Ecological Entomology

Ecological Entomology (2015), **40** (Suppl. 1), 36–44 DOI: 10.1111/een.12207

INSECTS AND ECOSYSTEM SERVICES SPECIAL ISSUE

Influential entomology: a short review of the scientific, societal, economic and educational services provided by entomology

SIMON R. LEATHER Crop and Environment Sciences, Harper Adams University, Newport, U.K.

Abstract. 1. Entomology as a written science probably originated with the ancient Greeks; Aristotle being regarded as the first published entomologist. It was, however, not until the Renaissance and the invention of the microscope that any further advances were made. The formation of national entomological societies in the early and mid-19th century heralded the blossoming of entomology as a scientific discipline.

2. The role of entomology in the development of ecology as a science is often overlooked, but important concepts in ecology such as the role and types of mimicry, the theoretical development of population dynamics and island biogeography all have their roots in the pioneering work of entomologists.

3. Insect products have long played a part in the economies of human civilizations stretching back several thousand years from the development of the silk industry in China to modern day uses of the excretory products of Hemiptera such as cochineal and shellac.

4. The study of entomology has had indirect applications in human medicine and genetics, such as the development of cryostorage techniques based on an understanding of the freeze-avoidance strategies of Antarctic insects to the direct use of Dipteran larvae in maggot debridement therapy.

5. Insects and their products have been used as sources of food by humans since before written records existed, the use of honey for example, being recorded in pre-historic cave drawings. Insects as recognisable entities such as lepidopteran larvae and adult locusts, play a significant role in the diets of some cultures, but increasingly, the idea that processed insect material can be used as mainstream human and livestock food is gaining ground with a number of commercial enterprises being formed.

6. Culturally insects have long inspired humans, from ancient Egypt and their veneration of scarab beetles, portrayal of insects in ancient Mesoamerican art, in European painting from the medieval period onwards and in literature, poetry, and the performing arts including cinema and music. Although the depiction of insects has not always been positive, it is undeniable that they have had a marked influence on human culture.

7. Insects have also influenced engineers, with their form and function inspiring the development of airless tyres, desert water collection devices and unmanned aerial vehicles.

Key words. Cultural, economics, education, entomology, entomophagy, history, influence, medicine, research, society.

Correspondence: Simon R. Leather, Department of Crop & Environment Sciences, Harper Adams University, Edgmond, Newport TF10 8NB, U.K. E-mail: sleather@harper-adams.ac.uk

Introduction

A question often posed by members of the public is 'what is the purpose of wasps?' This is because most members of the public only see wasps as a nuisance, rather than as the beneficial insects they can actually be. Equally, we might find ourselves faced with the question 'what use is entomology?' As entomologists this question baffles us, but given that the majority of the general public, thanks to the activities of the popular press and other media, believe that the only good insect, except perhaps for bees, is a dead one (Leather & Quicke, 2009, 2010), this is not surprising. Entomologists can sometimes be just as biased, 90% of the book *Insects and History*, (Cloudsley-Thompson, 1973) details with pestiferous and nuisance insects.

It is only relatively recently, despite its venerable age (Hooper, 1970; Westman, 1977; Ehrlich & Mooney, 1983) that the concept of ecosystem services, the theme of this conference, has done much to highlight the importance of insects to a more general audience (Gaston *et al.*, 2013; McKenzie *et al.*, 2013; Stanley *et al.*, 2013). That said, the general public's main perception of the ecosystem services afforded to the human race by insects is that of pollination (e.g. Bartomeus *et al.*, 2013; Cariveau *et al.*, 2013). Pest control services are also recognised to an increasing extent (e.g. Chaplin-Kramer *et al.*, 2013; Morandin *et al.*, 2014), although again as far as the general public are concerned this is probably largely confined to ladybirds.

As entomologists we are all very well aware that insects provide many more ecosystem services than pollination and pest control; the wide range of subjects covered by the keynote speakers at Ento '15 bear testament to this, covering as they do, dung beetles and other soil engineers (Beynon *et al.*, 2015), aquatic insects (Macadam & Stockan, 2015), and the role of insects in wood decomposition (Ulyshen, 2015), as well as the more well-known subjects of pollination (Birkin & Goulson, 2015; Dicks *et al.*, 2015) and crop protection (Bengtsson, 2015; Macfadyen *et al.*, 2015; Midega *et al.*, 2015; Schäkermann *et al.*, 2015). Even entomologists, however, may be surprised by the positive impact that insects and entomology have had, and continue to have, on the human race. Here I briefly review under a series of headings, the positive cultural services that insects and entomologists have had on our lives in terms of education, societal enhancement and non-entomological scientific, and medical advances.

Education and research

Herodotus (484 to 425 BC) is sometimes cited as the first entomologist (e.g. Essig, 1936), but I consider Aristotle (384 to 322 BC) to be the first published entomologist in that he appears to have made entomological observations himself (Essig, 1936; Morge, 1973), many of which were correct such as the three-part body plan, metamorphosis, the existence of the hardened exoskeleton, moulting behaviour and the fig–fig wasp mutualism, amongst others (Bodson, 1983). He did of course publish some incorrect facts such as that of the spontaneous generation of flies from dung, butterflies from leaves and bedbugs from sweat. It was not until the Renaissance that entomology was revived as a science (Southwood, 1977) and then really only as collections of past knowledge rather than the presentation of new facts; perhaps the most well-known being the multi-authored entomological text *Insectorum Theatrum* edited by Thomas Muffett (1634), although probably more famous as being Little Miss Muffet's father. It was, however, not until the invention of the microscope by Antony van Leeuwenhoek (1632–1723) which allowed Robert Hook (1635–1703) and Jan Swammerdam (1637–1680) to describe details of insect morphology previously unknown such as the compound eye and insect mouthparts (Hooke, 1665; Swammerdam, 1669) that the true complexity of the insect world was revealed. At the same time, the early experimental entomologist Franceso Redi (1626–1697), debunked the theory of spontaneous generation (Redi, 1668) an experiment that is still conducted in schools around the world to this day. The ability to distinguish minute differences in morphology enabled insect species description and systematics to blossom (e.g. Ray, 1705). The development of the binomial system of nomenclature by Linnaeus (1735), was a landmark publication and it and its subsequent editions, ensured that entomology as a science and cultural service, really begin to make an impact.

Table 1. Names and dates of foundation of some of the earliest entomological societies in the world.

Name of society/club	Date of establishment
The Aurelian Society*	1743
The Entomological Club	1826
Société Entomologique de France	1832
The Royal Entomological Society	1833
Société Entomologique de Belgique	1857
Entomological Society of Philadelphia†	1859
Entomological Society of Canada	1863
Società Entomologica Italiana	1869

*No longer in existence.
†Became the Entomological Society of America in 1906.

The next development in the history of entomology as a cultural service was the formation of entomological societies, the first being the Aurelian Society in London (1743), according to Southwood (1977), Aurelia was another name for the chrysalis of a butterfly. Over the next hundred years or so a number of entomological societies were formed (Table 1), many still in existence although the failure rate was fairly high (Southwood, 1977). Although the early societies were originally started because of an interest in collecting, this changed after the publication of *Darwin's Origin of the Species*, and they became more scientific and professional in nature. Today, even those specialist societies centred on insect orders, whose members are mainly amateurs, adopt a scientific approach to their collecting activities, publishing journals, books, and distribution maps.

Ecology

I have opted to give ecology a separate heading as I feel that there is a tendency for modern day ecologists, many of whom work on vertebrates, to overlook the contribution made to their science by entomologists. That said I will only give three brief case studies to illustrate the importance of entomology to ecologists. I will, however, consider the third case study in some detail.

Mimicry. Two early examples that have become textbook examples and are commonly referred to by vertebrate biologists (e.g. Schaefer *et al*., 2002; Sanders *et al*., 2006; Caro, 2014; Hartman *et al.*, 2014) are the concepts of Batesian mimicry (Bates, 1861) or protective or defensive mimicry, where a harmless organism takes on the appearance of a dangerous or venomous organism, and Müllerian mimicry (aposematism) (Müller, 1878) in which two or more dangerous species share warning signals. These concepts were based on many years of independent work by Bates and Müller in Brazilian rainforests and based on their observations of the Heliconiid butterflies that they collected there. Judging by the literature, those vertebrate biologists and ecologists working on amphibians and reptiles have been the most heavily influenced non-entomologists (see references already cited above) although of course the study of mimicry is still popular within the entomological world (Howse, 2013; Merrill *et al*., 2014).

Functional responses. The growth of animal populations and the interactions between predators and their prey has long been of interest to biologists and ecologists, although much of the early theoretical work was conducted by entomologists (e.g. Nicholson, 1933). It was, however, not until 1949, that the disparate conceptual strands of pre-war population dynamics were drawn together in one coherent whole in a paper that has had an immense influence on the study of population dynamics (Solomon, 1949). Solomon was the first ecologist to formalise the term ‘functional response’. This was an inspirational paper and despite its length, inspired early modern mathematical ecologists such as Holling (1959), with his famous disc equation, Watt (1965) modelling biological control strategies, Varley and colleagues working on predator–prey interactions (e.g. Varley & Edwards, 1957; Varley *et al.*, 1973), and through them to current cohort of modern ecologists. A truly influential piece of writing and a concept that is the mainstay of biological control research including my own (e.g. Wittman & Leather, 1997; Aqueel & Leather, 2012; Midthassel *et al*., 2014).

Island biogeography. Modern mathematical island biogeography [sometimes termed insular biogeography (e.g. Whitehead & Jones, 1969)], has its roots in plant ecology (Arrhenius, 1921, 1923) but it was not until the pioneering work of the entomologists Philip Darlington (Darlington, 1943, 1957) and E O Wilson (1961) and of course the publication of MacArthur and Wilson’s book in 1967, that it began to enter the consciousness of mainstream ecology. The paper that really attracted the attention of entomologists and was to have a huge influence on conservation biology was, however, Southwood (1961). This was an astonishingly influential paper although it took some years for its influence to be really appreciated. Southwood was curious as to why some tree species had more insect species associated with them than others. He made comparisons between trees in Britain, Russia, and Cyprus and demonstrated that those trees that were more common in those regions and had a wider distribution had more insect species associated with them. He also laid the foundations of invasion biology by showing that introduced trees tended to have fewer insects than native species. He hypothesised that the number of insects associated with a tree species was proportional to its recent history and abundance and were a result of host encounter rates and evolutionary adaptation to those hosts. Using Godwin’s data on the Quaternary records of plant remains (Godwin, 1956) he then tested this hypothesis, making the assumption that the pollen records could be used as a proxy for range as well as evolutionary age. For those tree species where the points were significantly above or below the line he hypothesised that those above the line were a result of having a large number of congeners and those below the line either as being taxonomically isolated and/or very well defended.

He further tested his ideas about the evolutionary nature of the relationship by looking at trees and insects in Hawaii, (Southwood, 1960) showing that there was a strong relationship between tree abundance and distribution and the numbers and specificity of their associated insect species (Fig. 1). Some years later Dan Janzen (Janzen, 1968) wrote

> *It is unfortunate that the data on insect-host plant relationships have not in general been collected in a manner facilitating analysis by MacArthur and Wilson’s methods (as is the case as well with most island biogeographical data). What we seem to need are lists of the insect species on various related and unrelated host plants, similarity measures between these lists (just as in Holloway and Jardine’s, 1968 numerical taxonomic study of Indo- Australian islands), knowledge of the rates of buildup of all phytophagous insect species on a host plant new to a region, where these species come from, etc. Obviously, the insect fauna must be well known for such an activity. The* ***English countryside*** *might be such a place; it has few “islands” (making replication difficult) but a very interesting* ***“island”*** *diversity, with such plants* ***as oaks being like very large islands and beeches being like very small ones****, if the equilibrium number of species on a host plant (Southwood, 1960; Elton, 1966) is any measure of island size.*

Janzen returned to the subject of trees as islands a few years later (Janzen, 1973), basing his ideas on the assumption that the number of herbivorous insects associated with a plant increases with the size of the host plant population (Opler, 1974) and firmly established that trees could be considered to be ecological islands. Opler (1974) also suggested that this approach could be used for predicting pest problems in agricultural systems, which did indeed prove to be the case (e.g. Strong *et al*., 1977; Rey *et al*., 1981), and that the concept of habitat islands and the species-area relationship could be used when designing and evaluating nature reserves, something which has come to pass (e.g. Higgs, 1981). Southwood’s 1961 data were later reanalysed using tree range based on the Atlas of the British Flora (Perring & Walters, 1962), to explain the patterns seen (Strong, 1974; Kennedy & Southwood, 1984).

It was the publication of this paper that really opened the floodgates of research in this area, and papers examining the species-area relationships of different insect groups and plant

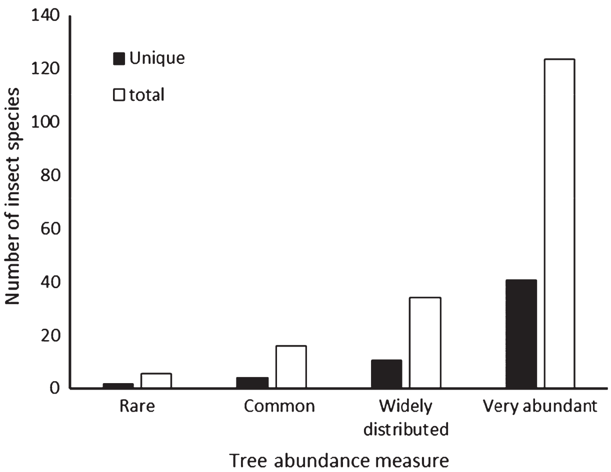

Fig. 1. Relationship between tree abundance and number of insect species associated with them (drawn using data from Southwood, 1960).

communities proliferated [e.g. leafhoppers (Claridge & Wilson, 1976), bracken (Rigby & Lawton, 1981), leaf miners (Claridge & Wilson, 1982), rosebay willow herb (MacGarvin, 1982), and Rosaceous plants (Leather, 1985, 1986)]. Although not nearly as popular an entomological subject as it was in the 1980s, people are still extending and refining the concept (e.g. Brändle & Brandl, 2001; Sugiura, 2010; Baje *et al*., 2014) and as well as inspiring at least two generations of entomologists and ecologists, including me, is still very relevant today.

A further very important development from island biogeography and of great importance in the world of conservation biology worldwide, was that of metapopulation theory which was championed and refined by two very eminent entomologists, Ilkka Hanski and Chris Thomas (e.g. Hanski & Gilpin, 1991; Thomas, 1994; Hanski *et al*., 1995).

Economics

Insects and allied arthropods are with us everywhere, even if we are unaware of their presence, from the follicle mites in our eyebrows to the detritivores roaming even the most fastidiously cleaned household. The negative effects of insects on human economies and societies through their roles a crop pests, medical, veterinary and household pests (e.g. Gullan & Cranston, 2011), are well known and recognised, but the important positive roles that insects have had on human economics and society are less appreciated.

In the introduction to his highly informative and interesting paper, Edward Melillo (2014) asks us to consider what three very different events have in common: 1781 – the surrender of General Cornwallis to Major-General Lincoln of the North American Continental Army, 1841, the founding of the Hereke Imperial Carpet Manufacture by Sultan Abdulmecid I, and in 1944, the release by Decca Records of an album by Ella Fitzgerald and The Ink Spots. As a clue, the British Army uniform at the time, was characterised by a red jacket, the carpets made by the Hereke Imperial Carpet Manufacture were, and still are made of silk, and in 1944, records were made of shellac. The answer is of course, insects; the red dye used by the British Amy was cochineal produced by crushing the cactus feeding bug *Dactylopius coccus* (Hemiptera), silk is produced by the silk worm, *Bombyx mori* (Lepidoptera) and shellac by the scale insect *Kerria lacca* (Hemiptera). Three insects that have had a huge economic and social impact on the human race. These products are all still used to this day, cochineal or as it appears on product labels, carmine, carminic acid, Natural Red 4 or E120 is present in food and drink products and cosmetics as is shellac which is also used in the sweet and pharmaceutical industry. It should also be noted that prior to the use of shellac for making records, sound was recorded using wax cylinders, yet another insect by-product. The economic and social consequences of these insect–human interactions are thoroughly documented in Melillo's paper so I do not propose to elaborate them further.

One further and perhaps overlooked effect of insects on the economic activity of nation states is their influence on the various postal services around the world (Foster, 2006). Insects figure prominently on the postage stamps of most countries (Fig. 2). In this role they play both an economic one, in that the stamps are bought for practical use, but also because of their beauty or aesthetic value, they also acquire added economic and cultural value as they are collected by philatelists. In this instance, they are playing a dual economic and cultural role, lying as they do on the borderline of economics and the arts.

Human medicine

The interactions between humans and insects in a medical context is generally seen in a negative context; malaria, sleeping sickness, the various arboviruses transmitted to humans, rickettsias, spirochaetes, *etcetera*; the list is long and frightening and the common factor blood-sucking insect vectors (Cloudsley-Thompson, 1973). This list of potentially fatal diseases is of course, not the whole story. From very early days, the detailed study of insect vectors has added greatly to our understanding of insect behaviour and the realisation that the study of vector ecology and biology was necessary to gain a full understanding of how to control them (e.g. Zetek, 1915; Phillips, 1930). An unexpected bonus of the study of vectors was the discovery by Julius Wagner-Jauregg that he could induce curative fevers in late-stage syphilitic patients suffering from dementia paralytica using infective *Anopheles* mosquitoes, 'fever therapy', for which he was awarded the Nobel Prize in 1927 (Whitrow, 1990). More recently, however, the most beneficial medical spin-off from entomology has been in the field of cryobiology.

For many years, the Society for Cryobiology annual meeting brought together the so-called 'cryopreservation blood and guts people' with the insect physiologists. Many sessions were run on the theme of 'What can medical-related scientists learn from nature i.e. from the natural systems in insects?' (J. S. Bale, pers. comm.). John Baust, Kenneth Storey, and Richard Lee were involved in this early work looking at freeze-tolerant animals (Baust, 1973; Baust & Lee, 1982) and their possible applications to cryostorage (Storey, 1990). This led on to the

Fig. 2. Examples of some of the many insect postage stamps that almost every country produces. Photograph by author.

application of cryobiology to diabetes research. Albeit the latter work used amphibians (Wolanczyk *et al*., 1990), which are not of course insects, but the idea of looking for ice-nucleating activity in the blood of freeze-tolerant vertebrates came from their early insect work (Baust, 1981). In addition, the ability to cryopreserve insect embryos has aided the cryostorage of *Drosophila* for genetic research which has in turn, implications for human medicine. The human cryopreservation people are also interested in the natural ability of some insects to achieve vitrification, which bypasses ice crystallisation, which is to be avoided to prevent tissue damage (Fuller & Paynter, 2004).

Another, and more direct use of insects in medicine, is the ancient, but now once again commonly used practice of applying maggots to wounds to remove necrotic tissue painlessly and hygienically; maggot debridement therapy (Shi & Shofler, 2014).

Food (entomophagy)

Insects have, given that they are still a large part of many people's diet, particularly in the tropics (Dezerefos & Witkowski, 2014), almost certainly been part of the human menu since we were hunter gatherers. There are, for example, cave paintings dating back to the ice age showing human exploitation of wild bees and honey (Pager, 1976). According to Southwood (1977), Aristotle states that cicadas are tastier when young and according to the *New Testament* (Mark 1 : 6), John the Baptist survived or a considerable time on locusts and wild honey. Insect larvae are a common source of protein, e.g. witchetty grubs, larvae of the Cossid *Endoxyla leucomochla*, cerambycid beetle larvae, and honey ants are an important protein and lipid source for Australian aboroginals (Cranston, 2010) whereas Mopane worms (Lepidopteran larvae) are a common dietary addition in southern Africa (e.g. Hope *et al*., 2009; Gondo *et al*., 2010). In some parts of the world, 5–15% of the protein in human diets comes from insects (Yen, 2009). Eating insects now seems to be an essential component of the modern reality TV show but more seriously, the concept of entomophagy for both humans and their livestock is becoming an every-day reality (Cerritos, 2009). Given the number of approaches I receive from people interested in starting up insect breeding factories with the aim of producing them for human consumption, it is likely that we will see processed insect protein playing a more prominent role in human diets even in those parts of the world where insects do not form a traditional part of their diet (Micek *et al*., 2014)

The arts

Insects and entomologists have had a role in human culture for millennia. As mentioned earlier, cave paintings of honey hunting in the Ice Ages exist, and images of insects were commonplace in ancient civilizations, scarabs, and locusts in Egypt for example (Southwood, 1977). In addition, there is a rich insect fauna to be found both adorning and forming artefacts from ancient Mesoamerica (Woodger, 2011). The beauty of insects has inspired artistic entomologists such as the two Henry Seymers (Vane-Wright & Hughes, 2005) and Maria Sibylla Merian famous for her book *Insects of Surinam* published in 1705. Insects appear in many classical paintings e.g. Albrecht Dürer's watercolour, *The Stag Beetle* dated 1505 and Justus Juncker's *Pear with Insects* from 1765 to name two early examples. Victorian fairy paintings were much influenced by insects e.g. Walter Morgan's *A Fairy Ring* where the wings of the fairies are closely modelled on those of swallowtail butterflies.

Insects commonly appear in literature, not always positively, although Aesop used insect imagery very successfully in his *Fables* urging us to be industrious as the ant and not to fritter away our time as the grasshopper did. Illustrations of Insects also appear in a number of medieval manuscripts, sometimes just as marginal doodles, but also as part of the main text (Briggs, 2014). Lewis Carrol's Alice in Wonderland spends some time in conversation with a large hookah smoking caterpillar and Roald Dahl's *James and The Giant Peach* details a wondrous journey in the company of assorted arthropods. We all love Eric Carle's *The Very Hungry Caterpillar* despite the entomological inaccuracies. More negatively, Franz Kafka utilises gruesome insect imagery in *Metamorphosis*, William Golding's *Lord of the Flies* addresses our dark side, and science-fiction writer Keith Roberts plays on our fears of wasps in his apocalyptic novel *The Furies*. On the other hand, Barbara Kingsolver enthralled us with her factually accurate story of the Monarch migration gone astray *in Flight Behavior*. Entomologists have also doubled up as novelists, some more famously than others, e.g. Vladimir Nabakov and Ernst Jünger. Poets have addressed insects directly e.g. *To a Louse* by Robert Burns, and *To a Butterfly* by William Wordsworth. Marvel and DC comics have over the years, featured 232 superheroes and villains either based on insects or with insect-like characteristics, e.g. Ant-man, Spider-Man, The Blue Beetle, Firefly, and many others (Da Silva *et al*., 2014).

In the world of cinema, insects have often played major roles, in most cases to the despair of watching entomologists e.g. *Beginning of the End* (1957) in which giant grasshoppers threaten Chicago, *Genocide* a Japanese disaster movie from 1968 in which all the insects in the world attack the human race, *The Swarm* (1978) starring Michael Caine as an entomologist battling African killer bees, *The Fly* (1986) starring Jeff Goldblum as the human-Dipteran hybrid, *Mosquito* (1995) in which mosquitoes feed on corpses from an alien spaceship crash with horrifying consequences, *Infested* (2002) in which insects eat their human hosts from the inside out, the list goes on. Not all insect-inspired films portray insects in a bad light, the charming but inaccurate *A Bug's Life* (1998) and *Antz* (1998) portray insects in a much more sympathetic manner and cartoon shorts often feature charming and amusing insect characters.

Insects have also inspired musicians and composers, Rimsky-Korsakov's *Flight of the Bumblebee*, the composer Bela Bartok collected insects as well as writing music inspired by their songs e.g. *Mikrocosmos, From the Diary of a Fly* (Rothenberg, 2013). Insects have also invaded the world of rock and roll from the names of groups, titles of albums, and tracks and of course as the subjects of songs (Coelho, 2000) and very few entomologists will not be familiar with Burl Ives' rendition of *The Ugly Bug Ball.*

It is clear that insects as a result of their ubiquity and variety, have inspired creative artists from all over the world, working in many different media, but not always to the benefit of insects or entomologists.

Engineering

Insects have also inspired engineers. Airless tyres based on the hexapod honeycomb design have been produced by the all-terrain vehicle manufacturer Polaris and went on sale at the end of 2013. The winner of the 2011 James Dyson award, Edward Linacre from Swinburne University of Technology in Melbourne based his design for a device, The Airdrop, to collect water from the air in desert environments on the Namib beetle, *Stenocares gracilipes,* which collects fog droplets on its elytra (Parker & Lawrence, 2001). Dragonflies and bees have provided inspiration for micro-drones, the DelFly Explorer and RoboBee developed respectively engineers at Delft Technical University in 2014 (de Croon *et al.*, 2012; Hennop, 2014) and Harvard University (Fuller *et al*., 2014). Biology as a source of engineering and technological solutions is now well recognised even to the extent of having a journal specifically devoted to the subject, *Bioinspiration & Biomietics* published under the auspices of the Institute of Physics with a high proportion of papers describing research inspired by insects.

Conclusion

Insects have had and continue to have a huge effect on the human race, both as pests and beneficials. Their cultural role is, however, often overlooked but that they have had a strong influence on the way we think about and perceive the natural world is undeniable. In some cultures, they have achieved near religious significance. Bushmen, for example, hold the praying mantis in very high regard because of its copulatory behaviour. The male being eaten by the female, is seen as a representation of the cycle of death and rebirth, a central tenet of many religions (Southwood, 1977). The early Christians believed that the bee reproduced without the help of a male, and it became a symbol of the Immaculate Conception and emblem of the Virgin Mary (Ferguson, 1954).

And if you ever need to answer the question posed at the beginning of this paper, this quotation from Simon Barnes (Barnes, 2014) will save you a lot of arm-waving.

But we should bless wasps every time we see one. Without wasps, the spread of knowledge across the history of human kind would have been desperately hampered. Because wasps invented paper. A wasp's nest is as exquisite a thing as you will see anywhere in the natural world. It is a glorious piece of architecture created from of wood pulp and spit, chewed up and manufactured into – paper. The Chinese cracked the technique a couple of thousand years ago and the rest is – in every sense – history.

I ask you, then, to raise your glass rather than your newspaper to the wasps you see as you take tea or drinks in the garden in the summer. These late-season hooligans live a highly evolved social life, are essential predators in a complex eco-system, they create a thing of genuine beauty, and without them, what would Shakespeare have written on? "I'll be waspish, best beware my sting," says Kate in The Taming of the Shrew.

Acknowledgements

Many thanks(?) to Archie Murchie for twisting my arm to give the plenary talk at Ento '15 in Dublin on which this paper is based. Also thanks to Fran Sconce for drawing my attention to some of the more bizarre literature sources. Finally thanks to all those colleagues who read and commented on earlier versions of this paper and to the two anonymous referees who drew my attention to some additional references that I had missed.

References

Aqueel, M.A. & Leather, S.R. (2012) Nitrogen fertiliser affects the functional response and prey consumption of *Harmonia axyridis* (Coleoptera: Coccinelldiae) feeding on cereal aphids. *Annals of Applied Biology*, **160**, 6–15.

Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.

Arrhenius, O. (1923) Statistical investigations in the constitution of plant associations. *Ecology*, **4**, 68–73.

Baje, L., Stewart, A.J.A. & Novotny, V. (2014) Mesophyll cell-sucking herbivores (Cicadellidae: Typhlocybinae) on rainforest trees in Papua New Guinea: local and regional diversity of a taxonomically unexplored guild. *Ecological Entomology*, **39**, 325–333.

Barnes, S. (2014) *Ten Million Aliens*. Short Books, London, U.K.

Bartomeus, I., Park, M.G., Gibbs, J., Danforth, B.N., Lakso, A.N. & Winfree, R. (2013) Biodiversity ensures plant-pollinator phenological synchrony against climate change. *Ecology Letters*, **16**, 1331–1338.

Bates, H.W. (1861) Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London*, **23**, 495–566.

Baust, J.G. (1973) Mechanisms of cryoprotection in freezing tolerant animal systems. *Cryobiology*, **10**, 197–205.

Baust, J.G. (1981) Biochemical correlates to cold hardening in insects. *Crybiology*, **18**, 186–198.

Baust, J.G. & Lee, R.E. (1982) Cryoprotectant triggering and diversity in two populations of overwintering *Eurosta solidaginis*. *Journal of Insect Physiology*, **28**, 431–436.

Bengtsson, J. (2015) Biological control as an ecosystem service: Partitioning contributions of nature and human inputs to yield. *Ecological Entomology*, **40**(S1), 45–55.

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. *Ecological Entomology*, **40**(S1), 124–135.

Birkin, L. & Goulson, D. (2015) Using citizen science to monitor pollination services. *Ecological Entomology*, **40**(S1), 3–11.

Bodson, L. (1983) The beginnings of entomology in Ancient Greece. *The Classical Outlook*, **61**, 3–6.

Brändle, M. & Brandl, R. (2001) Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology*, **70**, 491–504.

Briggs, S.J. (2014) Medieval manuscripts blog. *Bugs in Books*. [WWW document]. URL http://britishlibrary.typepad.co.uk/digitisedmanuscripts/2014/08/bugs-in-books.html [accessed on 19 December 2014].

Cariveau, D., Williams, N.H., Benjamin, F.E. & Winfree, R. (2013) Response diversity to land use occurs but does not consistenly stabilise ecosystem services provided by native pollinators. *Ecology Letters*, **16**, 903–911.

Caro, T. (2014) Antipredator deception in terrestrial vertebrates. *Current Zoology*, **60**, 16–25.

Cerritos, R. (2009) Insects as food: an ecological, social and economical approach. *CAB REviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, **4**, 1–9.

Chaplin-Kramer, R., De Valpine, P., Mills, N.J. & Kremen, C. (2013) Detecting pest control services across spatial and temporary scales. *Agriculture Ecosystems and Environment*, **181**, 206–212.

Claridge, M.F. & Wilson, M.R. (1976) Diversity and distribution patterns of some mesophyll-feeding leafhoppers of temperate trees. *Ecological Entomology*, **1**, 231–250.

Claridge, M.F. & Wilson, M.R. (1982) Insect herbivore guilds and species-area relationships: leafminers on British trees. *Ecological Entomology*, **7**, 19–30.

Cloudsley-Thompson, J.L. (1973) *Insects and History*. Weidenfeld & Nicholson, London.

Coelho, J. (2000) Insects in rock and roll. *American Entomologist*, **46**, 186–200.

Cranston, P.S. (2010) Insect biodiversity and conservation in Australasia. *Annual Review of Entomology*, **55**, 55–75.

de Croon, G.C.H.E., Groen, M.A., De Wagter, C., Remes, B., Ruisjink, R. & van Oudheusden, B.W. (2012) Design, aerodynamics and autonomy of the DelFly. *Bioinspiration and Biomimetics*, **7**, 025003.

Darlington, P.J. (1943) Carabidae of mountains and islands: data on the evolution of isolated faunas and on atrophy of wings. *Ecological Monographs*, **13**, 37–61.

Darlington, P.J. (1957) Zoogeography: The Geographical Distribution of Animals. John Wiley & Sons, Inc., New York, New York.

Da Silva, E.R., Coelho, L.B.N., dos Santos, E.L.S., Müller dos Campos, T.R., de Miranda, G.S., Araújo, T.C. *et al.* (2014) Marvle and DC characters inspired by insects. *Research Expo International Multidisciplinary Research Journal*, **4**, 10–136.

Dezerefos, C.M. & Witkowski, E.T.F. (2014) The potential of entomophagy and the use of the stinkbug, *Encosternum delegorguei* Spinola (Hemipera: Tessaratomidae), in sub-Saharan Africa. *African Entomology*, **22**, 461–472.

Dicks, L.V., Baude, M., Roberts, S.P.M., Phillips, J., Green, M. & Carvell, C. (2015) How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology*, **40**(S1), 22–35.

Ehrlich, P.R. & Mooney, H.A. (1983) Extinction, substitution, and ecosystem services. *Bioscience*, **33**, 248–254.

Elton, C.S. (1966) *The Pattern of Animal Communities*. Wiley, New York, New York.

Essig, E.O. (1936) A sketch history of entomology. *Osiris*, **2**, 80–123.

Ferguson, G. (1954) *Signs and Symbols in Christian Art*. Oxford University Press, Oxford.

Foster, W. (2006) Stamps of approval. *Antenna*, **30**, 120–12125.

Fuller, B. & Paynter, S. (2004) Cryobiology in reproductive medicine. *Reproductive Biomedicine Online*, **9**, 680–691.

Fuller, S.B., Karpelson, M., Censi, A., Ma, K.Y. & Wood, R.J. (2014) Controlling free flight of a robotic fly using an onboard vision sensor inspired by insect ocelli. *Journal of the Royal Society Interface*, **11**. DOI: 10.1098/rsif.2014.0281.

Gaston, K.J., Avila-Jiminez, M.L. & Edmondson, J.L. (2013) Managing urban ecosystems for goods and services. *Journal of Applied Ecology*, **50**, 830–840.

Godwin, H. (1956) *The History of the British Flora*. Cambridge University Press, Cambridge.

Gondo, T.J., Frost, P., Kozanyi, W., Stack, J. & Mushongahande, M. (2010) Linking knowledge and practice: assessing options for sustainable use of Mopane worms *(Imbasia belina)* in southern Zimbabwe. *Journal of Sustainable Development in Africa*, **12**, 281–305.

Gullan, P.J. & Cranston, P.S. (2011) *The Insects*. Wiley-Blackwell, Oxford, U.K.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics – brief history and conceptual domain. *Biological Journal of the Linnaean Society*, **42**, 3–16.

Hanski, I., Pakkala, T., Kuusaari, M. & Lei, G. (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, **72**, 21–28.

Hartman, R., Pope, K. & Lawler, S. (2014) Factors mediating co-occurrence of an economically valuable introduced fish and its native frog prey. *Conservation Biology*, **28**, 763–772.

Hennop, J. (2014) *Dutch scientists flap to the future with 'insect' drone* [WWW document]. URL http://phys.org/news/2014-02-dutch-scientists-future-insect-drone.html [accessed on 18 December 2014].

Higgs, A.J. (1981) Island biogeography theory and nature reserve design. *Journal of Biogeography*, **8**, 117–124.

Holling, C.S. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385–398.

Holloway, J.D. & Jardine, N. (1968) Two approaches to zoogeography: a study based on the distributions of butterflies, birds and bats in the Indo-Australian area. *Proceedings of the Linnaean Society of London*, **179**, 153–188.

Hooke, R. (1665) *Micrographia*. John Martyn, London, U.K.

Hooper, J.F. (1970) Economics, the ecosystem and conservation. *Journal of Range Management*, **23**, 148–150.

Hope, R.A., Frost, P.G.H., Gardiner, A. & Ghazoul, J. (2009) Experimental analysis of adoption of domestic Mopane worm farming technology in Zimbabwe. *Development Southern Africa*, **26**, 29–46.

Howse, P.E. (2013) Lepidopteran wing patterns and the evolution of satyric mimicry. *Biological Journal of the Linnean Society*, **109**, 203–214.

Janzen, D.H. (1968) Host plants as islands in evolutionary and contemporary time. *American Naturalist*, **102**, 592–595.

Janzen, D.H. (1973) Host plants as islands II. Competitive in evolutionary and contemporary time. *American Naturalist*, **107**, 786–790.

Kennedy, C.E.J. & Southwood, T.R.E. (1984) The number of species of insects associated with British trees: a re-analysis. *Journal of Animal Ecology*, **53**, 455–478.

Leather, S.R. (1985) Does the bird cherry have its 'fair share' of insect pests? An appraisal of the species-area relationships of the phytophagous insects associated with British *Prunus* species. *Ecological Entomology*, **10**, 43–56.

Leather, S.R. (1986) Insect species richness of the British Rosaceae: the importance of hostrange, plant architecture, age of establishment, taxonomic isolation and species-area relationships. *Journal of Animal Ecology*, **55**, 841–860.

Leather, S.R. & Quicke, D.L.J. (2009) Where would Darwin have been without taxonomy? *Journal of Biological Education*, **43**, 51–52.

Leather, S.R. & Quicke, D.L.J. (2010) Do shifting baselines in natural history knowledge threaten the environment? *Environmentalist*, **30**, 1–2.

Linnaeus, C. (1735) *Systemae Naturae*. Holmiae, Stockholm, Sweden.

Macadam, C.R. & Stockan, J.A. (2015) More than just fish food: ecosystem services provided by freshwater insects. *Ecological Entomology*, **40**(S1), 113–123.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Macfadyen, S., Kramer, E., Parry, H. & Schellhorn, N.A. (2015) Temporal change in vegetation productivity in grain production landscapes: linking landscape complexity with pest and natural enemy communities. *Ecological Entomology*, **40**(S1), 56–69.

MacGarvin, M. (1982) Species-area relationships of insects on host plants: herbivores on rosebay willowherbs. *Journal of Animal Ecology*, **51**, 207–223.

McKenzie, A.J., Emery, S.B., Franks, J.R. & Whittingham, M.J. (2013) Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? *Journal of Applied Ecology*, **50**, 1274–1280.

Melillo, E.D. (2014) Global entomologies: insects, empires, and the 'synthetic age' in world history. *Past and Present*, **223**, 233–270.

Merrill, R., Chia, A. & Nadeau, N.J. (2014) Divergent warning patterns contribute to assortative mating between incipient *Heliconius* species. *Ecology and Evolution*, **4**, 911–917.

Micek, J., Rop, O., Borkovcova, M. & Bednarova, M. (2014) A comprehensive look at the possibilities of edible insects as food in Europe – a review. *Polish Journal of Food and Nutrition Sciences*, **64**, 147–157.

Midega, C.A.O., Bruce, T.J.A., Pickett, J.A. & Khan, Z.R. (2015) Ecological management of cereal stemborers in African smallholder agriculture through behavioural manipulation. *Ecological Entomology*, **40**(S1), 70–81.

Midthassel, A., Leather, S.R., Wright, D.J. & Baxter, I.H. (2014) The functional and numerical response of *Typhlodromips swirskii* (Acari: Phytoseiidae) to the factitious prey *Suidasia medanensis* (Acari: Suidasidae) in the context of a breeding sachet. *Biocontrol Science and Technology*, **24**, 361–374.

Morandin, L.A., Long, R.F. & Kremen, C. (2014) Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape. *Agriculture Ecosystems and Environment*, **189**, 164–170.

Morge, G. (1973) Entomology in the Western World in antiquity and medieval times. *History of Entomology* (ed. by R. F. Smith, T. E. Mittler and C. N. Smith), pp. 40–45. Annual Reviews, Palo Alto, California.

Muffett, T. (1634) *Insectorum Sive Minimorum Animalium Theatrum*. Thomas Cotes for Benjamin Allen, London, U.K.

Müller, F. (1878) Ueber die Vortheile der Mimicry bei Schmetterlingen. *Zoologischer Anzeiger*, **1**, 54–55.

Nicholson, A.J. (1933) The balance of animal populations. *Journal of Animal Ecology*, **2**, 132–178.

Opler, P.A. (1974) Oaks as evolutionary islands for leaf-mining insects. *American Scientist*, **62**, 67–73.

Pager, H. (1976) Cave paintings suggest honey hunting activities in the Ice Age times. *Bee World*, **7**, 9–14.

Parker, A.R. & Lawrence, C.R. (2001) Water capture by a desert beetle. *Nature*, **414**, 33–34.

Perring, F.J. & Walters, S.M. (1962) Atlas of the British Flora. BSBI Nelson, London, U.K. & Edinburgh, U.K.

Phillips, J.F.V. (1930) The application of ecological research methods to the tsetse (*Glossina* spp.) problem in Tanganyika territory: a preliminary account. *Ecology*, **11**, 713–733.

Ray, J. (1705) *Methodus Insectorum*. Royal Society, London, U.K.

Redi, F. (1668) *Esperienze intorno alla generazione degl'insetti*. All'insegna della Stella, Florence, Italy.
Rey, J.R., McCoy, E.D. & Strong, D.R. (1981) Herbivore pests, habitat islands, and the species area relation. *American Naturalist*, **117**, 611–622.
Rigby, C. & Lawton, J.H. (1981) Species-area relationships of arthropods on host plants: herbivores on bracken. *Journal of Biogeography*, **8**, 125–133.
Rothenberg, D. (2013) *Bug Music: How Insects gave us Rhythm and Noise*. St. Martin's Press, New York, New York.
Sanders, K.L., Malhotra, A. & Thorpe, R.S. (2006) Evidence for a Mullerian mimetic radiation in Asian pitvipers. *Proceedings of the Royal Society B*, **273**, 1135–1141.
Schäkermann, J., Pufal, G., Mandelik, Y. & Klein, A.-M. (2015) Agro-ecosystem services and dis-services in almond orchards are differentially influenced by the surrounding landscape. *Ecological Entomology*, **40**(S1), 12–21.
Schaefer, H.C., Vences, M. & Veith, M. (2002) Molecular phylogeny of Malagasy poison frogs, genus *Mantella* (Anura: Mantellidae): homoplastic evolution of colour pattern in aposematic amphibians. *Organisms Diversity & Evolution*, **2**, 97–105.
Shi, E. & Shofler, D. (2014) Maggot debridement therapy: a systematic review. *British Journal of Community Nursing* (Suppl. 12), **19**, s6–s13.
Solomon, M.E. (1949) The natural control of animal populations. *Journal of Animal Ecology*, **18**, 1–35.
Southwood, T.R.E. (1960) The abundance of the Hawaiian trees and the number of their associated insect species. *Proceedings of the Hawaiian Entomological Society*, **17**, 299–303.
Southwood, T.R.E. (1961) The number of species of insect associated with various trees. *Journal of Animal Ecology*, **30**, 1–8.
Southwood, T.R.E. (1977) Entomology and mankind. *American Scientist*, **65**, 30–38.
Stanley, D.A., Gunning, D. & Stout, J.C. (2013) Pollinators and pollination of oilseed rape crops (*Brassica napus* L.) in Ireland: ecological and economic incentives for pollinator conservation. *Journal of Insect Conservation*, **17**, 1181–1189.
Storey, K.B. (1990) Biochemistry of natural freeze tolerance in animals: molecular adaptations and applications to cryopreservation. *Biochemistry and Cell Biology*, **68**, 687–698.
Strong, D.R. (1974) The insects of British trees: community equilibrium in ecological time. *Annals of the Missouri Botanical Gardens*, **61**, 692–701.
Strong, D.R., McCoy, E.D. & Rey, J.R. (1977) Time and the number of herbivore species: the pests of sugarcane. *Ecology*, **58**, 167–175.
Sugiura, S. (2010) Associations of leaf miners and leaf gallers with island plants of different residency histories. *Journal of Biogeograpgy*, **37**, 237–244.
Swammerdam, J. (1669) *Historia Insectorum Generalis*. Dreunen, Utrecht, The Netherlands.
Thomas, C.D. (1994) Extinction, colonization, and metapopulations – environmental tracking by rare species. *Conservation Biology*, **8**, 373–378.
Ulyshen, M.D. (2015) Insect-mediated nitrogen dynamics in decomposing wood. *Ecological Entomology*, **40**(S1), 97–112.
Vane-Wright, R.I. & Hughes, H.W.D. (2005) *The Seymer Legacy: Henry Seymer and Henry Seymer Jnr of Dorset and their Entomological Paintings with a Catalogue of Butterflies and Plants (1755–1783)*. Forrest Text, Tresaith, U.K.
Varley, G.C. & Edwards, R.L. (1957) The bearing of parasite behaviour on the dynamics of insect host and parasite dynamics. *Journal of Animal Ecology*, **26**, 471–477.
Varley, G.C., Gradwell, G.R. & Hassell, M.P. (1973) Insect Population Ecology. Blackwell Scientific, Oxford, U.K.
Watt, K.E.F. (1965) Community stability and the strategy of biological control. *Canadian Entomologist*, **97**, 887–895.
Westman, W.E. (1977) How much are nature's services worth? *Science*, **197**, 960–964.
Whitehead, D.R. & Jones, C.E. (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution*, **23**, 171–179.
Whitrow, M. (1990) Wagner-Jauregg and fever therapy. *Medical History*, **34**, 294–310.
Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist*, **95**, 169–193.
Wittman, E.J. & Leather, S.R. (1997) Compatability of *Orius laevigatus* Fieber (Hemiptera: Anthocoridae) with *Neoseiulus (Amblyseius) cucumeris* Oudemans (Acari: Phytoseiidae) and *Iphiseius (Amblyseius) degenerans* Berlese (Acari: Phytoseiidae) in the biocontrol of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae). *Experimental and Applied Acarology*, **21**, 523–538.
Wolanczyk, J.P., Storey, K.B. & Baust, J.G. (1990) Ice nucleating activity in the blood of the freeze-tolerant frog, *Rana sylvatica*. *Cryobiology*, **27**, 328–335.
Woodger, M. (2011) Insects in the art and mythology of ancient Msoamerica (Part 1). *Antenna*, **35**, 97–101.
Yen, A.L. (2009) Entomophagy and insect conservation: some thoughts for digestion. *Journal of Insect Conservation*, **13**, 667–670.
Zetek, J. (1915) Behavior of *Anopheles albimanus* Wiede. and *tarsimaculata* Goeldi. *Annals of the Entomological Society of America*, **8**, 221–271.

Accepted 17 March 2015
First published online 5 May 2015