R., Huttunen, K.L., Kuemmerlen, M., Monteith, D., et al., 2018. Effects of changing climate on European summer invertebrate communities: a long-term data analysis. *Sci. Total Environ.* 621, 588–599. <https://doi.org/10.1016/j.scitotenv.2017.11.242>.
- Kameoka, S., Kiyono, H., 2003. *A Survey of the Rhinoceros Beetle and Stag Beetle Market in Japan*. Traffic East Asia, Tokyo, Japan.
- Karban, R., Black, C.A., Weinbaum, S.A., 2000. How 17-year cicadas keep track of time. *Ecol. Lett.* 3, 253–256. <https://doi.org/10.1046/j.1461-0248.2000.00164.x>.
- Kenis, M., Sileshi, G., Mbata, K., Chidumayo, E., Meke, G., Muatintse, B., 2006. Towards

- conservation and sustainable utilization of edible caterpillars of the miombo. In: Presentation to the SIL Annual Conference on Trees for Poverty Alleviation, 9 June 2006, Zürich, Switzerland.
- Kowler, J.T., Flint, P.W.H., Flint, S., 2016. Trichoptera (Caddisflies) caught by the Rothamsted light trap at Rowardennan, Loch Lomondside throughout 2009. *Glasg. Nat.* 26, 35–42.
- Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S., 2004a. Species coextinctions and the biodiversity crisis. *Science* 305, 1632–1634. <https://doi.org/10.1126/science.1101101>.
- Koh, L.P., Sodhi, N.S., Brook, B.W., 2004b. Ecological correlates of extinction proneness in tropical butterflies. *Conserv. Biol.* 18, 1571–1578. <https://doi.org/10.1111/j.1523-1739.2004.00468.x>.
- Kotze, D.J., O'Hara, R.B., 2003. Species decline - but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* 135, 138–148. <https://doi.org/10.1007/s00442-002-1174-3>.
- Krämer, B., Poniatowski, D., Fartmann, T., 2012. Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. *Biol. Conserv.* 152, 253–261. <https://doi.org/10.1016/j.biocon.2012.03.038>.
- Krosby, M., Wilsey, C.B., McGuire, J.L., Duggan, J.M., Nogueira, T.M., Heinrichs, J.A., et al., 2015. Climate-induced range overlap among closely related species. *Nat. Clim. Chang.* 5, 883–886. <https://doi.org/10.1038/nclimate2699>.
- Kurze, S., Heinken, T., Fartmann, T., 2018. Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species. *Oecologia* 188, 1227–1237. <https://doi.org/10.1007/s00442-018-4266-4>.
- Kwak, M.L., 2018. Australia's vanishing fleas (Insecta: Siphonaptera): a case study in methods for the assessment and conservation of threatened flea species. *J. Insect Conserv.* 22, 545–550. <https://doi.org/10.1007/s10841-018-0083-7>.
- Kytö, M., Niemelä, P., Larsson, S., 1996. Insects on trees: population and individual response to fertilization. *Oikos* 75, 148–159. <https://doi.org/10.2307/3546238>.
- Latham, P., 2003. *Edible Caterpillars and Their Food Plants in Bas-Congo*. Mystole Publications, Canterbury.
- Leandro, C., Jay-Robert, P., Vergnes, A., 2017. Bias and perspectives in insect conservation: a European scale analysis. *Biol. Conserv.* 215, 213–224. <https://doi.org/10.1016/j.biocon.2017.07.033>.
- Leather, S.R., 2013. Institutional vertebratism hampers insect conservation generally; not just saproxylic beetle conservation. *Anim. Conserv.* 16, 379–380. <https://doi.org/10.1111/acv.12068>.
- Lister, B.C., Garcia, A., 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. *PNAS* 115, E10397–E10406. <https://doi.org/10.1073/pnas.1722477115>.
- Lokeshwari, R.K., Shantibala, T., 2010. A review on the fascinating world of insect resources: reason for thoughts. *Psyche* 2010, 207570. <https://doi.org/10.1155/2010/207570>.
- Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *BioScience* 56, 311–323. [https://doi.org/10.1641/0006-3568\(2006\)56\[311:TEVOES\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2).
- Macadam, C.R., Stockan, J.A., 2015. More than just fish food: ecosystem services provided by freshwater insects. *Ecol. Entomol.* 40, 113–123. <https://doi.org/10.1111/een.12245>.
- Macgregor, C.J., Williams, J.H., Bell, J.R., Thomas, C.D., 2019. Moth biomass increases and decreases over 50 years in Britain. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-019-1028-6>.
- Mammides, C., 2019. European Union's conservation efforts are taxonomically biased. *Biodivers. Conserv.* 28, 1291–1296. <https://doi.org/10.1007/s10531-019-01725-8>.
- Mammola, S., Cardoso, P., Culver, D.C., Deharveng, L., Ferreira, R.L., Fišer, C., et al., 2019a. Scientists' warning on the conservation of subterranean ecosystems. *BioScience* 69, 641–650. <https://doi.org/10.1093/biosci/biz064>.
- Mammola, S., Piano, E., Cardoso, P., Vernon, P., Domínguez-Villar, D., Culver, D.C., et al., 2019b. Climate change going deep: the effects of global climatic alterations on cave ecosystems. *The Anthropocene Review* 6, 98–116. <https://doi.org/10.1177/2053019619851594>.
- McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., et al., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* 10, 995–1015. <https://doi.org/10.1111/j.1461-0248.2007.01094.x>.
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. Royal Soc. B* 271, 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>.
- Millennium Ecosystem Assessment, 2003. *Ecosystems and Human Well-being: A Framework for Assessment*. Island Press, Washington, D.C.
- Misof, B., Liu, S., Meusemann, K., Peters, R.S., Donath, A., Mayer, C., et al., 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346, 763–767. <https://doi.org/10.1126/science.1257570>.
- Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., et al., 2004. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX, Mexico City.
- Moritz, C., 1999. Conservation units and translocations: strategies for conserving evolutionary processes. *Hereditas* 130, 217–228. <https://doi.org/10.1111/j.1601-5223.1999.00217.x>.
- Morley, E.L., Jones, G., Radford, A.N., 2014. The importance of invertebrates when considering the impacts of anthropogenic noise. *Proc. Royal Soc. B* 281, 20132683. <https://doi.org/10.1098/rspb.2013.2683>.
- Morris, B., 2004. *Insects and Human Life*. Berg Publisher, Oxford.
- Münsh, T., Helbing, F., Fartmann, T., 2019. Habitat quality determines patch occupancy of two specialist Lepidoptera species in well-connected grasslands. *J. Insect Conserv.* 23, 247–258. <https://doi.org/10.1007/s10841-018-0109-1>.
- New, T.R., 2005. 'Inordinate fondness': a threat to beetles in south east Asia? *J. Insect Conserv.* 9, 147–150. <https://doi.org/10.1007/s10841-005-1309-z>.
- Ng, K., Barton, P.S., Blanchard, W., Evans, M.J., Lindenmayer, D.B., Macfadyen, S., et al., 2018. Disentangling the effects of farmland use, habitat edges, and vegetation structure on ground beetle morphological traits. *Oecologia* 188, 645–657. <https://doi.org/10.1007/s00442-018-4180-9>.
- Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J.I., et al., 2018. Research trends in ecosystem services provided by insects. *Basic Appl. Ecol.* 26, 8–23. <https://doi.org/10.1016/j.baec.2017.09.006>.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. *PNAS* 104, 19891–19896. <https://doi.org/10.1073/pnas.0706375104>.
- Owens, A.C.S., Lewis, S.M., 2018. The impact of artificial light at night on nocturnal insects: a review and synthesis. *Ecol. Evol.* 8, 11337–11358. <https://doi.org/10.1002/ece3.4557>.
- Pachepey, E., Crawford, J.W., Bown, J.L., Squire, G., 2001. Towards a general theory of biodiversity. *Nature* 410, 923–926. <https://doi.org/10.1038/35073563>.
- Pearse, I.S., Altermatt, F., 2013. Extinction cascades partially estimate herbivore losses in a complete Lepidoptera-plant food web. *Ecology* 94, 1785–1794. <https://doi.org/10.1890/12-1075.1>.
- Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., et al., 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Glob. Change Biol.* 19, 2303–2338. <https://doi.org/10.1111/gcb.12143>.
- Platts, P.J., Mason, S.C., Palmer, G., Hill, J.K., Oliver, T.H., Powney, G.D., et al., 2019. Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups. *Sci. Rep.* 9, 15039. <https://doi.org/10.1038/s41598-019-51582-2>.
- Poniatowski, D., Fartmann, T., 2010. What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? *J. Insect Conserv.* 14, 637–645. <https://doi.org/10.1007/s10841-010-9293-3>.
- Poniatowski, D., Stuhldreher, G., Löffler, F., Fartmann, T., 2018. Patch occupancy of grassland specialists: habitat quality matters more than habitat connectivity. *Biol. Conserv.* 225, 237–244. <https://doi.org/10.1016/j.biocon.2018.07.018>.
- Powney, G.D., Cham, S.S.A., Smallshire, D., Isaac, N.J.B., 2015. Trait correlates of distribution trends in the Odonata of Britain and Ireland. *Peer J* 3, e1410. <https://doi.org/10.7717/peerj.1410>.
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019. Widespread losses of pollinating insects in Britain. *Nat. Commun.* 10, 1018. <https://doi.org/10.1038/s41467-019-08974-9>.
- Prasad, B., 2007. *Insect diversity and endemic bioresources*. In: Singh, N.I. (Ed.), *Endemic Bio-resources of India – Conservation and Sustainable Development With Special Reference to North East India*, pp. 275–291 Dehra Dun, India.
- Preston, D.L., Henderson, J.S., Johnson, P.T.J., 2012. Community ecology of invasions: direct and indirect effects of multiple invasive species on aquatic communities. *Ecology* 93, 1254–1261. <https://doi.org/10.1890/11-1821.1>.
- Price, R.D., Hellenenthal, R.A., Palma, R.L., 2003. *World checklist of chewing lice with host associations and keys to families and genera*. In: Price, R.D., Hellenenthal, R.A., Palma, R.L., Johnson, K.P., Clayton, D.H. (Eds.), *The Chewing Lice: World Checklist and Biological Overview*. Illinois Natural History Survey Special Publication 24. pp. 1–448.
- Price, B.W., Barker, N.P., Villet, M.H., 2007. Patterns and processes underlying evolutionary significant units in the *Platypleura stridula* L. species complex (Hemiptera: Cicadidae) in the Cape Floristic Region, South Africa. *Mol. Ecol.* 16, 2574–2588. <https://doi.org/10.1111/j.1365-294X.2007.03328.x>.
- Ramos-Elorduy, J., 2006. Threatened edible insects in Hidalgo, Mexico and some measures to preserve them. *J. Ethnobiol. Ethnosc.* 2, 51. <https://doi.org/10.1186/1746-4269-2-51>.
- Ratcliffe, N.A., Mello, C.B., Garcia, E.S., Butt, T.M., Azambuja, P., 2011. Insect natural products and processes: new treatments for human disease. *Insect Biochem. Mol. Biol.* 41, 747–769. <https://doi.org/10.1016/j.ibmb.2011.05.007>.
- Régnier, C., Achaz, G., Lambert, A., Cowie, R.H., Bouchet, P., Fontaine, B., 2015. Mass extinction in poorly known taxa. *PNAS* 112, 7761–7766. <https://doi.org/10.1073/pnas.1502350112>.
- Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., et al., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* 94, 849–873. <https://doi.org/10.1111/brv.12480>.
- Rewicz, T., Grabowski, M., MacNeil, C., Bączela-Spychalska, K., 2014. The profile of a 'perfect' invader – the case of killer shrimp, *Dikerogammarus villosus*. *Aquat. Invasions* 9, 267–288. <https://doi.org/10.3391/ai.2014.9.3.04>.
- Ripple, W.J., Wolf, C., Newsome, T.M., Galetti, M., Alamgir, M., Crist, E., et al., 2017. World scientists' warning to humanity: a second notice. *BioScience* 67, 1026–1028. <https://doi.org/10.1093/biosci/bix125>.
- Ripple, W.J., Wolf, C., Newsome, T.M., Barnard, P., Moomaw, W.R., 2019. World scientists' warning of a climate emergency. *BioScience* biz088. <https://doi.org/10.1093/biosci/biz088>.
- Rohr, R.P., Saavedra, S., Bascompte, J., 2014. On the structural stability of mutualistic systems. *Science* 345, 1253497. <https://doi.org/10.1126/science.1253497>.
- Roubinet, E., Birkhofer, K., Malsher, G., Staudacher, K., Ekkob, B., Traugott, M., Jonsson, M., 2017. Diet of generalist predators reflects effects of cropping period and farming system on extra- and intraguild prey. *Ecol. Appl.* 27, 1167–1177. <https://doi.org/10.1002/eap.1510>.
- Roy, D.B., Sparks, T.H., 2000. Phenology of British butterflies and climate change. *Glob. Change Biol.* 6, 407–416. <https://doi.org/10.1046/j.1365-2486.2000.00322.x>.
- Roy, H.E., Brown, P.M.J., Adriaens, T., Berkvens, N., Borges, I., Clusella-Trullas, S., et al., 2016. The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. *Biol. Invasions* 18, 997–1044. <https://doi.org/10.1007/s10530->

- 016-1077-6.
- Saavedra, S., Stoffler, D.B., Uzzi, B., Bascompte, J., 2011. Strong contributors to network persistence are the most vulnerable to extinction. *Nature* 478, 233–235. <https://doi.org/10.1038/nature10433>.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., et al., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>.
- Samways, M.J., 2019. *Insect Conservation – A Global Synthesis*. CABI (600 pp.).
- Samways, M.J., Barton, P., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., et al., 2020. Solutions for humanity on how to conserve insects. *Biol. Conserv. In this issue*.
- Saunders, M.E., 2018. Ecosystem services in agriculture: understanding the multi-functional role of invertebrates. *Agric. Forest Entomol.* 20, 298–300. <https://doi.org/10.1111/afe.12248>.
- Schabel, H.G., 2006. *Forest Entomology in East Africa: Forest Insects of Tanzania*. Springer, Dordrecht.
- Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T., et al., 2016. The broad footprint of climate change from genes to biomes to people. *Science* 354, aaf 7671. <https://doi.org/10.1126/science.aaf7671>.
- Schmidt, A.K.D., Balakrishnan, R., 2015. Ecology of acoustic signalling and the problem of masking interference in insects. *J. Comp. Physiol. A*. 201, 133–142. <https://doi.org/10.1007/s00359-014-0955-6>.
- Schoolmeesters, P., 2019. Scarabs: world Scarabaeidae database (version Jan 2019). In: Roskov, Y., Ower, G., Orrell, T., Nicolson, D., Bailly, N., Kirk, P.M. (Eds.), *Species 2000 & ITIS Catalogue of Life*. Naturalis, Leiden. <http://www.catalogueoflife.org/>col.
- Schowalter, T.D., Noriega, J.A., Tscharnkte, T., 2018. Insect effects on ecosystem services – introduction. *Basic Appl. Ecol.* 26, 1–7. <https://doi.org/10.1016/j.baec.2017.09.011>.
- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarli, D., et al., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574, 671–674. <https://doi.org/10.1038/s41586-019-1684-3>.
- Severns, P.M., Warren, A.D., 2008. Selectively eliminating and conserving exotic plants to save an endangered butterfly from local extinction. *Anim. Conserv.* 11, 476–483. <https://doi.org/10.1111/j.1469-1795.2008.00203.x>.
- Sheikh, K., 2017. Brood awakening: 17-year Cicadas emerge 4 years early. May 26 Scientific American <https://www.scientificamerican.com/article/brood-awakening-17-year-cicadas-emerge-4-years-early/>.
- Shortall, C.R., Moore, A., Smith, E., Hall, M.J., Woiwod, I.P., Harrington, R., 2009. Long-term changes in the abundance of flying insects. *Insect Conserv. Diver.* 2, 251–260. <https://doi.org/10.1111/j.1752-4598.2009.00062.x>.
- Silverman, J., Brightwell, R.J., 2008. The Argentine ant: challenges in managing an invasive unicolonial pest. *Annu. Rev. Entomol.* 53, 231–252. <https://doi.org/10.1146/annurev.ento.53.103106.093450>.
- Sirois-Delisle, C., Kerr, J.T., 2018. Climate change-driven range losses among bumblebee species are poised to accelerate. *Sci. Rep.* 8, 14464. <https://doi.org/10.1038/s41598-018-32665-y>.
- Skaldina, O., Sorvari, J., 2019. Ecotoxicological effects of heavy metal pollution on economically important terrestrial insects. In: Kesari, K. (Ed.), *Networking of Mutagens in Environmental Toxicology*. Springer, Cham, pp. 137–144.
- Smith, V.S., Ford, T., Johnson, K.P., Johnson, P.C.D., Yoshizawa, K., Light, J.E., 2011. Multiple lineages of lice pass through the K-Pg boundary. *Biol. Lett.* 7, 782–785. <https://doi.org/10.1098/rsbl.2011.0105>.
- Smithsonian, 2019. BugInfo: Insects as Pets. Department of Systematic Biology, Entomology Section, National Museum of Natural History, in Cooperation With Public Inquiry Services. Smithsonian Institution. <https://www.si.edu/spotlight/buginfo/pets>.
- Stagoll, K., Lindenmayer, D.B., Knight, E., Fischer, J., Manning, A.D., 2012. Large trees are keystone structures in urban parks. *Conserv. Lett.* 5, 115–122. <https://doi.org/10.1111/j.1755-263X.2011.00216.x>.
- Stork, N.E., 2018. How many species of insects and other terrestrial arthropods are there on Earth? *Annu. Rev. Entomol.* 63, 31–45. <https://doi.org/10.1146/annurev-ento-020117-043348>.
- Stork, N.E., Habel, J.C., 2014. Can biodiversity hotspots protect more than tropical forest plants and vertebrates? *J. Biogeogr.* 41, 421–428. <https://doi.org/10.1111/jbi.12223>.
- Stork, N.E., Stone, M., Sam, L., 2016. Vertical stratification of beetles in tropical rainforests as sampled by light traps in North Queensland, Australia. *Austral Ecol* 41, 168–178. <https://doi.org/10.1111/aec.12286>.
- Storkey, J., Macdonald, A.J., Bell, J.R., Clark, I.M., Gregory, A.S., Hawkins, N.J., et al., 2016. Chapter one – the unique contribution of Rothamsted to ecological research at large temporal scales. *Adv. Ecol. Res.* 55, 3–42. <https://doi.org/10.1016/bs.aecr.2016.08.002>.
- Strayer, D.L., 2010. Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshw. Biol.* 55, 152–174. <https://doi.org/10.1111/j.1365-2427.2009.02380.x>.
- Strona, G., Bradshaw, C.J.A., 2018. Co-extinctions annihilate planetary life during extreme environmental change. *Sci. Rep.* 8, 16724. <https://doi.org/10.1038/s41598-018-35068-1>.
- Stuhldreher, G., Fartmann, T., 2014. When habitat management can be a bad thing: effects of habitat quality, isolation and climate on a declining grassland butterfly. *J. Insect Conserv.* 18, 965–979. <https://doi.org/10.1007/s10841-014-9704-y>.
- Sunny, A., Diwakar, S., Sharma, G.P., 2015. Native insects and invasive plants encounters. *Arthropod Plant Interact.* 9, 323–331. <https://doi.org/10.1007/s11829-015-9384-x>.
- Swart, R.C., Pryke, J.S., Roets, F., 2019. The intermediate disturbance hypothesis explains arthropod beta-diversity responses to roads that cut through natural forests. *Biol. Conserv.* 236, 243–251. <https://doi.org/10.1016/j.biocon.2019.03.045>.
- Termaat, T., van Strien, A.J., van Grunsven, R.H.A., De Knijf, G., Bjelke, U., Burbach, K., et al., 2019. Distribution trends of European dragonflies under climate change. *Divers. Distrib.* 25, 936–950. <https://doi.org/10.1111/ddi.12913>.
- Thébaud, E., Fontaine, C., 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856. <https://doi.org/10.1126/science.1188321>.
- Themis, J.-L., 1997. *Des insectes à croquer: Guide de découverts*. Les Éditions de l'Homme, Québec.
- Thielens, A., Bell, D., Mortimore, D.B., Greco, M.K., Martens, L., Joseph, W., 2018. Exposure of insects to radio-frequency electromagnetic fields from 2 to 120 GHz. *Sci. Rep.* 8, 3924. <https://doi.org/10.1038/s41598-018-22271-3>.
- Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J., Asher, J., et al., 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303, 1879–1883. <https://doi.org/10.1126/science.1095046>.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–845. <https://doi.org/10.1126/science.1060391>.
- Tourmant, P., Joseph, L., Goka, K., Courchamp, F., 2012. The rarity and overexploitation paradox: stag beetle collections in Japan. *Biodivers. Conserv.* 21, 1425–1440. <https://doi.org/10.1007/s10531-012-0253-y>.
- Turbelin, A.J., Malamud, B.D., Francis, R.A., 2017. Mapping the global state of invasive alien species: patterns of invasion and policy responses. *Glob. Ecol. Biogeogr.* 26, 78–92. <https://doi.org/10.1111/geb.12517>.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>.
- Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biol. Conserv.* 143, 2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>.
- Union of Concerned Scientists, 1992. World scientists' warning to humanity. <http://www-formal.stanford.edu/jmc/progress/ucs-statement.txt>, Accessed date: 22 October 2019.
- Valente-Neto, F., De Oliveira Roque, F., Rodrigues, M.E., Juen, L., Swan, C.M., 2016. Toward a practical use of Neotropical odonates as bioindicators: testing congruence across taxonomic resolution and life stages. *Ecol. Indic.* 61, 952–959. <https://doi.org/10.1016/j.ecolind.2015.10.052>.
- Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., et al., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307. <https://doi.org/10.1111/1365-2435.12356>.
- van Schalkwyk, J., Pryke, J.S., Samways, M.J., 2019. Contribution of common vs. rare species to species diversity patterns in conservation corridors. *Ecol. Indic.* 104, 279–288. <https://doi.org/10.1016/j.ecolind.2019.05.014>.
- Vaughan, I.P., Gotelli, N.J., 2019. Water quality improvements offset the climatic debt for stream macroinvertebrates over twenty years. *Nat. Commun.* 10, 1956. <https://doi.org/10.1038/s41467-019-09736-3>.
- Verdú, J.R., Lobo, J.M., Sánchez-Piñero, F., Gallego, B., Numa, C., Lumaret, J.P., et al., 2018. Ivermectin residues disrupt dung beetle diversity, soil properties and ecosystem functioning: an interdisciplinary field study. *Sci. Total Environ.* 618, 219–228. <https://doi.org/10.1016/j.scitotenv.2017.10.331>.
- Villalobos-Jiménez, G., Dunn, A., Hassall, C., 2016. Dragonflies and damselflies (Odonata) in urban ecosystems: a review. *Eur. J. Entomol.* 113, 217–232. <https://doi.org/10.14411/eje.2016.027>.
- Villéger, S., Miranda, J.R., Hernandez, D.F., Moullot, D., 2012. Low functional β -diversity despite high taxonomic β -diversity among tropical estuarine fish communities. *PLoS One* 7 (7), e40679. <https://doi.org/10.1371/journal.pone.0040679>.
- Vorster, C., Samways, M.J., Simaika, J.P., Kipping, J., Clausnitzer, V., Suhling, F., Dijkstra, K.-D.B., 2020. Development of a new continental-scale index for freshwater assessment based on dragonfly assemblages. *Ecol. Indic.* 109, 105819. <https://doi.org/10.1016/j.ecolind.2019.105819>.
- Wagner, D.L., 2019. Global insect decline: comments on Sánchez-Bayo and Wyckhuys (2019). *Biol. Conserv.* 233, 332–333. <https://doi.org/10.1016/j.biocon.2019.03.005>.
- Wagner, D.L., Van Driesche, R.G., 2010. Threats posed to rare or endangered insects by invasions of nonnative species. *Annu. Rev. Entomol.* 55, 547–568. <https://doi.org/10.1146/annurev-ento-112408-085516>.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebe, T.J.C., et al., 2002. Ecological responses to recent climate change. *Nature* 416, 389–395. <https://doi.org/10.1038/416389a>.
- Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>.
- Wertheim, B., Sevenster, J.G., Eijs, I.E.M., Van Alphen, J.J.M., 2000. Species diversity in a mycophagous insect community: the case of spatial aggregation vs. resource partitioning. *J. Animal Ecol.* 69, 335–351. <https://doi.org/10.1046/j.1365-2656.2000.00396.x>.
- Whiting, M.F., Whiting, A.S., Hastriter, M.W., Dittmar, K., 2008. A molecular phylogeny of fleas (Insecta: Siphonaptera): origins and host associations. *Cladistics* 24, 677–707. <https://doi.org/10.1111/j.1096-0031.2008.00211.x>.
- Williamson, M., Griffiths, B., 1996. *Biological Invasions*. Springer, Netherlands.
- Wilson, E.O., 1992. *The Diversity of Life*. Harvard University Press, Cambridge, Massachusetts.
- Witzemberger, K.A., Hochkirch, A., 2011. *Ex situ* conservation genetics: a review of molecular studies on the genetic consequences of captive breeding programmes for endangered animal species. *Biodivers. Conserv.* 20, 1843–1861. <https://doi.org/10.1007/s10531-011-0074-4>.
- Wood, P.J., Armitage, P.D., 1997. Biological effects of fine sediment in the lotic

- environment. *Environ. Manag.* 21, 203–217. <https://doi.org/10.1007/s002679900019>.
- Wood, P.J., Greenwood, M.T., Agnew, M.D., 2003. Pond biodiversity and habitat loss in the UK. *Area* 35 (2), 206–216.
- Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philos. Trans. Royal Soc. B* 365, 2093–2106. <https://doi.org/10.1098/rstb.2010.0055>.
- Zvereva, E.L., Kozlov, M.V., 2010. Responses of terrestrial arthropods to air pollution: a meta-analysis. *Environ. Sci. Pollut. Res.* 17, 297–311. <https://doi.org/10.1007/s11356-009-0138-0>.