Antenna

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Royal Entomological Society

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Submissions are made by email to *antenna@royensoc.co.uk* and reviewed by *Antenna's* editorial team. There are no page charges for publication in *Antenna*, where we encourage use of full colour figures and photographs to accompany text. Standard articles are normally 1,000–3,000 words in length and submitted with four to eight images (file should be original size of image taken and not reduced in size nor cropped heavily).

Cover Picture: Acorn and Nut Weevil on a type of Foxtail grass seed head. Tim Crabb, see page 106.

Editorial

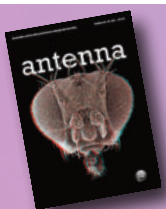
I don't think we've ever done this before. Sadly, every entomologist eventually re-joins the carbon cycle. An obituary in *Antenna* for those who have contributed greatly to entomology and to the Society is always appropriate. Few, if any, though, can have contributed more to both than Simon Leather, who died tragically young by modern standards. He joined the Society as a Fellow in 1978 and held a committee and/or editorial position pretty much ever since. He contributed hugely to the body of knowledge covering both forest and agricultural entomology and inspired the new generation of entomologists like no other. This issue is dedicated to him. Stuart Reynold's Research Spotlight majors on Simon's passion, aphids. The six articles that follow are written by Simon's students, then Allan Watt provides a moving obituary. Maya Leonard reviews Simon's amazing new book. Simon's legacy will live on for a very long time. Indeed, it will be self-perpetuating.

The Society has a new strategy, about which you will already have heard a lot. The exciting launch is described herein. Fulfilment of the strategy will be supported by RES staff, many of whom are new to the Society. You will now be able to put faces to the names.

In the previous issue, we said thanks and cheerio to our long-serving editor, Dave George. This time we say thanks and a fond farewell to Hugh Loxdale as an associate editor. With this issue, I have been helped considerably by Tom Pope, who worked with Simon Leather for many years. I'm delighted to say that he has apparently enjoyed the editorial experience so much that he will step up from being an associate editor to an editor. We will also be joined from the next issue by Dafydd Lewis as an editor. Not only that, but we have four, yes four, new associate editors. Patrick Vyvyan has lived for a long time in Chile and will encourage contributions from that part of the world. Jes Bartlett will do the same for Scandinavia and Moses Musonda for parts of Africa. If you would like to represent another part of the world, please let me know. Jane Phillips and Andrew Boardman will lower the average age of the editorial board and help ensure that *Antenna*'s content meets the aspirations of younger members. Welcome to you all. *Antenna*'s future is looking very strong indeed!

Very many thanks to all contributors.

Richard Harrington



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Index and online copies

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Antenna

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Letter from the President

It does not seem possible that my term as President of the Royal Entomological Society is coming to an end. It has been such a privilege to work alongside you all. I am very honoured to be part of our amazing entomological community. I am very much looking forward to my continued connections and collaborations through the Society but delighted that Professor Jane Hill will be the next President. I know the Society will flourish under her leadership and with the wider membership who show their commitment in so many diverse and incredible ways. I will look forward to a little extra time with the ladybirds!

The launch of the Royal Entomological Society Strategy 2022–2025 was the culmination of consultation far and wide across the membership; an amazing celebration of the collective insights from so many of you. I have also been keenly following the progress with the Grand Challenges and these will inform and underpin our future directions. The ideas captured through the collaborative Grand Challenges process are diverse and far-reaching, spanning engagement and outreach to blue skies research with many opportunities for interdisciplinary approaches. These are certainly exciting times for insect science with increasing recognition of the importance of insects to people everywhere.

So, as I step aside as President, I would like to express my thanks to the amazing trustees and staff members that I have worked with on Council – I am indebted to them for the immense amount of time, energy and expertise each and every one of them has devoted to the Society. The work involved in guiding the Society through this time of rapid, and in some ways dramatic, change has been demanding for everyone. I am extremely appreciative of the dedicated and thoughtful way in which everyone has approached the myriad of tasks presented to them. I would also like to welcome all the new staff members, committee members and everyone taking on new roles across the Society.

I have happy memories of my time with the Society and I am looking forward to more. We will continue to share entomological adventures together – it won't surprise anyone that I have many more ladybird tales to tell (interspersed with parasitic wasps and flies and even the occasional moth … and all the other amazing insects that never cease to capture my imagination). The Society will be there to support your entomological journey too and I look forward to hearing your exciting stories along the way.

Over to you Jane…I am quite sure you will have joyous times as President and I know the Society will gain much from you too.

Helen Roy
President
Royal Entomological Society

Correspondence

Pieris brassicae in New Zealand

I am mystified by the report in the article on *Pieris brassicae* in New Zealand (*Antenna* **45**(4) 173–175) to the effect that the NZ authorities consider that species a threat to endangered endemic Fabaceae. The obligate relationship of this butterfly with glucosinolate-producing plants was first documented by Verschaffelt in 1910 – it is one of the classic histories in chemical ecology – and has been amply validated ever since. I do not know of a single credible report of *P. brassicae* on any Fabaceous host. Some endemic South American pierines have associations with both Fabaceae and Brassicaceae, but I know of only one species (*Tatochila distincta*) recorded on both (by me!). Whence comes this decision by the NZ folks?

Arthur M. Shapiro
University of California, Davis

Response from John Feltwell:

The reasons why the Large White butterfly has become such a successful species with over 100 species of foodplants is indeed because it has mostly exploited the chemical-rich Cruciferae (c. >50%) for its own aposematic defences as well as relying on four other plant families which are within its list of 'Principal Families' of foodplants. It is also known from eight species from seven other 'Secondary Families' (see Foodplants chapter in the author's 1982 book in *Series Entomologica*, pp 97–117). Keeping the butterfly's options open seems to me a good evolutionary strategy in a changing biodiverse floral world, and keeping a good eye out for the Large White seems rather sensible for the NZ authorities.

John Feltwell
Wildlife Matters

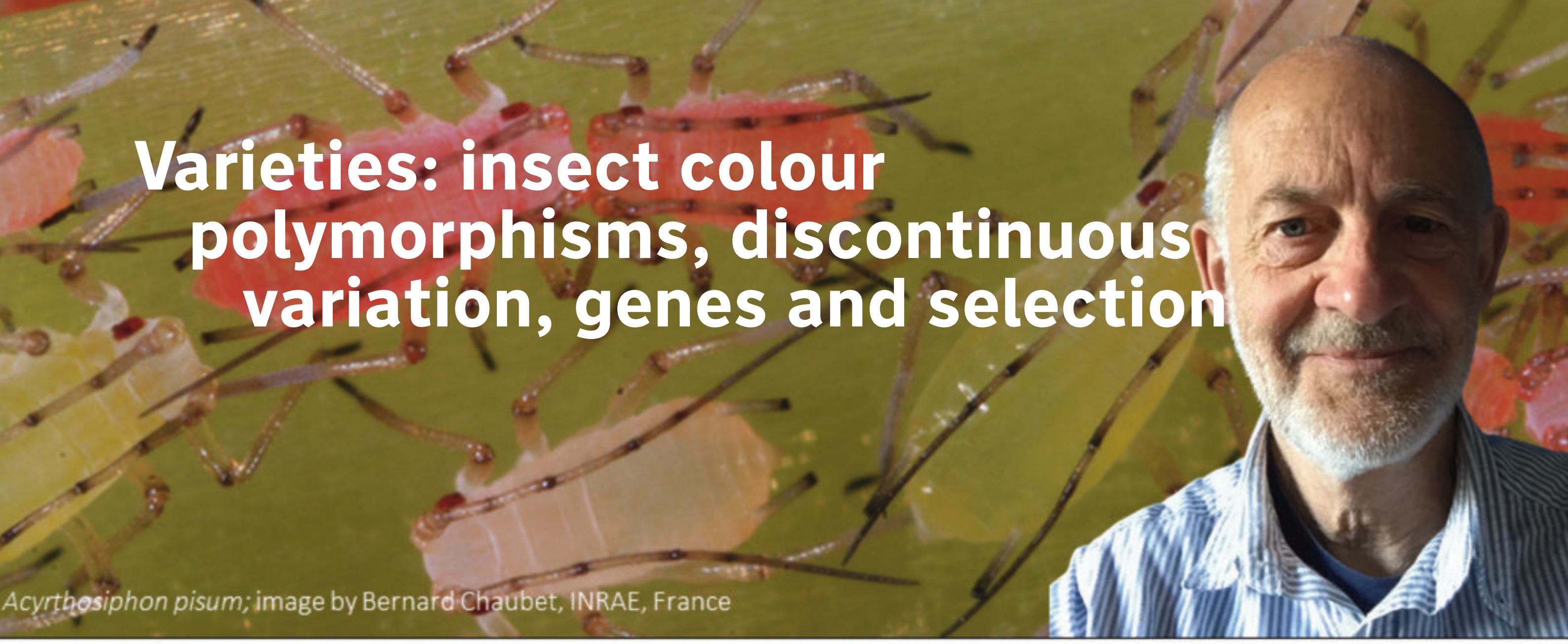
Response from Arthur Shapiro

Fine. But the authenticated hosts are all glucosinolate-rich plants*, e.g.*, *Capparis* and *Tropaeolum*. I regard non-glucosinolate-plant records as spurious unless proven otherwise.

Furthermore, the use of serially-transmitted glucosinolates as chemical defence by *P. brassicae* larvae, alluded to by Feltwell, has been seriously challenged; for example, see Müller *et al.* (2003; *Chemoecology* **13**, 47–54). This paper is very widely overlooked. It is far more rigorous than the usually-cited Aplin *et al.* (1975; *Journal of Entomology Series A, General Entomology* 50**,** 73–78), which it very effectively contradicts.

Arthur M. Shapiro
University of California, Davis

Varieties: insect colour polymorphisms, discontinuous variation, genes and selection



Acyrthosiphon pisum; image by Bernard Chaubet, INRAE, France

RESEARCH SPOTLIGHT

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Organisms belonging to the same species are sometimes highly variable in appearance

Variation: the raw material for evolution

Organisms belonging to the same species are sometimes highly variable in appearance. This is a problem for taxonomists; when shape and colour are not uniform within the available specimens, it's tricky to describe a species in the first place, and thereafter difficult to be sure that you have classified it correctly. But variation is interesting in itself. Why does it occur and how is it maintained? This article is specifically about one particular kind of variation termed **polymorphism**, the situation where discrete heritable forms co-occur within a species. Polymorphism is important because when variation is heritable it is the raw material of evolution. Colour polymorphism is particularly easy to investigate and has been historically important in developing ideas about how the genetic structures of populations evolve (McKinnon *et al.* 2010). The famous case of industrial melanism in the geometrid moth *Biston betularia* (Cook, 2018) will quickly come to mind, but in the present article aphids emerge as the main characters, although other insects set the scene and put in occasional appearances as the plot develops.

Polymorphism matters because phenotypic variation is required for adaptive evolution; without genetic variation, natural selection would have nothing to select. Charles Darwin was aware of this and in his great work *On the Origin of Species* (Darwin, 1859) he paid particular attention to the existence within species of 'varieties'. Although he clearly recognised their centrality in thinking about the evolution of life, Darwin wasn't very incisive about what either varieties or species actually were. He said:
"No one definition (of species) has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. Generally the term includes the unknown element of a distinct act of creation. The term "variety" is

Polymorphism matters because phenotypic variation is required for adaptive evolution

almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved".

This passage nevertheless makes clear that the kind of variety that is subject to natural selection is necessarily heritable.

Of course, Darwin didn't use the term 'polymorphism' because that word was not yet used in a biological context in the mid-nineteenth century. As far as I can tell, it was first used in print by the pioneer of genetics, William Bateson[1] (1894, page 42), who said: "*Nature abounds with examples of colour-polymorphism*". But in fact, he used the P-word very sparingly, and evidently preferred the terms 'monomorphic' and 'dimorphic' (*e.g.*, Bateson *et al.*, 1892); nevertheless, the word 'polymorphic' seems to have trickled into general scientific use at around this time. A paper in German by Jacobson (1910) used "*polymorphismus*"; two in English that soon followed were by Gerould (1911) and Fryer (1914). All of these works (as it happens) refer to colour variation in insects. Doubtless I have missed other publications from this eventful period in the history of genetics, but it appears that insects figured prominently from the start in the development of the idea of polymorphism. By 1930, R.A. Fisher was able to use 'polymorphism' (although still very infrequently) in its modern scientific sense in his hugely influential book "*The Genetical Theory of Natural Selection*". To describe polymorphism's separate forms, Julian Huxley (1955) invented the word 'morph', a term which we still use. He also said that he personally liked the term 'morphism' better than 'polymorphism', but no-one seems to have since taken any notice of his preference.

The discontinuous distributions of William Bateson

Polymorphism is surprisingly tricky to define. A much-quoted attempt by E.B. Ford (1945) is as follows: "*the occurrence together in the same habitat of two or more distinct genetic forms of a species in such proportion that the rarest of them cannot be maintained by recurrent mutation*". I want to call our attention to two aspects of this formulation. First, Ford specifically excluded genetic variation that is caused by recurrent mutation as a valid polymorphism. He did this because he was himself particularly interested in polymorphisms that were maintained by natural selection. But in fact, over the last 50 years a large part of the literature about polymorphism has specifically concerned exactly that class of polymorphisms that *is* explained by recurrent mutation and the subsequent genetic drift of selectively neutral alleles. This is because such 'silent' polymorphisms are good markers for tracing phylogenies, evidently something that Ford didn't foresee as possible.

Polymorphism is surprisingly tricky to define

Second, a key word here is 'distinct'; a similar but slightly stronger term often used today is 'discrete'. This 'distinctness' is basically a statistical concept, and it derives directly from Bateson's early work, summed up in his book of 1894 on variation. I confess here that I'm a fan of Bateson. His approach is nicely illustrated by a study of forceps length in the earwig *Forficula auricularia* (Bateson *et al.*, 1892). Discovering by chance that the remarkably dense populations of earwigs on the Farne Islands (a tiny archipelago off the coast of Northumberland) included an unusually high proportion of long-forceped males, Bateson took a sample of 1,000 insects (actually he got his daughter to collect them!) and measured all of the 583 males to show that the distribution was bimodal (Fig. 1A). More than 100 years later, Tomkins (1999) showed that forceps length in male *F. auricularia* is indeed due to a gene–environment interaction.

Bateson's statistical approach can also be applied to colour polymorphism but, in this case, it is not a matter of measuring but of categorising. An example of how Bateson approached this can be seen in a paper from 1895, in which he reported that while doing fieldwork in Granada, Spain, he had investigated the colour morphs of the chrysomelid beetle *Gonioctena variabilis*, which (as implied by its specific name) is exceptionally variable in appearance (Fig. 1B). Bateson catalogued the various colour forms and observed that although all colour types were present in both sexes, their distribution differed between male and female. He also found that intermediate forms were less common than the main categories of spotted and striped, red, green and melanic. A point of interest is the complete lack in his paper of tests of 'statistical significance'; in the last decade of the nineteenth century, you evidently just looked at the distribution and formed an opinion about it. How different from today! Impressively, Bateson began by reassuring himself that *G. variabilis* was indeed a single species, noting that the frequencies of colour morphs seen in mating pairs were distributed as expected from their frequency in the general population.

In the end, Bateson was unable to come up with a coherent model of how polymorphism was maintained in the beetle population. Nevertheless, he evidently gained satisfaction by concluding the paper with a parting shot at Alfred Russel Wallace, with whom he was having an argument about whether polymorphism 'matters' to the animal concerned (Wallace thought that it was unimportant). Bateson responded testily: "*I do not find Mr. Wallace offering evidence, and I am not even aware that he has even hazarded a guess*". I find it astonishing that the up-and-coming young man (he was 34) was prepared to be so rude in public to the then most eminent living evolutionist. It's also interesting that these two prominent men were so intransigent in their positions; in fact, the answer to this question is not at all obvious, and the debate about whether genetic polymorphisms are adaptive or neutral has continued more or less ever since (see for example

[1] Bateson is an important figure in this article. He was a Fellow of the Royal Entomological Society. See Figure 1Ad.

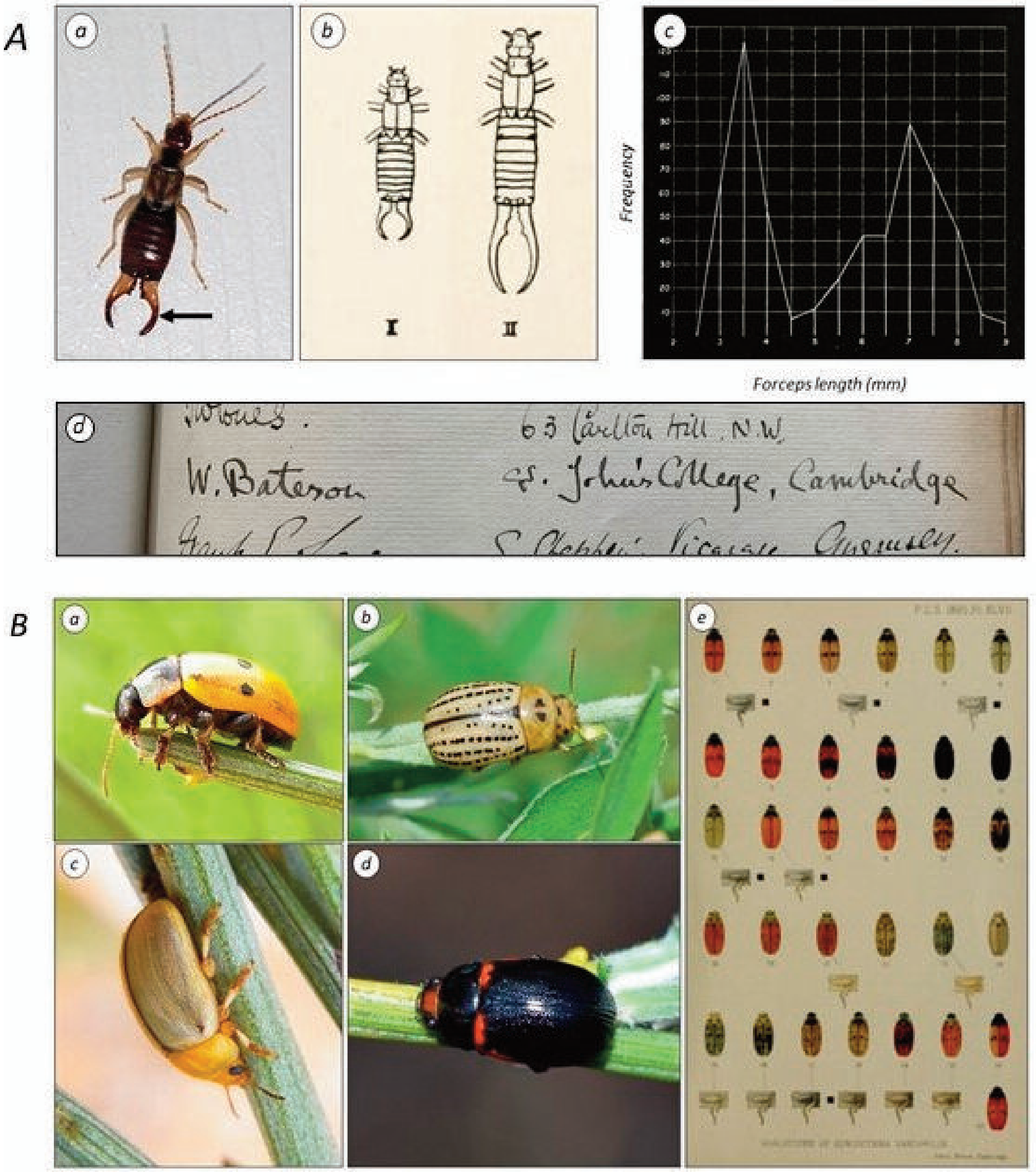

Fig 1. William Bateson's work on polymorphic insects. ***A a*** The earwig *Forficula auricularia* (Dermaptera, Forficulidae), arrow shows abdominal forceps. ***b*** Drawing from Bateson (1892) to show short (I) and long (II) forceps forms. ***c*** Frequency distribution of different forceps lengths in male *F. auricularia* (n = 583). ***d*** Bateson's signature in the Royal Entomological Society's Obligation Book (1893). ***B a–d*** Four examples of variable colouration in the beetle *Gonioctena variabilis* (Chrysomelidae). ***B e*** Drawings of *G. variabilis* colour morphs from Bateson (1895).
Images: ***A a*** Photo by Eugene Zelenko, Creative Commons 4.0 International; ***A b,c*** from Bateson (1894) pp 40–41. ***A d*** photo by Simon Ward, Royal Entomological Society. ***B a,c*** photos by Sigo CC BY-SA 3.0; ***B b,d*** photos by José Rafael González López, with permission. ***B e*** From Bateson (1895) Plate 47.

Lewontin, 1974, and Maynard-Smith, 1975).

All this is of interest, because at that time Bateson, the future geneticist, was unable to explain polymorphism in terms of the segregation of genes (the word 'gene' hadn't even been invented then – it was only introduced by Johannsen in 1909). While Bateson was measuring earwigs and categorising beetle colours, Mendel's now famous pioneer research on the inheritance of discrete variation in pea plants still lay unnoticed in the archives. It was only rediscovered in 1900 by Hugo de Vries and Carl Correns, who immediately called attention to its importance in relation to hybridisation in plant breeding. It was Bateson himself who realised that Mendel's work implied the existence of particulate inheritance (Bateson, 1901), coined the word 'genetics' to describe the new science that underlay it, and gave a full account of the matter in his important book of 1909. Bateson indeed deserves great credit not only as the godfather of genetics, but also as the progenitor of

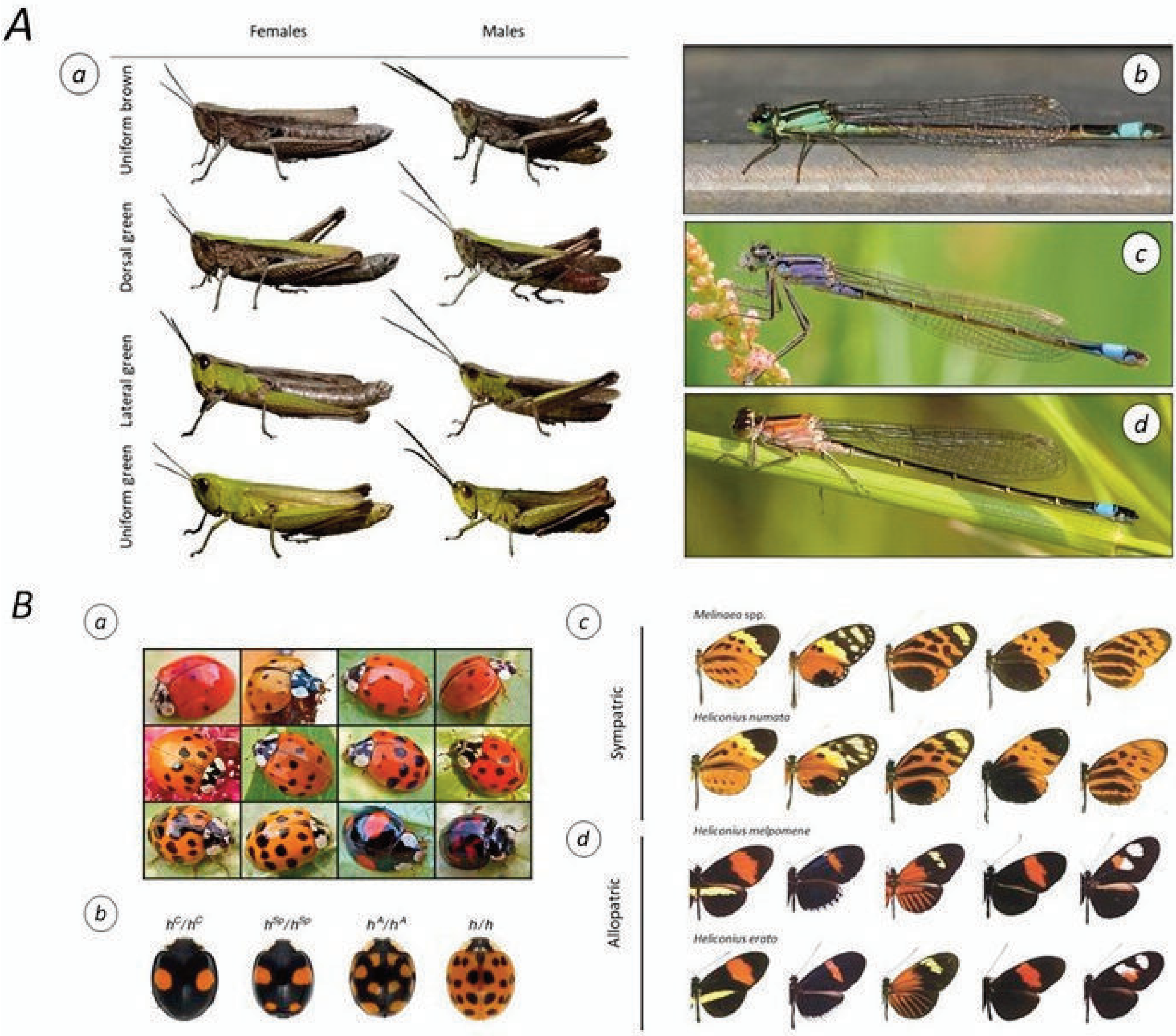

Fig 2. Examples of colour polymorphisms in insects. ***A a*** green-brown polymorphism in the steppe grasshopper *Chorthippus dorsatus*. ***A b–d*** Recently emerged blue-tailed damselflies *Ischnura elegans* (Odonata, Zygoptera) adopt one of the three morphic forms as shown here; ***b*** green ***c*** violet (violacea) ***d*** pink (*rufescens*), ***B a*** the highly variable elytral colours of the ladybird beetle *Harmonia axyridis* (Coccinellidae). ***B b*** Four major alleles of *pannier* that determine the beetle's elytral colour patterns. h^C, *conspicua*; h^{Sp}, *spectabilis*; h^A, *axyridis*; *h*, *succinea*. ***B c–d*** polymorphic wing patterned forms of Müllerian mimic butterflies. ***B c*** Sympatric polymorphism; Row 1, five different species of the genus *Melinaea* (Ithomiiinae), sympatric in northern Peru; Row 2, five comimetic polymorphic forms of *Heliconius numata* from the same geographic area. ***B d*** Allopatric polymorphism; Row 3, five polymorphic forms of *H. melpomene* from different parts of South America; Row 4, five polymorphic forms of *H. erato*, which are Müllerian comimetic forms from the same geographic zones as in row 3.
Images: ***A a*** graphic from Winter *et al.* (2021), with permission; ***A b and c*** photos by Andrew Makeham <http://www.makeham.org/odonata/>, with permission.; ***A d*** photo by Jörg Hempel, CC BY-SA 3.0. ***B a*** composite photo © entomart with permission; ***B b*** figure is from Ando *et al.* (2018), CC BY-SA 4.0; ***B c–d*** figure is from Joron *et al.* (2006) (lettering modified from original), CC BY-SA.

polymorphism. But our idols almost always have feet of clay, and Huxley (1955) called attention to the fact that Bateson could never reconcile his interest in the discontinuity that characterises polymorphism with his allegiance to Darwin's conviction (itself due to Lyell) that evolution took place gradually. He was also very late to acknowledge that Mendel's Laws strongly supported the chromosome theory of heredity.

By the way, one particular case in which variation in morphology is maintained within a population is by convention arbitrarily excluded from consideration as polymorphic. This is the quite obviously discontinuous distribution of sexually-related traits between males and females. Even though Ford's stated criteria would clearly include sexual dimorphism as an example of polymorphism, in practice it has always been regarded as a special case, to be considered separately.

Insect colour polymorphisms

Bateson (1894) commented that "*Nature abounds with colour-polymorphism*" and backed up his assertion with numerous examples that included many insects, although he didn't attempt to count them. In those days, it seems, the comparative method was about argument rather than counting and measuring. Now it's different, of course. According to Galeotti *et al.* (2003), 334 species of bird (about 3.5% of them) show colour polymorphism. As far as I know, there is no comparable estimate available for the number of colour polymorphic insects, nor the fraction of known species (I wish someone would do this!), but there are certainly many familiar examples.

I have already mentioned the case of the chrysomelid beetle, *Gonioctena variabilis,* investigated by Bateson (1895). I will choose a few more instances, such as the green–brown polymorphisms of

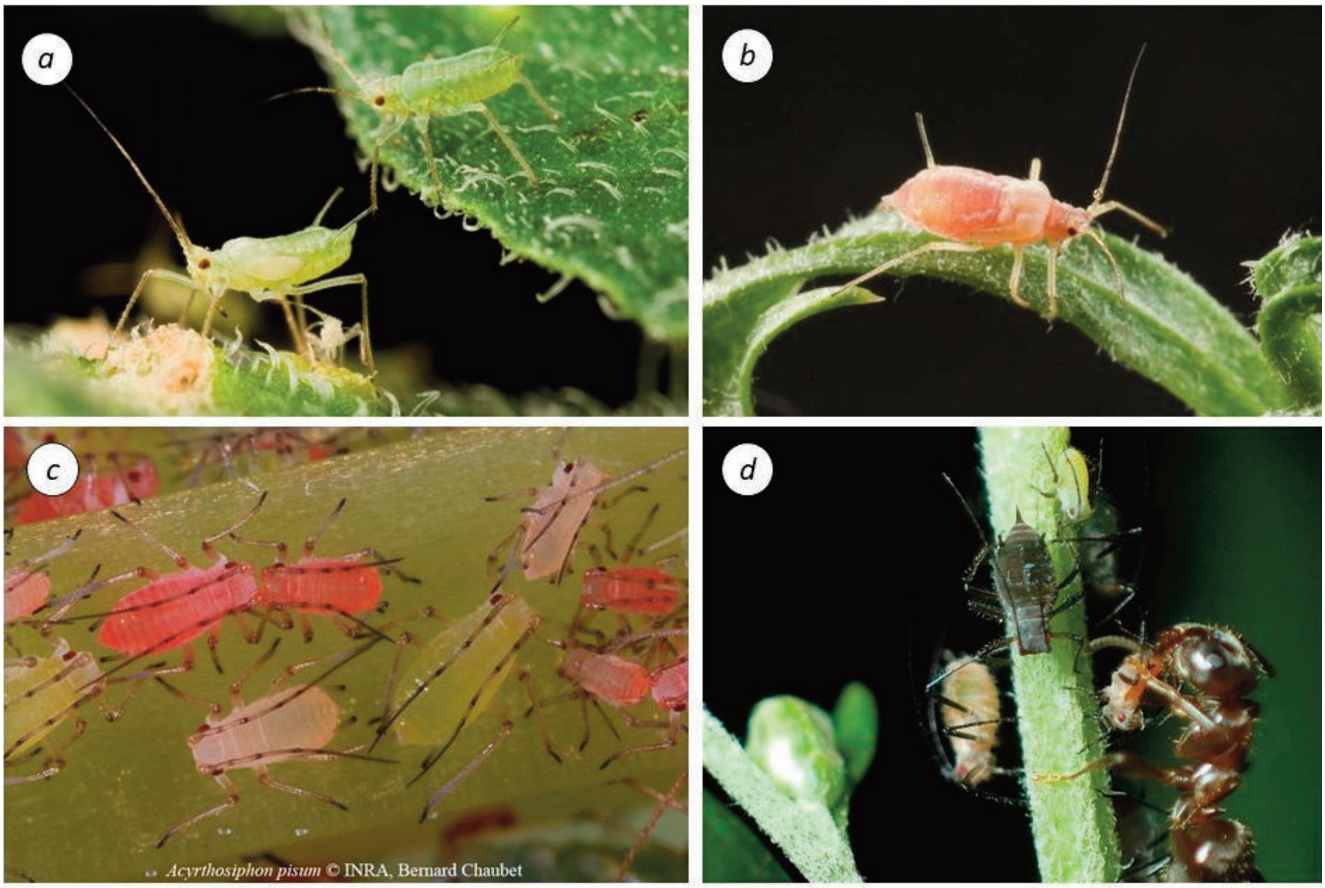

Fig 3. Colour polymorphic aphids.
a Green morphs of the potato aphid, *Macrosiphum euphorbiae;* ***b*** Red morph of *M. euphorbiae*; ***c*** red and green morphs of the pea aphid *Acyrthosiphon pisum*; ***d*** 'pink' and 'green' morphs of the mugwort aphid *Macrosiphoniella yomogicola* together with an attending ant *Lasius japonicus*. In this species the colours of the colour morphs change with reproductive maturity and the black aphid at the centre of the image is a 'green' morph, while the two aphids at the side are immature and are still pink.
Images: ***a*** and ***b*** photo copyright Rothamsted Research; ***c*** photo by Bernard Chaubet, INRAE with permission; ***d*** photo from Watanabe *et al.* (2018), reproduced under Creative Commons Attribution Licence CC BY 4.0.

many grasshoppers (Fig. 2Aa); Winter *et al.* (2021) showed that the colour morphs of this insect are best explained by inheritance at three autosomal loci, one locus influencing the ability to show green colour (dominant), and two loci each with a recessive allele suppressing green on the dorsal side and the lateral side, respectively; these occur equally in females and males. Another example shown in Fig. 2Ab–d concerns the polymorphic colours of teneral female (but not male) damselflies; Abbott *et al.* (2008) found that the frequency of these three morphs is subject to year-to-year fluctuations in selection pressure (probably negative frequency-dependent selection), when compared to a neutral genetic marker. Figure 2Ba–b illustrates the highly variable elytral colours of ladybird beetles (Coccinellidae), best explained by polymorphism at a single gene, *pannier*, four major alleles of which determine the beetle's elytral colour patterns. h^C, *conspicua*; h^{Sp}, *spectabilis*; h^A, *axyridis*; *h*, *succinea* (Ando *et al.*, 2018). Finally, Fig. 2Bc–d shows the well-known alternative wing-pattern forms of Müllerian mimetic butterflies in the genus *Heliconius*. These butterflies sequester distasteful chemicals from their diet and advertise the fact by their aposematic colours, benefitting by sharing the warning colour patterns on their wings. In one case (Fig. 2Bc) a single *Heliconius* species has several polymorphic wing colour patterns that each co-mimic a different sympatric model species, while in another case (Fig. 2Bd) shared polymorphic patterns that are common to two different *Heliconius* species have evolved allopatrically (Joron *et al*., 2006) (Fig. 2B). The wing patterns of all these species involve genes within a single genetic locus. The tight linkage among these genes means that the locus appears to act as a 'supergene' controlling multiple aspects of wing pattern formation, resulting in the long-term persistence of recognisable polymorphic alternative phenotypes. The genes concerned include *optix* (controls red, brown and orange colours), *cortex* (black colour), *aristaless* (white and yellow colours), and *WntA* (size and shape of pattern elements). This complex topic is reviewed by Nadeau (2018). There isn't space here to relate these interesting entomological stories in full; instead I'm simply making the point that many insects display adaptive and selectable colour polymorphisms.

Polymorphic aphids

The rest of this article is mostly about the colour varieties of aphids, many species of which have both red and green morphs that occur together in mixed populations (reviewed by Tsuchida, 2016) (Fig. 3). Before I go any further, though, I had better remind the reader that polymorphism is a completely different phenomenon from polyphenism, which is where *all* members of a species are capable of adopting alternative phenotypes according to environmental circumstances (Simpson *et al*., 2011). In the latter case (unlike polymorphism) all of the required genes for all alternative phenotypes are necessarily encoded in the same genome, and thus the question of selection between morphs within a polymorphism doesn't arise. Many insects are polyphenic (locusts are a good example), but aphids are masters of the art (Ogawa *et al*., 2014), and their complex life cycles alternate between winged and wingless forms, and also sexual and asexual forms. I'm calling attention to this because unfortunately, many papers about aphid polyphenism actually call this 'polymorphism', despite the fact that it obviously isn't. The problem is seen mostly in older literature, but papers still appear where this error is perpetuated.

The best studied example of an aphid colour polymorphism is *Acyrthosiphon pisum* (pea aphid), which has both red and green morphs that occur together in mixed populations (Fig. 3*A*). But there are plenty of other examples of colour polymorphic aphids. Here are just a few: *Myzus persicae* (peach–potato aphid) (Kerns *et al*., 1998); *Macrosiphum euphorbiae* (potato aphid) (https://www.cabi.org/isc/datasheet/32154); and *Sitobion avenae* (English grain aphid) (Alkedhir *et al.,* 2010; Tougeron *et al.,* 2021). Hille Ris Lambers (1966) mentions both *Macrosiphum rosae* and *Metopolophium dirhodum* as colour dimorphic. All of these aphids have similar red–green colour dimorphisms (Fig. 3). In *Macrosiphoniella yomogicola* (mugwort aphid)*,* the immature forms are red–green dimorphic but in the reproductive stages the same forms are respectively orange-brown and black (Watanabe *et al.,* 2016). *Chromaphis juglandicola* (walnut aphid) displays a yellow–white dimorphism (Wani *et al.,* 2015).

The genetics of the red–green polymorphism in *A. pisum* have been studied (Caillaud *et al*., 2010); aphid colour inheritance is determined by a single autosomal, biallelic locus, *colorama*. The direction of the cross has no influence on colour, showing that cytoplasmic effects and/or maternally-inherited symbionts are normally unimportant in this species (but see below). Other colours are sometimes seen, including orange and light green (Valmalette *et al*., 2012). In many cases, however, the variation in colour is not exclusively genetic but also influenced by environmental factors, with some aphid clones being exclusively colour-monomorphic, while in others alternative colours of aphid can be produced according to temperature, time of year, state of crowding (Jenkins *et al*., 1999), and especially light intensity (*e.g., S. avenae*: Alkedhir *et al.,* 2010; Tougeron *et al.,* 2021). This means that this aphid is polymorphic for a gene that is conditionally expressed, but it is still a polymorphism, so there exists within the population a stable mix of genes that affect colour.

Aphid colours are most commonly due to carotenoid pigments. Most animals are unable to synthesise carotenoids for themselves, but aphids do so, the required genes having been derived by horizontal gene transfer from a fungal donor at some point in the past. While green aphids possess only α-, β- and γ carotenes, the red (or pink) colour of red morphs is due to the production of additional carotenoid pigments (torulene and dehydro-γ,Ψ-carotene) not possessed by green aphids. Interestingly, all red clones of pea aphids have a 30 kb genomic insertion that encodes a single carotenoid desaturase that is absent from green individuals; a spontaneous mutant line that had lost its red colour was shown to have a mutation in this gene, so that we can be sure that this is the gene responsible for colour polymorphism in this species (Moran *et al.,* 2010).

Natural selection and aphid colour polymorphism

Like lots of other insects, aphids reproduce sexually only once a year, but every summer, parthenogenetic female aphids colonise host plants to produce huge numbers of asexual offspring. Their reproductive potential is so prodigious that it has been calculated that a single cabbage aphid, *Brevicoryne brassicae*, would, if left unchecked, produce 1.56 x 10^{24} progeny by the end of the season (Sabrosky, 1952). Harrington (1994) estimated that a single individual of *M. persicae* has the reproductive potential to produce a layer 149 km deep over the whole surface of the Earth in a year. That this does not happen in practice (thank goodness!) is due to massive losses when host seeking, as well as adverse weather, prodigious predation, parasitism and disease among progeny, but the point about the profligacy of aphid reproduction is that there is plenty of opportunity for natural selection under varying environmental conditions.

We don't have good information about the frequency with which the genes encoding the red colour morph have arisen in the past, nor the ease with which they spread in the population. As noted above, a genomic insertion is a likely cause, at least in pea aphids. The presence of red–green polymorphism in multiple aphid species suggests that it may have had a remote origin and that the polymorphism has persisted across species boundaries (as has happened with some other polymorphisms – Gray, 2006). But we also can't rule out the possibility that red-green polymorphisms may come and go, once the ability to synthesise the red pigment has been acquired, due perhaps to later inactivating point mutations within the carotenoid desaturase gene. The red morph gene may also acquire the capacity for environmental regulation; since this appears to happen regularly on a seasonal basis, it may depend on an asexually heritable epigenetic effect rather than on mutation. Another possibility is that on at least some occasions, colour change is due to the acquisition of a new bacterial endosymbiont; the facultative symbiont "*Candidatus* Rickettsiella viridis" changes pea aphid colour from red to green (Tsuchida *et al*., 2014). Interestingly, the symbiont does not itself synthesise the carotenoid pigments necessary for colour change, but somehow it causes the aphid to do so in an unknown way (Nikoh *et al*., 2018).

Whatever the cause, all that is required is for a heritable change to make some difference to fitness, and for selection pressure to be maintained. It is extremely unlikely that being red or green is selectively neutral (in other words, as Bateson would have said, body colour 'matters' to the aphid). Although there are examples of naturally occurring polymorphisms that appear to be maintained by selectively neutral processes such as genetic drift, migration and dispersal, and founder effects (reviewed by Bond, 2007), I suggest that the sheer reproductive power of asexual reproduction in aphids argues against this.

The one thing that we can be fairly sure about is that sexual selection is unlikely to play a big part in the evolution of aphid colour forms, since their rapidly growing summer populations are made up only of females. Sexual reproduction usually occurs annually in aphid life cycles, and in some species not at all (Loxdale *et al.,* 2020). Consequently, we must concentrate on natural selective forces that act on asexual female reproduction.

It is possible that a coloured phenotype might be naturally selected because it is in itself beneficial, by affecting the rate of (asexual) reproduction or alternatively survival. Both of these factors can conceivably be affected by behaviour; it is known that red aphids are more active and disperse more freely, both by walking and by producing a higher proportion of winged offspring in response to crowding or attack by predators (Braendle *et al.,* 2001). On the other hand, green pea aphids produce more offspring than red morphs (Markkula, 1963), which might be facilitated by the enhanced accumulation of proteins by green aphids. It seems unlikely that aphid colour would contribute directly to reproductive fitness, but this might occur through improved nutrition. Although Ahsaei *et al.* (2013) found that green and red morphs of *A. pisum* do not differ in total energy reserves, red aphids accumulate significantly more carbohydrate and lipids, while green morphs have more protein. This is in accord with the greater activity and energy expenditure of the red morph, and the higher reproductive output of the green morph. In this case, therefore, we might attribute the initial spread of red-colour-determining genes into aphid populations to their success in adapting resource allocation in favour of mobility over reproduction. The mechanism for this isn't known, but a hormonal signal seems likely.

Alternatively, red colouration might directly promote survival. Several studies have found that the red–green dimorphism of aphids is sometimes associated with reduced susceptibility to insecticides and that overuse of insecticide sprays is strongly associated with the increase of the proportion of red morphs (Kerns *et al*., 1998; Chen *et al*. 2018; Tian *et al.* 2020). In the best investigated case (Harlow *et al.,* 1990), the resistance appeared to be mediated by increased levels of metabolic degradation through increased esterase levels. The genes encoding colour aren't likely to be directly responsible for insecticide resistance, but if they are closely linked they might be swept along together by strong selection at the resistance locus. Since other cases of esterase-based insecticide resistance in aphids involve not only gene translocation and amplification but also epigenetic regulation (reviewed by Bass *et al*., 2014), application of a similar scenario to *M. persicae nicotianae* raises the possibility of linkage between the gene(s) conferring altered colour to the red morph and a translocated gene that causes reduced insecticide susceptibility; it is also possible, however, that the genetic change resulting in insecticide resistance occurs entirely separately within a red-coloured clone and is then selected by chronic exposure to the chemicals in question.

Balancing selection and colour polymorphism

But once a phenotypic polymorphism has arisen and spread into the population, how can it be maintained? This would have to be through some form of balancing selection (Hedrick, 2007). The most frequently discussed kind of balancing selection is heterozygote advantage, where an individual possessing both of two alternative alleles is more fit than are those that are homozygous (*i.e.*, having two copies of one or the other allele). But since summer aphids don't reproduce sexually, this kind of selection can't happen here.

The most likely cause for colour polymorphism in aphids is that selection on colour is frequency-dependent, so that when the proportion of one morph is below a critical level it is favoured. This would then either establish a stable polymorphism at that level, or perhaps selection would fluctuate in time so that each colour morph was alternately favoured. The selection would be exerted by predators, parasites and perhaps pathogens. One particular version of this idea is called 'apostatic selection'; this refers to the case where predators try to maximise their efficiency in hunting by learning the characteristics of the most frequently encountered prey and then specialising in attacking it (Bond, 2007). In the longer term, the same sort of process could operate through evolutionary change in other natural enemies like parasites and pathogens which, although they don't individually 'learn' the characteristics of the most frequently occurring host, might nevertheless evolve to be more effective in targeting it (Gibson *et al.,* 2020).

Selective pressure on colour morphs might also fluctuate differentially in time (*e.g.*, with the season) leading to genetic adaptation. This is known to occur in *Drosophila* (Machado *et al.,* 2021). It seems entirely reasonable that host plant quality would vary seasonally, and either background leaf colour or nutrient availability might influence the survival of aphid colour morphs. Starvation causes loss of red colour in red morphs of pea aphids, indicating that the maintenance of red colour is expensive (Tabadkani *et al*., 2013; Wang *et al*., 2019) and that selection based on resource availability would 'make a difference' to the relative fitness of colour morphs.

Alternatively, selection might fluctuate in space, so that aphids present in one type of environment would be favoured but would be at a disadvantage in others. This might well arise for aphids according to host plant species, or even their position on a single host plant, in both cases based either on visibility to predators and parasites or on nutrient flow. Geographically fluctuating selection might allow a colour morph that was at a disadvantage in one place to prosper in another, creating what would amount to allopatric polymorphism. Strictly speaking, allopatric allelic variation is not a proper polymorphism if it is maintained by lack of gene flow between the morph populations. Such separation might in the end lead to speciation, but a sufficiently high frequency of migration between the different zones would oppose this and allow the maintenance of an overall stable polymorphism. In that case, the polymorphism would be maintained by the different selective forces acting in different geographic zones. Hedrick (2006) has reviewed this topic and concludes that although heterogeneous environments have in some cases been responsible for genetic polymorphisms in animals such situations are not common.

As noted above, in the case of aphids we expect any balancing selective forces to be based on natural selection. The most obvious way for this to work would be through differential mortality, which in aphids is very high. Losey *et al*. (1997) showed that the red and green morphs of *A. pisum* are differentially susceptible to the parasitoid *Aphidius ervi* (a braconid wasp) and the predator *Coccinella septempunctata* (a ladybird). They found that green aphids are subject to higher rates of parasitism than red ones, while predators attack red morphs more often than green. It appears that this is because predators use visual cues to locate their prey, and that red aphids are more easily detected on green plants, while parasitoids are less reliant on visual cues (Harmon *et al*., 1998). Modelling showed that biased density-dependent parasitism and/or predation on different morphs could adequately explain maintenance of the colour polymorphism. Other studies have supported this idea. Libbrecht *et al.* (2007) confirmed in laboratory behavioural studies which controlled for many possibly confounding factors that the parasitoid *A. ervi* prefers to attack green rather than red morphs of the pea aphid when both are available. This preference might be adaptive to the wasp in that it avoids intraguild competition among the natural enemies of the aphid, by reducing the risk of successfully parasitised aphids being eaten by predators like ladybirds. Farhoudi *et al*. (2014) found that, like ladybirds, a different predator, the gall midge *Aphidoletes aphidimyza* (Cecidomyiidae), also prefers red morphs of *A. pisum*.

But the situation appears to be more complicated than this. Balog *et al.* (2013) found that while predators do indeed tend to target red-coloured pea aphids, the actual susceptibility of red morphs to predation is dependent on the mixture of colour morphs presented to the predator (in this case the ladybird *Adalia bipunctata*). Red morphs survive best when they are present at 25% of the exposed aphid population. At all other ratios, the fitness of red morphs is less than that of green morphs, presumably because the predator's 'choice' of prey is also colour-frequency dependent. In the field it was found that the red:green ratio in pea aphid populations is always close to 1:3. The authors concluded that this is because the red aphids "choose to associate with green morphs" at the favourable ratio, and that this is an evolutionarily stable strategy on the part of the red morph that can stabilise the polymorphism without any direct contribution from parasitoid mortality. I am unsure about this; it's not clear what behavioural mechanism could account for this choice. I'd like to see some modelling of whether the predator's frequency-dependent prey preference could be responsible for adjusting the red:green ratio to the 'magic' 1:3 level.

An alternative way in which aphid colour polymorphism may be maintained comes from work on a different species by Agawa *et al.* (1995), who investigated mortality in naturally occurring mixed populations of red and green *Macrosiphoniella yomogicola* on its natural host plants, *Artemisia* spp. It was found that while mortality was not related to population density, in three out of five datasets mortality was negatively related to population colour diversity. The authors initially suggested that a possible hypothesis to explain this is that enhanced diversity in colour polymorphism decreases the efficiency of searching for prey by predators. This would be similar to the mechanism proposed by Balog *et al*. (2013) for behavioural association between morphs of *A. pisum*. But subsequently it was discovered (Watanabe *et al*., 2016) that *M. yomogicola* is remarkably free from predation because it is protected by attending ants, *Lasius japonicus*. The ants defend the aphids by attacking potential predators and parasites in exchange for a harvest of sugar-rich honeydew. To an ant, the quality of honeydew from green aphids is better than that from red morphs. Despite this, the ants strongly prefer to farm colonies with intermediate proportions of red–green colour morphs, peaking with roughly one-third red, two-thirds green. The ants even manipulate the reproductive rate of the aphids to maintain this ratio, increasing the fecundity of the preferred green morphs while leaving that of the red morphs unchanged (Watanabe *et al*. 2018). It isn't clear how this is done, nor why the ants choose to maintain the polymorphism in this way. If they prefer to tend the green morphs, why don't they simply eliminate the red ones? One suggestion is that red aphids are better at producing sexual offspring in the autumn, and that to maintain a fraction of red morphs optimises the probability of the (perennial) ant nest being able to find aphids next year.

Is polymorphism intrinsically a good thing?

The then doyen of ecological and population geneticists, Theodosius Dobzhansky, consistently asserted that polymorphism was in itself beneficial to the organism at the population or species level. He supported this with many studies on populations of *Drosophila melanogaster* that differed in various chromosomal characteristics, summarising this work in in his book *Genetics and the Origin of Species* (1951). He said that populations with polymorphic phenotypes would inevitably be better adapted to fluctuating environmental conditions (*i.e.*, those presumably experienced by most organisms). Dobzhansky's argument was strongly criticised by Cain *et al.*, (1954) and Fisher (1958) on the grounds that it was not properly explained how this increased adaptiveness could be conferred. More recently, Forsman *et al.* (2008) and Forsman (2016) have attempted to provide counterarguments in favour of Dobzhansky's idea, but in my view, these are unpersuasive.

Really, the problem with Dobzhansky's proposal is that it is at heart a group selectionist argument, a concept that since the work of G.C. Williams (1966) has been generally considered to be just wrong. Although there are still pockets of resistance to the idea that natural selection can act only at the level of the individual (or below that level, in the case of 'selfish' genes), the remaining arguments in favour of any kind of group selection are controversial and are anyway concerned only with the evolution of altruism in eusocial animals (see West *et al.*, 2007).

I think that the only way to explain how polymorphism could in itself be advantageous, would be to use the same sort of arguments that are used to explain the benefits of sexual recombination (Barton, 2009). In essence, this is that polymorphism could function to bring together new favourable combinations of potentially adaptive genes so that all are available to confer fitness benefits in the same genome, which would be advantageous in a variable environment. How could this happen? One possible scenario is to envisage the existence of a gene that enables polymorphism by differentially regulating alternative alleles at another locus. The enabling gene would always confer a benefit in the presence of a varying environment and would thus be favoured. The snag is that it seems inevitable that such an enabling gene would quickly become fixed in the population; its existence could then only be detected by the loss of fitness when it was disabled. But Barton (2009) indicates that for this sort of mechanism to work, the mutation rate would need to be high, which we know not to be the case in aphids.

Actually, as we have seen, such complicated scenarios seem unnecessary. The most likely explanations for the maintenance of insect colour polymorphisms involve fluctuating selective benefits to individuals in the form of survival or fecundity. It therefore seems to me that there is no good reason to suppose that adaptive colour polymorphisms are maintained by anything other than fluctuating natural selection, and there is no need to suppose that there is any benefit in polymorphism *per se.*

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There is no need to suppose that there is any benefit in polymorphism *per se.*

References

Abbott, J.K. *et al.* (2008) *Molecular Ecology* **17**, 1597–1604.
Agawa, H. *et al.* (1995) *Ecological Research* **10**, 301–306.
Ahsaei, S.M. *et al.* (2013) *European Journal of Entomology* **110**, 241–245.
Alkhedir, H. *et al.* (2010) *Journal of Insect Physiology* **56**, 1999–2005.
Ando, T. *et al.* (2018) *Nature Communications* **9**, 38–43.
Balog, A. *et al.* (2013) *Journal of Evolutionary Biology* **28**, 545–552.
Barton, N.H. (2009) Why sex and recombination? *Cold Spring Harbor Symposia in Quantitative Biology* **74**, 187–195.
Bass, C. *et al.* (2014) *Insect Biochemistry and Molecular Biology* **51**, 41–51.
Bateson, W. *et al.* (1892) *Proceedings of the Zoological Society of London* **1892**, 585–594.
Bateson, W. (1894) *Materials for the Study of Variation, Treated with Especial Regard to Discontinuity in the Origin of Species*. pp 598. London, UK. Macmillan and Co.
Bateson, W. (1895) *Proceedings of the Zoological Society* **1895**, 850–860.
Bateson, W. (1901) *Journal of the Royal Horticultural Society* **25**, 54–61.
Bateson, W (1909) *Mendel's Principles of Heredity*. Cambridge UK, Cambridge University Press.
Bond, A.B. (2007) *Annual Review of Ecology, Evolution and Systematics* **38**, 489–514.
Braendle, C. *et al.* (2001) *Journal of Insect Behavior* **14**, 497–509.
Caillaud, M.C. *et al.* (2010) *Journal of Insect Science* **10**, 95.
Cain, A.J. *et al.* (1954) *American Naturalist* **88**, 321–326.
Chen, X.D. *et al.* (2018) *Insect Science* **26**, 843–852.
Cook, L.M. (2018) *Biological Journal of the Linnean Society* **125**, 862–866.
Darwin, C.R. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London, John Murray.
Dobzhansky, T. (1951). *Genetics and the Origin of Species*. 3rd edition, revised. pp 364. New York, USA. Columbia University Press.
Farhoudi, F. *et al.* (2014) *Journal of Insect Behavior* **27**, 776–785.
Fisher, R.A. (1930) *The Genetical Theory of Natural Selection.* pp 272. Oxford, UK, Clarendon Press.
Fisher, R.A. (1958) *Journal of Ecology* **46**, 289–293.
Ford, E.B. (1945) *Biological Reviews of the Cambridge Philosophical Society* **20**, 73–88.
Forsman, A. *et al.* (2008) *Ecology* **89**, 34–40.
Forsman, A. (2016) *Molecular Ecology* **25**, 2693–2698.
Fryer, J.C.F. (1914). *Philosophical Transactions of the Royal Society of London* B **204**, 227–254.
Galeotti, P. *et al.* (2003) *Journal of Evolutionary Biology* **16**, 635–646.
Gerould, J.H. (1911) *The American Naturalist* **45**, 257–283.
Gibson, A.K. *et al.* (2020) *Biology Letters* **16**, 20200210.
Gray, S.M. *et al.* (2006) *Trends in Ecology and Evolution* **22**, 71–79.
Harlow, C.D. *et al.* (1990) *Journal of Economic Entomology* **83**, 2130–2135.
Harmon, J.P. *et al.* (1998) *Oecologia* **115**, 287–292.
Harrington, R. (1994) *Antenna* **18**, 50–51.
Hedrick, P.W. (2006) *Annual Review of Ecology, Evolution and Systematics* **37**, 67–93.
Hedrick, P.W. (2007) *Current Biology* **17**, R230–R231.
Hille Ris Lambers, D. (1966) *Annual Review of Entomology* **11**, 47–78.
Huxley, J.S. (1955) *Heredity* **9**, 1–52.
Jacobson, E. (1910). *Tijdschrift voor Entomologie* **52**, 125–157.
Jenkins, R.L. *et al.* (1999). *Physiological Entomology* **24**, 171-178.
Johannsen, W. (1909) *Elemente der exakten Erblichkeitslehre*. Jena, Germany, Gustav Fischer.
Joron, M. *et al.* (2006) *PLOS Biology* **4**, e303.
Kerns, D.L. *et al.* (1998) *Southwestern Entomologist* **23**, 115–122.
Lewontin, R.C. (1974) The Genetic Basis of Evolutionary Change New York, USA, Columbia University Press.
Libbrecht, R. *et al.* (2007) *Journal of Insect Behavior* **20**, 25–32.
Losey, J.E. *et al.* (1997) *Nature* **388**, 269–272.
Loxdale, H.D. *et al.* (2020) *Biological Journal of the Linnean Society* **129**, 507–531.
Machado, H.E. *et al.* (2021) *eLife* **10**, e67577.
Markkula, M. (1963) *Annales Agriculturae Fenniae* **2**, 1–30.
Maynard Smith, J. (1975) *The Theory of Evolution* 3rd edition. Harmondsworth, UK, Penguin.
McKinnon, J.S. *et al.* (2010) *Molecular Ecology* **19**, 5101–5125.
Moran, N.A. *et al.* *Science* **328**, 624–627.
Nadeau, N.J. (2016) Genes controlling mimetic colour pattern variation in butterflies. *Current Opinion in Insect Science* **17**, 24–31.
Nikoh, N. *et al.* (2018) *MBIO* **9**, e00890-18.
Ogawa, K. *et al.* (2014) *Frontiers in Physiology* **5**, 1–11.
Sabrosky, C.W. (1952) How many insects are there? In: *Insects. The Yearbook of Agriculture* (ed. Stefferud, A.) Washington, USA, US Department of Agriculture.
Simpson, S.J. *et al.*, (2011) *Current Biology* **21**, R738–R749.
Tabadkani, S.M. *et al.* (2013) *Physiology & Behavior* **110–111**, 221–225.
Tian, F. *et al.* (2020) *Pesticide Biochemistry and Physiology* **163**, 193–199.
Tomkins, J.L. (1999) *Behavioral Ecology and Sociobiology* **47**, 1–8.
Tougeron, K. *et al.* (2021) *Evolutionary Ecology* **35**, 147–162.
Tsuchida, T. *et al.* (2014) *Applied and Environmental Microbiology* **80**, 525–533.
Tsuchida, T. (2016) *Current Opinion in insect Science* **17**, 74–80.
Valmalette, J.C. *et al.* (2012) *Scientific Reports* **2**, 579–587.
Wang, X-X. *et al.* (2019) *Frontiers in Physiology* **10**, 197.
Wani, S.A. *et al.* (2015) *Journal of Entomology and Zoology Studies* **3**, 28–31.
Watanabe, S. *et al.* (2016) *Science Advances* **2,** e16006.
Watanabe, S. *et al.* (2018) *Scientific Reports* **8**, 2313.
West, S.A. *et al.* (2007) *Journal of Evolutionary Biology* **20**, 415–432.
Williams, G.C. (1966) *Adaptation and Natural Selection, a Critique of some Evolutionary Thought*. pp 328. Princeton, N.J., USA, Princeton University Press.
Winter, G. *et al.* (2021) *Heredity* **127**, 66–78.

Is a 'silo' mentality to research holding back integrated pest management?

Fig. 1: *Orius laevigatus* a predator of thrips and other soft-bodied pests. Image: ©Tom Pope

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The success or impact of a scientist is increasingly determined by measurable outcomes of their research

Collaborations were achieved in a voluntary and non-hierarchical way across disciplines in order to share experience and ultimately to build new knowledge

The success or impact of a scientist is increasingly determined by measurable outcomes of their research. These outcomes include financial income and publications, which in turn are often measured by recording numbers of papers published, journal impact factors and h-index scores. These pressures often have the effect of creating smaller teams, within which research goals are narrowly focused, thereby creating a 'silo' mentality within universities and research institutes (Nagy, 2014). This is done with the belief that these smaller teams are better able to deliver the measurable outcomes that will further the careers of those within each team. Simon Leather was a vocal advocate for resisting this approach to research and instead maintained a collegiate or community approach to research that sought to decouple and liberate researchers from their silo(s). By taking this approach, collaborations were achieved in a voluntary and non-hierarchical way across disciplines in order to share experience and ultimately to build new knowledge. There are many examples where Simon took this collegiate approach at Harper Adams, often stimulating discussion by raising topical questions. In this article we look at how a more collaborative, collegiate approach could benefit the development and application of Integrated Pest Management (IPM) as it celebrates its 50th anniversary year.

The concept of using microbial and invertebrate natural enemies (Fig. 1) in glasshouses and protected crops has been a reality for more than fifty years (*e.g.*, Chant, 1961) and has been successfully incorporated into many IPM programmes. Indeed, in many of these programmes, augmentative releases of these natural enemies are the main method of pest control (*e.g.*, Messelink *et al.*, 2014). Protected cropping systems are, however, relatively amenable to the use of natural enemies; environmental conditions are stable and under the direct control of the grower, pest problems are easily monitored and the introduction and spread of beneficial organisms within the crop similarly tractable. Easy to deploy 'packages' of natural enemies and the use of commercially-produced pollinators mean that the use of conventional synthetic pesticides is, in many situations, almost eradicated.

The situation in broad scale agriculture is very different. Crops are grown at much larger scales and, although inputs are under the grower's control, the crops are subject to the vagaries of weather. The *Holy Grail* for pest managers is a future where the use of beneficial organisms in these field-grown crops is as accepted and commonplace as in protected cropping systems (Fig. 2). There are some success stories through the introduction of non-native natural enemies (classical biological control), the most well-known being the *Icerya purchasi* (Cottony-cushion scale) in Californian orchards, which was successfully controlled using a suite of introduced natural enemies in the 1880s (Heimpel *et al.*, 2017). However, most successes are confined to warm 'island habitats' or in forestry (Kenis *et al.*, 2017).

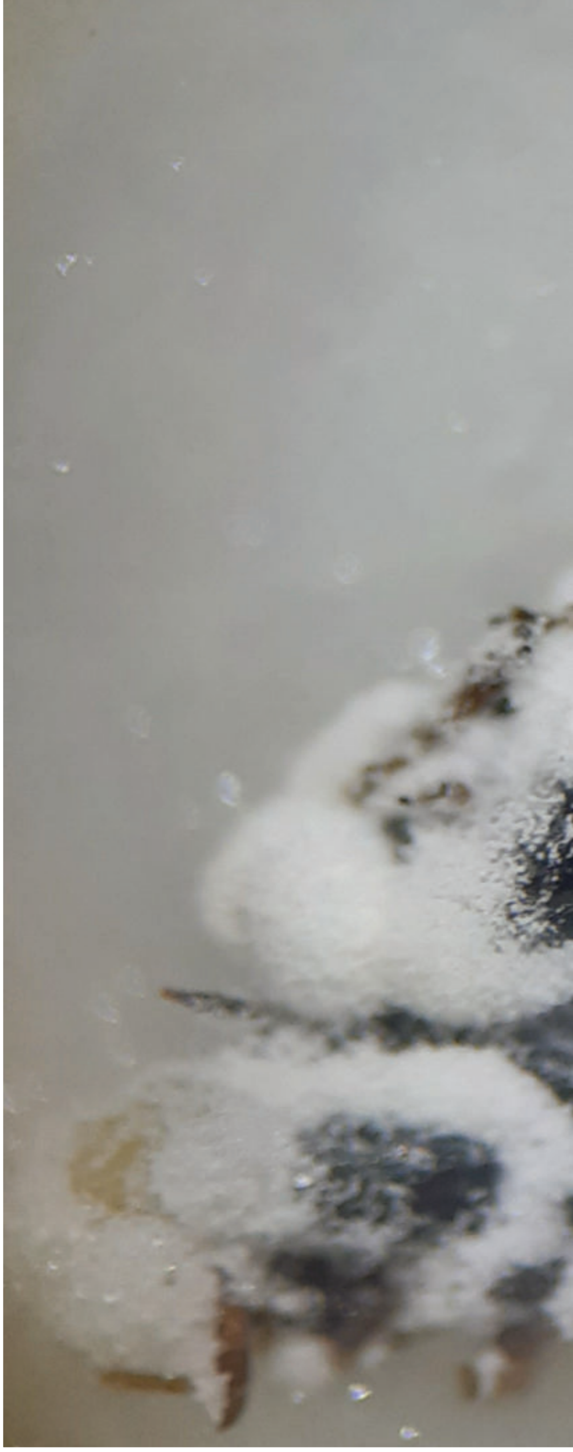
Perhaps the biggest challenge to the use of beneficial organisms for crop protection is the silo mentality of researchers. This is apparent in the fact that, while there has been considerable research activity in the individual elements of IPM, there has been comparatively little progress in developing the holistic science of IPM itself (Stenberg, 2017). A good example of this is the apparent lack of focus on use of

> **Perhaps the biggest challenge to the use of beneficial organisms for crop protection is the silo mentality of researchers**

conservation biological control in broadscale agriculture in recent years. As a concept, conservation biological control is commonly defined as "the modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effects of pests" (Eilenberg *et al.*, 2001). This is a slight modification of the original definition of DeBach (1974), which ends with the words "and/or judicious use of pesticides in order to conserve and/or increase natural enemies already present". The idea of using the natural enemies that are already present to improve pest control is not new. Thompson (1930) refers to this as "*intensification of action of natural enemies present in the area*" and more than 200 years ago we can find a similar suggestion regarding the control of hop aphids by ladybirds "*if we could but discover a mode of increasing these insects at will, we might not only, as Dr. Darwin has suggested, clear our hot-houses of aphides by their means, but render our crops of hops much more certain than they now are*" (Kirby *et al.*, 1816).

In the first half of the last century, it had been known for some time that the distribution of agricultural pests at the beginning of the season is not even, with pests being initially more abundant at the crop edges than in the centre (Petherbridge *et al.*, 1942), but it was not until the 1960s that the importance of hedges and hedgerows in providing shelter for beneficial and pest insects was highlighted in a number of studies (*e.g.*, Lewis, 1964, 1969a, b; Lewis *et al.*, 1962). The physical properties of hedges were shown to influence the distribution of pests and natural enemies within the crop, again with pests often being associated initially with field edges (van Emden, 1965; Pollard, 1968; Bardner *et al.*, 1974). The predatory bug, *Anthocoris nemorum*, for example, was less abundant in hedges where the bottom vegetation had been removed, but was found as far as 30 metres into a crop where the adjacent hedge bottom was retained (Pollard,

Fig. 2: An adult *Psylliodes chrysocephala* (Cabbage stem flea bee killed by the fungus *Beauveria bassiana*. Image: ©Claire Hoarau



1968). Conversely, hedges and surrounding non-crop habitats were shown to have no positive effects on the abundance of syrphid predators in adjacent cabbage crops (Pollard, 1971). By the late 1970s the idea that hedges and other non-cropped parts of a farm could be managed in an environmentally-friendly way without loss of profit was gaining some support (Lloyd, 1979).

During the 1980s, the interest in hedges and field boundaries grew. Several studies showed that field boundaries were beneficial for overwintering polyphagous predators, especially carabids and staphylinids (Sotherton, 1984, 1985). Importantly, it was shown that these polyphagous predators migrated in spring from the field boundaries into cereal crops and within 40–100 days (depending on species) were present in significant numbers 100 metres into the crop (Coombes *et al*., 1986). At the same time, in response to the poor establishment of game-bird populations, the introduction of 'conservation headlands' became a common feature of many UK farms. In this practice, the outermost 6 metres of fields were left unsprayed to provide a plentiful supply of invertebrate 'chick food' (Sotherton *et al*., 1989). An innovative approach to further enhance the populations of natural enemies within crops was to create areas of 'non-crop' habitat (grass-sown earth banks) in the centre of fields (Thomas *et al*., 1991). A similar idea was tested in Switzerland, where weedy strips were established in a winter wheat field. Carabid beetle numbers were significantly increased (Lys *et al*., 1994).

tle)

Although the general methods to manage habitats to enhance populations of natural enemies are now well-known and documented (*e.g.*, Landis *et al*., 2000; Gurr *et al*., 2003), research on the use of what are now termed ecosystem service providers has traditionally been limited to beneficial arthropods that attack insect herbivores, seed feeders and weeds (*e.g.*, Hinz *et al.,* 2014; Rowley *et al.,* 2017). Other ecosystem service providers, however, could be called upon, including vertebrates, microbes and plants themselves in an approach known as 'ecostacking', see https://www.ecostack-h2020.eu/. Ecostacking aims to deliver the effects of these organisms synergistically, rather than cumulatively (Hokkanen, 2017), and in doing so to unlock the potential of IPM (Stenberg, 2017). However, to do this requires collaboration between researchers with different expertise *e.g.*, entomologists, ecologists, microbiologists, nematologists, chemists, engineers, economists *etc*. These collaborations would lead to development of more effective, and perhaps most importantly, reliable crop protection systems where conservation biological control is used together with other IPM-compatible tools. These tools may include improved pest monitoring, economic thresholds, host plant resistance and a wider range of controls that may include products based on microbes or plant extracts (botanicals) and collectively often referred to as biopesticides.

A prime example of the challenge we face in developing collaborations is in integrating or 'ecostacking' the use of biopesticides with other IPM-compatible tools. Biopesticides can be defined as *a mass-produced agent manufactured from a living microorganism or a natural product and sold for the control of plant pests* (Chandler *et al.*, 2011). These products are often seen as 'green' alternatives to conventional synthetic pesticides. However, both the term 'biopesticide' and the concept of using these products as direct replacements for synthetic pesticides point to the silo mentality persisting in crop protection. This is because to see biopesticides on their own as solutions for crop protection (Rodgers, 1993) would simply repeat the mistakes of the synthetic chemical pesticide era, where each product was seen as a 'silver bullet' (Chandler *et al.,* 2011). Furthermore, the term 'biopesticide' exists alongside 'biocontrol' and 'biological control', creating confusion and the potential for researchers to occupy a subject area defined by a specific term. In order to address these concerns, the International Biocontrol Manufacturers Association (IBMA) proposed the use of the term 'bioprotectant' in 2018 as a collective concept, namely invertebrate biocontrol agents, microbials, semiochemicals (Fig. 3) and natural substances (IBMA, not dated).

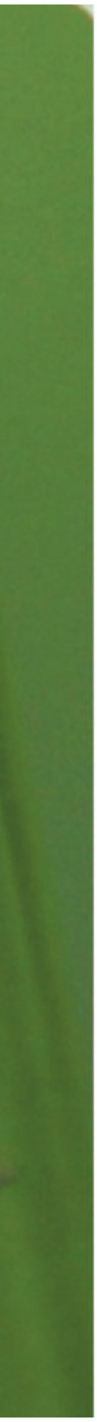
The rapid increase in the development and uptake of mass-produced agents manufactured from living microorganisms in particular (*e.g.*, Lacey *et al.*, 2015) has been driven by a range of attractive properties that characterise these products. These include increased selectivity, reduced development costs, and self-perpetuating control compared to conventional synthetic chemical pesticides. However, as is true for conservation biological control, the true potential of products based on microbials or other bioprotectants will come only when they are used within an IPM programme (Chandler *et al.*, 2011). This is because it is only with careful selection of IPM tools that farmers and growers will benefit from synergistic interactions. Indeed, synergistic interactions have already been reported between different microbials, microbials and semiochemicals and microbials and synthetic chemical pesticides for example (*e.g.*, Roditakis *et al.*, 2000; Furlong *et al.*, 2001; Ansari *et al.*, 2008; Shah *et al.*, 2008) highlighting the promise of this approach. But perhaps just as importantly, careful selection of IPM tools would avoid antagonistic interactions such as the non-target effects of bioprotectants (*e.g.*, Chaisson *et al.,* 2004; Ansari *et al.*, 2005).

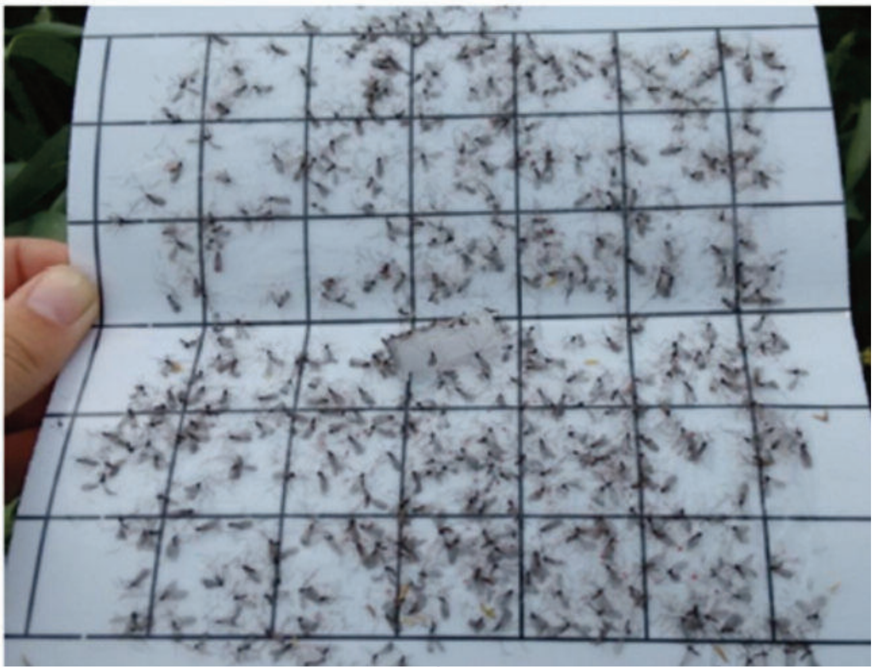
Herein lies the problem! While the term 'IPM' celebrates its 50th anniversary this year and the concept has been accepted and

Collaborative working will be essential if IPM programmes are to become more than the sum of their parts

Fig. 3: Pheromone-based monitoring system developed for the cereal crop pest *Haplodiplosis marginata* (Saddle gall midge). Image: ©Tom Pope

incorporated in public policies and regulations, the holistic science of IPM is still to be developed (Stenberg, 2017). Abolition of silos and collaborative working will be essential if IPM programmes are to become more than the sum of their parts and farmers are to benefit from synergistically combining conventional practices with biological controls, biopesticides and other novel approaches to crop protection. To this end, steps must be taken to encourage research that develops the concept of IPM rather than the individual IPM-compatible tools. Similarly, measures of academic success must be broadened to reflect the value of knowledge transfer and knowledge exchange activities that will ultimately promote the adoption and success of IPM. While there is clearly a long way to go, it can only be hoped that it doesn't take another 50 years of IPM research to unlock the true potential of this approach to crop protection. Indeed, the role of open, collaborative research is already clear from available evidence, which indicates higher levels of IPM adoption amongst farmers who proactively seek out information from impartial sources (Creissen *et al.*, 2021).





References

Ansari, M.A. *et al.* (2005) *BioControl* **50**, 465–475.
Ansari, M.A. *et al.* (2008) *Entomologia Experimentalis et Applicata* **129**, 340–347.
Bardner, R. *et al.* (1974) *Bulletin of Entomological Research* **64**, 141–160.
Chandler, D. *et al.* (2011) *Philosophical Transactions of the Royal Society B* **366**, 1987–1998.
Chant, D.A. (1961) *Canadian Entomologist* **93**, 437–443.
Coombes, D.S. *et al.* (1986) *Annals of Applied Biology* **108**, 461–474.
Creissen, H.E. *et al.* (2021) *Pest Management Science* **77**, 4148–4158.
Eilenberg, J. *et al.* (2001) *BioControl* **46**, 387–400.
Furlong, M.J. *et al.* (2001) *Journal of Economic Entomology* **94**, 344–356.
Gurr, G.M. *et al.* (2003) *Basic and Applied Ecology* **4**, 107–116.
Heimpel, G.E. *et al.* (2017) *BioControl* **63**, 27–37.
Hinz, H.L. *et al.* (2014) *Invasive Plant Science and Management* **7**, 565–579.
Hokkanen, H.M.T. (2017) *Arthropod-Plant Interactions* **11**, 741–742.
IBMA (not dated) Definition - Bioprotection as the global term for all biocontrol technologies. Available at: https://ibma-global.org/wp-content/uploads/2020/12/ibmadefinitionleafletweb.pdf
Kenis, M. *et al.* (2017) *Biological Invasions* **19**, 3401–3417.
Kirby, W. *et al.* (1816) *An Introduction to Entomology*, Longman, Hurst, Rees, Orme & Brown, London, UK.
Lacey, L.A. *et al.* (2015) *Journal of Invertebrate Pathology* **132**, 1–41.
Landis, D.A. *et al.* (2000) *Annual Review of Entomology* **45**, 175–201.
Lewis, T. (1964) *Scientific Horticulture* **17**, 74–84.
Lewis, T. (1969a) *Journal of Applied Ecology* **6**, 443–452.
Lewis, T. (1969b) *Journal of Applied Ecology* **6**, 453–458.
Lewis, T. *et al.* (1962) *Annals of Applied Biology* **50**, 299–311.
Lloyd, R.J. (1979) *Landscape Research* **4,** 18–22.
Lys, J.A. *et al.* (1994) *Entomologia Experimentalis et Applicata* **73**, 1–9.
Messelink, G.J. *et al.* (2014) *BioControl* **59**, 377–393.
Nagy, J. (2014) *Procedia - Social and Behavioral Sciences* **141**, 101–109.
Petherbridge, F.R. *et al.* (1942) *Annals of Applied Biology* **29**, 380–392.
Pollard, E. (1968) *Journal of Applied Ecology* **5**, 109–123.
Pollard, E. (1971) *Journal of Applied Ecology* **8**, 751–780.
Rodgers, P.B. (1993) *Pesticide Science* **39**, 117–129.
Roditakis, E. *et al.* (2000) *Annals of Applied Biology* **137**, 329–335.
Rowley, C. *et al.* (2017) *Biological Control* **115**, 112–118.
Shah, F.A. *et al.* (2008) *Biological Control* **44**, 111–115.
Sotherton, N.W. (1984) *Annals of Applied Biology* **105**, 423–429.
Sotherton, N.W. (1985) *Annals of Applied Biology* **106**, 17–21.
Sotherton, N.W. *et al.* (1989) *The Entomologist* **108**, 135–143.
Stenberg, J.A. (2017) *Trends in Plant Science* **22**, 759–769.
Thomas, M.B. *et al.* (1991) *Journal of Applied Ecology* **28**, 906–917.
Thompson, W.R. (1930) *Annals of Applied Biology* **17**, 306–338.
van Emden, H.F. (1965) *Journal of Applied Ecology* **2,** 171–196.

The value of long-term insect monitoring

Fig. 1: Common sycamore aphids feeding on sycamore buds. Photo: © Tom Pope, with permission.

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According to a recent investigation into science productivity "*Researchers face increasing pressure to produce results in ever shorter timeframes, with negative consequences*" (Oxford Economics, 2021). The study, led by Oxford Economics and commissioned by the science and technology company Merck, involved surveys of 3,500 individuals responsible for oversight of research projects in a range of sectors across seven countries. Seventy five percent of respondents felt that shorter funding cycles are leading to less research in new, unexplored areas. The same proportion felt that pressure to produce results or publish papers has increased over the past 10 years.

Similar trends arguably hold true for disciplines such as entomology. In the face of short-termist publishing and reporting pressures, the capacity and motivation to collect and curate long-term data may become jeopardised, even though such datasets are essential to enable more comprehensive understanding of how environmental drivers affect biodiversity. Publications from such datasets can be sparse in early years, as their value increases with the duration of recording. It is only after many years that dynamics in multiple

"Researchers face increasing pressure to produce results in ever shorter timeframes, with negative consequences"

(Oxford Economics, 2021)

environmental drivers, such as weather and land use, begin to create 'natural experiments' allowing sufficient statistical power for robust hypothesis testing. Furthermore, collecting such data requires an intense curiosity and motivation, which is at risk of being crowded out by other demands on time.

In light of this, it is remarkable how some professional and amateur entomologists have managed to maintain several of these valuable data collection schemes. One example is a 20-year dataset on the phenology of a tri-trophic interaction collected by Professor Simon Leather at Silwood Park, Ascot from 1993 to 2021 (Senior *et al.*, 2020). Weekly counts were conducted from March to November, with remarkably few missing weeks, to count the number of two aphid species, *Drepanosiphum platanoidis* (Common sycamore aphid) (Fig. 1) and *Periphyllus testudinaceus* (Common periphyllus aphid), as well as parasitism rates by wasps (various Hymenoptera species) and budburst of *Acer pseudoplatanus* (Sycamore) trees. The study revealed trophic mismatches in phenology between aphids with their host plant and parasitoids, based on differing weather cues. Warmer temperatures in late winter (February) delayed aphid emergence yet advanced parasitoid attack. In contrast, the sycamore trees were most affected by warmer early spring (March–April) temperatures, advancing their budburst.

Quantifying the abundance of aphids each week allowed for analysis of the effects of this phenological mismatch on their population sizes, whilst accounting for direct weather effects and intra- and inter-specific density-dependence effects. It turns out that aphid population growth rates appear currently resilient to a delayed emergence relative to sycamore budburst, at least partly due to strong buffering effects of density dependence (Senior *et al.*, 2020). But continued monitoring is important. Climate change can weaken the effects of density dependence (Ouyang *et al.*, 2014; an insight from another long-term study, this one a 37-year study of Cotton bollworm). The effects of climate on the Hymenopteran parasitoids are also worth closely monitoring. Beyond advancing earlier, some have been shown to completely stop diapausing in milder conditions if sufficient resources are available (Andrade *et al.*, 2016) and other species completely lose their winter diapause (Tougeron *et al.*, 2017).

Unfortunately, with the passing of the dedicated collector of this dataset, monitoring of the sycamore–aphid–parasitoid system at Silwood Park no longer continues. Taking on the legacy of such intensive data collection would be a major task. The longevity of long-term schemes may need careful consideration with regards to the effort devoted to individual sites, which also comes at the opportunity cost of being able to cover many locations. Other long-running insect-monitoring schemes, such as the UK Butterfly Monitoring Scheme (https://ukbms.org/) or Rothamsted light-trap and suction-trap networks (https://www.rothamsted.ac.uk/insect-survey), focus on a less intensive sampling methodology, and so can cover hundreds of sites through a network of volunteers. Such schemes are not set up to deliver insights on multi-trophic interactions, however. One promising avenue is the development of coordinated networks for long-term ecological experiments, such as the Long-Term Ecosystem Research (LTER) network in Europe (https://elter-ri.eu/) recently extended to collect socio-ecological data. This draws benefits from intensive data collection across space and time. Such broad spatial and temporal replication provides more power to detect important signals of environmental change, linking them to drivers and informing development of appropriate management interventions as needed. Suffice to say, UK insect-monitoring schemes are much more powerful when they link to standardised approaches carried out across the European continent and beyond. Such schemes reveal how biodiversity transcends national borders and ties us all together (*e.g.*, Hu *et al.*, 2021). In addition to a deep dedication to aphid ecology, Professor Simon Leather was also strongly outspoken about UK ties to Europe. Developing new long-term insect monitoring that bridges national boundaries would certainly be something he would approve of.

References

Andrade, T.O. *et al.* (2016) *Oecologia* **180**, 877–888.

Hu, G. *et al.* (2021) *PNAS* **118**, e2102762118.

Ouyang, F. *et al.* (2014) *Ecology and Evolution* **4**, 3362–3374.

Oxford Economics (2021) The State Of Scientific Research Productivity. Oxford Economics & Merck (Nov 2021). Available at: https://www.merckgroup.com/en/productive-science.html (Accessed: 17 March 2022)

Senior, V.L. *et al.* (2020) *Global Change Biology* **26**, 2814–2828.

Tougeron, K. *et al.* (2017) *Oecologia* **183**, 619–629.

Forests, insects and integrated pest management: topics of an unexpected career

As a research entomologist at Forest Research (FR), I study insects that are associated with trees, particularly the species that are considered pests due to their causing detrimental damage to trees and forests. The core focus of my research is the development and improvement of Integrated Pest Management (IPM) methods within a forestry context. FAO (2020) defines IPM as *"an ecosystem approach to crop production and protection that combines different management strategies and practices to grow healthy crops and minimise the use of pesticides"*. This IPM approach was developed in the 1970s in response to the overuse of chemical pesticides in agriculture (Wainhouse, 2005), although the "integrated control concept" existed 20 years earlier (Stern *et al.*, 1959, p81). IPM can be categorised into eight principles: prevention, monitoring, risk assessment, non-chemical methods, pesticide selection, reduced pesticide use, anti-resistance strategies, and evaluation (Barzman *et al.*, 2015).

"An ecosystem approach to crop production and protection that combines different management strategies and practices to grow healthy crops and minimise the use of pesticides"

In my role this includes the development of monitoring (*e.g.,* Sukovata *et al.*, 2020) and non-chemical control methods (*e.g.,* Moore *et al.*, 2019) for forest pests, such as *Hylobius abietis* (Large pine weevil) and *Dendrolimus pini* (Pine-tree lappet moth) (Fig. 1a, b). I also run FR's biocontrol programme for *Dendroctonus micans* (Great spruce bark beetle), for which we breed and release the predatory beetle *Rhizophagus grandis* (Fig. 1c). My interest in pest management led me to question how, where, and why IPM is (or isn't) being used in the forest industry and to identify the drivers and barriers to uptake. In 2020 I embarked on a PhD to investigate this topic further.

Less than ten years ago I knew nothing of IPM and little of insects in general. I was working for the National Trust helping conserve the collections of stately homes. My career as a forest entomologist stems not from a childhood fascination with bugs, but from discovering museum pests (such as furniture beetles and clothes moths) when I was working with historic collections. This discovery led me to a post-graduate open day at Harper Adams University where I first met Professor Simon Leather, who was to become a key figure in my early entomological life. Having done an undergraduate degree in Fine Art, I had attended the open day expecting to be advised to return once I had gained some science qualifications. After a fairly informal discussion, which I only realised afterwards was an interview, Simon offered me a provisional place on the IPM Master's and convinced me to abandon my job for a year's unpaid leave so that I could study full-time. During that year I felt completely out of my depth on multiple occasions and often questioned my decision. With support and encouragement from Simon and other staff and students, however, I persevered and my knowledge, skills, confidence, and grades slowly improved. By the time we were choosing topics for our research projects I was hooked and had decided I wanted to change careers and become a forest entomologist.

Forests and the insects associated with them fascinated me because they are both extraordinary and essential to the health of the planet (Fig. 2). Forests comprise and support a wealth of biodiversity and provide crucial ecosystem and societal services (Sing *et al.*, 2015). Insects, such as those that feed on roots, bark or leaves, perform vital ecosystem functions, such as nutrient cycling, and are a crucial trophic level of the food chain (Scudder, 2017). Under certain conditions, however, insect herbivory can cause extensive tree damage or mortality. Damage is driven by environmental changes, forest management practices or insect species being introduced to areas where trees have no natural defences. Protecting trees and forests by preventing or reducing insect damage is therefore necessary, and IPM offers a sustainable and ecological approach.

My ambition to become a forest entomologist meant I was keen to choose a Master's research project on a related topic. Opportunely, Simon had worked at Forest Research earlier in his career, publishing on forest pests including Large pine weevil (Leather *et al.*, 1999), Pine beauty moth (Watt *et al.*, 1991) and many other species (Day *et al.*, 1997). He kindly contacted several of his

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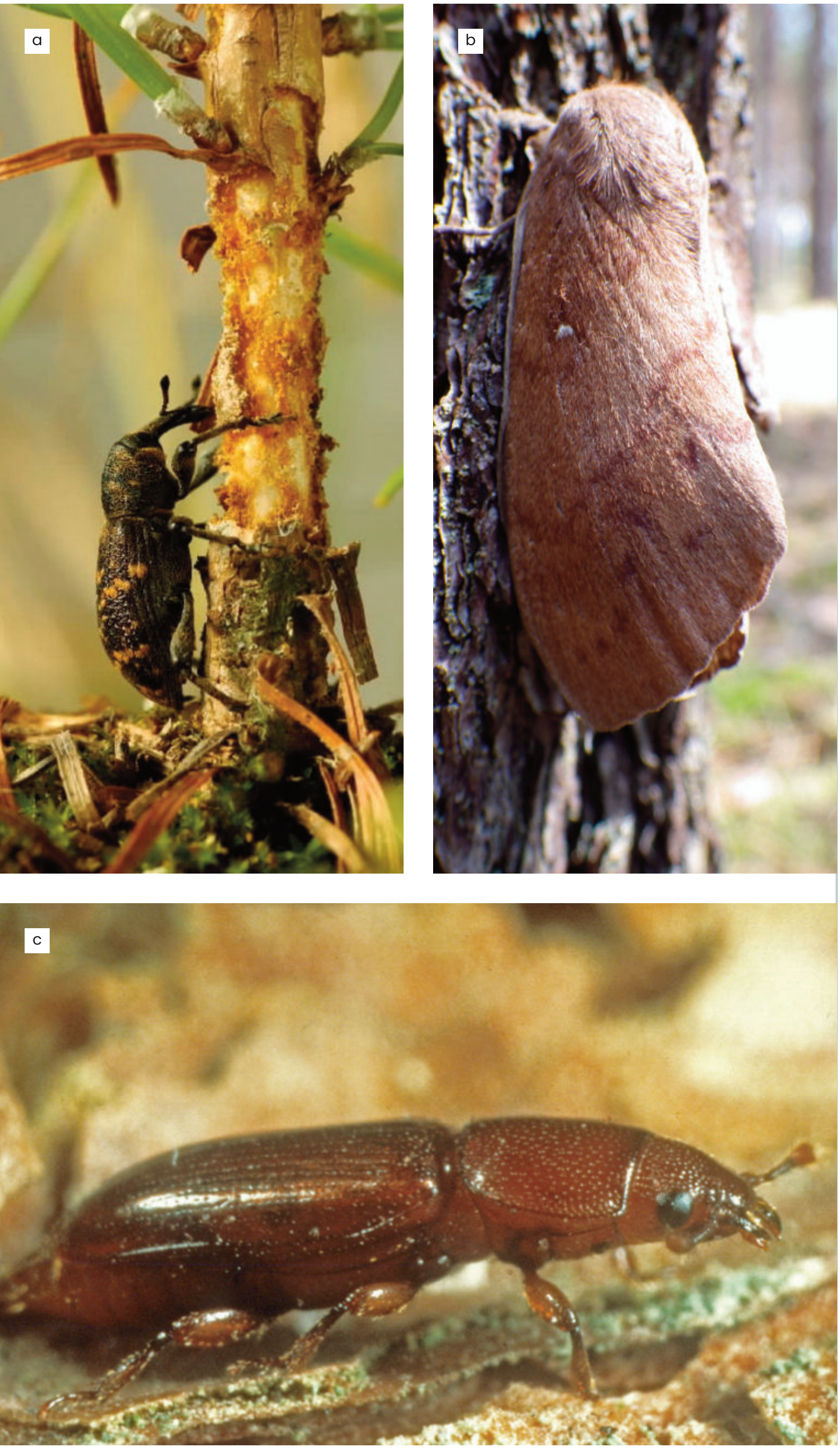

Fig. 1: a) *Hylobius abietis* (Large pine weevil), b) *Dendrolimus pini* (Pine-tree lappet moth), c) *Rhizophagus grandis*. Images: ©Crown Copyright, Forest Research.

former colleagues who helped construct a suitable study on the feeding preferences and behaviour of the Large pine weevil. Despite several challenges, I successfully completed the project and went on to pass my MSc with Distinction. After this intense year of learning, plus several voluntary and short-term roles (including at Natural England and Oxford University Museum of Natural History), I managed to follow in Simon's footsteps and secure a temporary contract at Forest Research in 2015. Since then, I have branched out from weevils, and now have a permanent role, but my focus remains IPM in forestry. Simon remained a constant supporter throughout my fledgling entomological career and would arrange to meet me whenever he was visiting Scotland. It was with his encouragement that in 2020 I embarked on a part-time PhD at the University of Edinburgh (supported by SRUC, FR and the Scottish Forestry Trust) to evaluate and enhance the use of IPM in UK Forestry.

My decision to study this topic was based on an accumulating sense that there was a mismatch between forest pest management research and practice. This was reinforced by anecdotal evidence from industry stakeholders that indicated there was both an interest in, and a need for, improved and alternative pest management methods. This seems a pertinent concern given the substantial economic impacts that insect pests have on forests in the UK, with annual management costs estimated to be between £4million and £11million (Williams *et al.*, 2010; Defra, 2018; Willoughby *et al.*, 2020). Integrated control strategies, including insect pest management, have also been identified by Defra (2013) as a key evidence gap within UK Plant Health policy. Although developing and improving an IPM approach may seem an ideal solution, there is first a need to assess existing knowledge, practices and attitudes towards IPM in UK forestry. My PhD is therefore investigating this knowledge gap, gathering evidence of existing forest pest management methods, and identifying strengths, weaknesses, opportunities, and challenges.

Developing a comprehensive IPM approach and implementing robust, sustainable practices is particularly critical now as UK trees and forests are facing the dual threats of climate change and the globalisation of trade. Both are facilitating a rise in the arrival and establishment of pest and pathogen threats (Freer-Smith *et al.*, 2017) (Fig. 3). Improved surveillance methods may be partly responsible for this rise, but the scale of threat is illustrated by the 600+ insect species listed on the UK plant health risk register as a direct or indirect threat to UK trees (Defra, 2021). The likelihood of these threats being introduced is amplified by the UK being the second largest net importer of forest products after China (Forest Research, 2020). The additional implications of increased demand, changing suppliers and new trading routes resulting from EU exit are not yet clear and could increase or decrease the risk of insect pest incursions into the UK.

Annual temperature rises and more frequent extreme weather events resulting from climate change are also promoting larger insect pest populations. Warmer temperatures enable larger pest populations to survive over winter, shorten life cycles and aid distribution flights over further distances. Additionally, more frequent storms, flooding and drought increase tree stress, which reduces tree defence resources and raises their susceptibility to insect pests. Planting the right tree (*e.g.,* species, provenance) in the right place (*e.g.,* soil type, elevation, exposure) can help promote tree health and thereby reduce susceptibility to pests. Increasing tree species diversity also builds forest resilience against pests and diseases (Deal *et al.*, 2014). The UK forest industry is, however, largely reliant on one tree species (Sitka spruce, *Picea sitchensis*), which accounts for 51% of conifer woodlands in GB (Forest Research, 2020). This leaves the industry particularly vulnerable to insect pests of spruce, such as *Dendroctonus micans* (Great spruce bark beetle), *Ips typographus* (Larger eight-toothed European spruce bark beetle) and *Elatobium abietinum* (Green spruce aphid). These insect pest threats also challenge the UK's ambitious tree planting and forest expansion targets.

As well as requiring additional or revised methods for dealing with these increasing levels of insect pest threats, UK forestry risks losing existing pest management

Fig. 2: Showing my tree appreciation. Image: ©Ashleigh Whiffin.

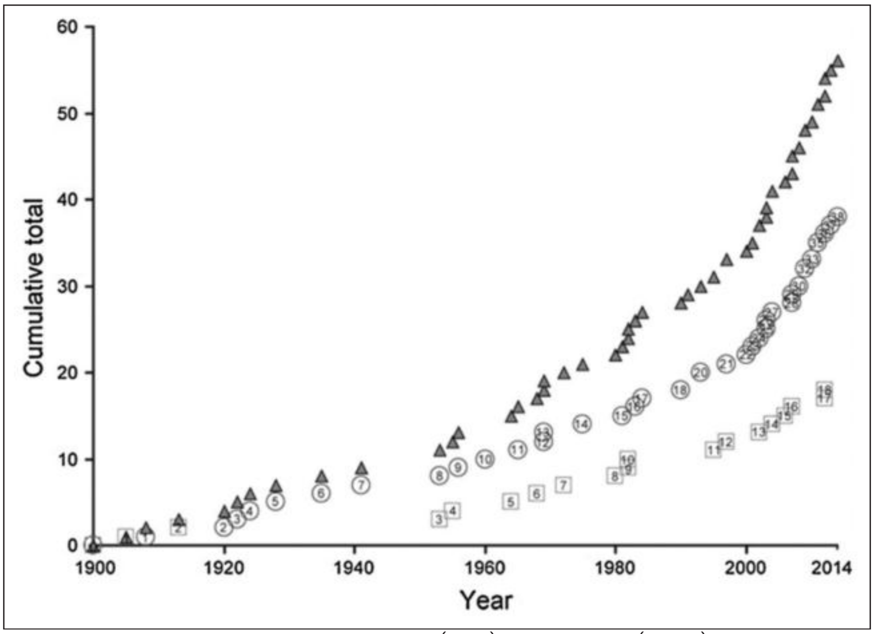

Fig. 3: The cumulative numbers of new tree pathogens (circle) and insect pests (square) identified in the UK between 1900 and 2014. The total accumulated numbers of pathogens and pests are also shown (grey triangle). (Reproduced from Freer-Smith *et al.*, 2017, p3173, with permission)

tools. Four (of five) insecticides currently relied upon for the management of *Hylobius abietis* (Large pine weevil) and *Thaumetopoea processionea* (Oak processionary moth) are at medium or high risk of withdrawal (Evans, 2020). The need for alternative, sustainable controls is therefore increasing. Research has tended to focus on monitoring and control methods for individual insect pests, rather than broader IPM approaches that incorporate a range of options to ensure optimum management. Recent technical advancements such as smart sensors (Kumar *et al.*, 2021) and geospatial technologies including unmanned aerial vehicles (UAVs) (Maslekar *et al.*, 2020; Nageswara Rao *et al.*, 2020) also offer innovative solutions.

My research intends to address some of the pest management challenges that the UK forest industry currently faces, with the aim of finding practical, cost-effective solutions based on an IPM approach. My hope is that this research will build on the work of peers past and present to help nurture and protect healthy and resilient forests and their thriving ecosystems. I have no doubt that trees, forests and especially the insects that inhabit them will continue to fascinate me and I will always be indebted to Simon Leather for helping me discover these remarkable small creatures which have huge impacts.

References

Barzman, M. *et al.* (2015) *Agronomy for Sustainable Development* **35**, 1199–1215.
Day, K.R. *et al.* (1997) *Forests and Insects*. 18th Edition. Chapman and Hall, UK.
Deal, R.L. *et al.* (2014) *Forestry* **87**, 193–208.
Defra (2013) *UK National Action Plan for the Sustainable Use of Pesticides (Plant Protection Products)*. York, UK.
Defra (2018) *Tree Health Resilience Strategy*. London, UK.
Defra (2021) *The UK Plant Health Risk Register*. Available at: https://secure.fera.defra.gov.uk/phiw/riskRegister/ (Accessed: 24 April 2021).
Evans, A. (2020) *Potential Impacts Arising from Pesticide Withdrawals to Scotland's Plant Health PHC2018 / 15 - Project Final Report.*
FAO (2020) Available at: http://www.fao.org/pest-and-pesticide-management/ipm/integrated-pest-management/en/ (Accessed: 12 November 2020).
Forest Research (2020) *Forestry Statistics 2020, Forest Research*. Available at: https://www.forestresearch.gov.uk/tools-and-resources/statistics/forestry-statistics/forestry-statistics-2020/.
Freer-Smith, P.H. *et al.* (2017) *Biodiversity and Conservation* **26**, 3167–3181.
Kumar, R. *et al.* (2021) *IEEE Consumer Electronics Magazine* **10**, 51–56.
Leather, S.R. *et al.* (1999) *Bulletin of Entomological Research* **89**, 3–16.
Maslekar, N.V. *et al.* (2020) Chapter 2 in Chakravarthy A.K. (ed.) *Innovative Pest Management Approaches for the 21st Century*. Springer, Singapore.
Moore *et al.* (2019). *SBRI End of Phase 1 Report Form*. Can Do Innovation Challenge Fund.
Nageswara Rao, P.P. *et al.* (2020) Chapter 1 in Chakravarthy A.K. (ed.) *Innovative Pest Management Approaches for the 21st Century*. Springer, Singapore.
Scudder, G.G.E. (2017) *Insect Biodiversity*. John Wiley & Sons Ltd, Chichester, UK.
Sing, L. *et al.* (2015) *Ecosystem Services and Forest Landscape Management*, Forestry Commission, Edinburgh.
Stern, V.M. *et al.* (1959) *Hilgardia* **29**, 81–101.
Sukovata L. *et al.* (2020) *Agricultural and Forest Entomology* **22**, 319–327.
Wainhouse, D. (2005) *Ecological Methods in Forest Pest Management*. Oxford University Press, Oxford, UK.
Watt, A.D. *et al.* (1991). *Forest Ecology and Management* **39**, 211–221.
Williams, F. *et al.* (2010) *The economic cost of invasive non-native species on Great Britain. Technical report*, CABI Proj No VM10066.
Willoughby, I.H. *et al.* (2020) *Forestry* **93**, 694–712.

PhD supervision – from both sides

The enthusiasm and charm of the man who interviewed me, Simon Leather, and who saw sufficient capability in me, won me over

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I discovered a thirst for learning rather late and, ten years after most of my peers, charged through agricultural college (National Certificate in Horticulture (Arboriculture) at Merrist Wood) and an undergraduate degree (Ecology and Conservation at University of Sussex) to find myself hanging out under the Wisteria of Imperial College's Silwood Park campus embarking on a PhD. To be honest, I hadn't thought that much about aphids before then and had applied haphazardly, more based on distance from home than topic. The enthusiasm and charm of the man who interviewed me, Simon Leather, and who saw sufficient capability in me, won me over. He assured me that working to better understand the biology and ecology of *Tuberolachnus salignus* (Giant willow aphid) (Fig. 1) would be useful, interesting and a tremendous learning experience, and that he would direct me as much, or as little, as was needed.

Silwood Park in the late 1990s was an extraordinary educational experience. The cohort of students was zinging with drive. The postdocs were diverse, social, always happy to answer our questions and give advice. The supervision I received was superior. The campus had a cohesion and collegiality holding a diverse array of ecologists together. There were 'nozzle heads' working on reducing pesticide use, entomologists working to understand pests and beneficials, applied ecologists working to understand the natural world, and theorists who made interpretive leaps. They drank and ate together, helped any student who came along, and the breadth of our work benefitted hugely. In the midst of all this I was very lucky to have Simon. He advised, encouraged, laughed and helped me bash my work into a suitable shape.

In any potential academic life, a PhD is a critically formative stage.

You learn so many things in those few years. It's a time of maturing and self-direction, of focus and synthesis, of skill development and of finding a place in the vastness of science. Like many of Simon's students, my PhD had an 'industrial partnership'. The Game Conservancy Trust had an interest in the landscape-level change that might be brought about by substantial expansion of short rotation coppice willows as biofuels, and thus in the potential insect pests that might affect productivity in this system. An 'industrial partner' helps root the applied side of much entomological work and is often a route to impact. I've tried often to do the same for my students. In

Fig. 1. *Tuberolachnus salignus* (Giant willow aphid). © Tom Pope

many ways, chatting and exploring these possibilities with the people we encounter at conferences and dinners is part of the supervisory arts. These conversations act to build links for future work to have direct relevance to problems faced (or anticipated), and help with diversifying funding streams. I was set an excellent example in this.

Right from the start I was encouraged to 'stand up and talk'. Simon made me give departmental seminars, sent me to the Royal Entomological Society student meeting, to the British Ecological Society annual meeting and pushed me to give talks long before I had any results to talk about. This worked. I was soon able to give lectures confidently. It improved my experimental design, exposed me to a wider theoretical base and helped me to avoid many pitfalls. Learning how to manage difficult, sometimes unanswerable, questions modestly but robustly is vital for surviving conferences and helps us to flesh-out our own understanding of a topic in which we hope to develop some expertise.

Trying to squeeze three field seasons out of a three-and-a-half-year PhD is a real challenge and you have to hit the ground running. Fortunately for me, *Tuberolachnus salignus* (Giant willow aphid) was a forgiving insect to study and fed on an even more forgiving plant. I had no problem with replication (and learnt rapidly about pseudo-replication), and the aphid's reproductive capacity (Collins *et al.*, 2001a, b) gave me stock to complete synchronous experiments (when you have to work seven days a week) efficiently. Simon helped me plan. He gently pointed out unrealistic ambition, kept in touch and encouraged me to publish. Our first papers are formative in so many ways. We learn the writing style and conventions of academic communication (which have thankfully shifted from formality to clarity over the past couple of decades). If we are

Giant willow aphid biology and ecology

What we know:

- This aphid can form large infestations that are sufficient to kill small trees, but this is rare (Collins *et al.,* 2006).
- They are sufficiently large and coordinated to repel many potential predators with synchronous kicking.
- Their honeydew contains the trisaccharide, melezitose, in addition to several disaccharides and, together, these can influence soil biota and feed back to tree architecture and performance (Milcu *et al.*, 2015).
- They are obligately parthenogenetic.

What we don't know:

- Where they go in winter. They can vanish from field sites, and many avenues have been explored to identify either over-wintering morphs or sites, but none has offered a convincing explanation.
- How they are 'bound as a species' and remain globally morphologically conserved if there is no sexual recombination.
- How high they fly. Colonisation patterns suggest they may travel substantial distances in large leaps. Is this through flight or high-level wind-borne dispersal?
- What biocontrol will be effective. Fungal pathogens seem more viable than predators or parasitoids for this species.

lucky, we are reviewed by people who understand that this is an 'early work' and who phrase their critiques supportively. These early works are not usually our best papers, but learning to take the criticism, absorb the advice and respond intelligently is a key life skill. My early papers are small bricks in the wall of entomological understanding. The aphid in question is now troublesome to New Zealand's Manuka Honey production (Sopow *et al.*, 2017), and the papers are contributing some of the basic biological underpinnings to the researchers there.

I was so very lucky to be well-supervised and, in Simon, retained a source of pragmatic advice for the next twenty-five years. What, and how, he taught me both academically and in approach to life will stay with me, and feeds through to my students. I will always aspire to good communication, careful listening and to providing sound advice.

References

Collins, C.M. *et al.* (2001a) *European Journal of Entomology* **98**, 177–182.
Collins, C.M. *et al.* (2001b) *Agricultural and Forest Entomology* **3**, 183–189.
Collins, C.M. *et al.* (2006) *Annals of Applied Biology* **138**, 133–140.
Milcu, A. *et al.* (2015) *Pedobiologia* **58**, 119–127.
Sopow, S.L. *et al.* (2017) *Agricultural and Forest Entomology* **19**, 225–234.

Life in death

Figure 1. *Cicindela campestris* (Green tiger beetles) in the collection at National Museums Scotland (NMS).

Collections can be used to answer an array of questions, from tracking changes in species distribution to examining morphological adaptations in response to environmental drivers

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As a curator, a large proportion of my time is spent advocating for entomology by using the preserved bodies of dead insects (Fig. 1). I have to say, this isn't the direction I thought I would take… let's rewind for a moment. I was properly introduced to insects during my forensic science BSc at the University of Derby. This culminated in a fascination with forensic entomology and participation in research on insect succession (see Barnes *et al.*, 2019). For a short time, I dreamt of pursuing forensic entomology further. It's what motivated me to enrol on the Entomology MSc at Harper Adams. However, it didn't take long for Professor Simon Leather to convince me to explore other entomological avenues, and so I diversified and carried out my research project on *Halyzia sedecimguttata* (Orange ladybird).

Following my MSc, I initially felt a little lost. Most of my cohort were pursuing PhDs, but I felt that this option wasn't right for me. Whilst applying for jobs, I volunteered at the Natural History Museum, and it's there that I became besotted with collections. So, when an opportunity came up at National Museums Scotland (NMS) I grabbed it with both hands and haven't let go yet (Fig. 2)!

When you talk of insect collections and museums, many people will think of quiet stores full of cabinets and drawers, housing row upon row of neatly pinned specimens – an army of dead insects. What many will overlook, however, is the accompanying data labels. They're often overshadowed by the beauty of the specimens themselves, but the labels are of equal importance. Whether impaled on a pin or nestled in a tube of ethanol, data labels contain all the key information relating to the preserved specimen (such as the collecting locality, date and habitat) – they hold its scientific value. With this ecological information, collections can be used to answer an array of questions, from tracking changes in species distribution to examining morphological adaptations in response to environmental drivers. The reality is that a preserved insect is not

Figure 2. Ashleigh, in the entomology store at the National Museums Collection Centre, Edinburgh.

truly dead if it's accompanied by high quality data.

Museums hold great appeal for me, not only for the collections themselves, but because they provide many opportunities to engage with a broad audience, from researchers and local natural history groups to schools and families. This is facilitated through a variety of different mediums, be it a tour of the collection or public event, a display (Fig. 3) or exhibition or a blog – there are so many ways to advocate for insects!

Simon's passion for outreach was infectious and I caught that bug from him early on in my studies. By far, the most enjoyable form of outreach is in-person events, when you can engage with people one-to-one and see the wonder in their eyes when they see insects in a new light. However, preaching our entomological gospel one person at a time does not reach enough people to make a real impact. Fortunately, something that Simon introduced many of his students to was the benefits of Twitter (Fig. 4) – and aren't we so very glad he did! Social media has become an effective tool for communicating insect science to a wider audience (Côté *et al.*, 2018; Hulcr *et al.*, 2019). It's also a space to be creative and make useful connections within the community. The outcomes are sometimes surprising, and for me a highlight has been a collaboration with Australian taxonomist Dr Bryan Lessard on the use of social media as a tool for public engagement for entomology collections (Lessard *et al.*, 2017). Throughout the pandemic, it has been a vital outlet and alongside Zoom and YouTube, social media allowed us to continue to engage people with entomology when other options were off the table.

In my spare time, I volunteer as co-organiser of the National Silphidae Recording Scheme – one of many citizen science initiatives working to encourage recording of some of the lesser-known insect groups. Together with Matthew Esh and Richard Wright, we've been collating records of carrion beetles since 2016, to better understand their ecology, distribution and conservation status. Thanks to a community of dedicated biological recorders, we have accrued over 30,000 records! This doesn't just comprise recent efforts. To get a look at the full picture, historical records were

required too, and where do we go to find these… to the museums of course! As well as databasing our collection of 800 British and Irish specimens at NMS, I also travelled to several other museums to hunt down those old records. This wealth of information recently enabled the creation of a collaborative new book on the Histeridae, Sphaeritidae and Silphidae of Britain and Ireland (Lane *et al*, 2020) (Fig. 5). The opportunity to increase awareness, knowledge and recording of these groups has been really exciting, and it was a privilege to be a part of this work.

One of the highlights of my job is the fieldwork. It feeds into research and helps develop the collection. The museum collection also grows via donations, and some are from formal survey work by paid professionals – we even have some of Simon's specimens from his time working for the

Figure 3. Engaging the next generation with insects on display at the museum. ©National Museums Scotland.

Figure 4. Professor Simon Leather conference tweeting from his laptop (2017).

Figure 5. The Histeridae, Sphaeritidae and Silphidae of Britain and Ireland, alongside some of the Carrion beetle specimens at NMS.

Figure 6. Ichneumonid wasps collected by Simon, in the NMS collection.

Forestry Commission in Scotland (Fig. 6). For the most part, museum collections have largely been built up by volunteers: decades of passionate people utilising much of their spare time to collect and record our insect fauna. Collections are an incredible resource, providing a window to the past and the potential to solve problems long into the future. We must continue to develop and utilise them for the benefit of our dear insect populations and to honour those who devoted their time to their creation. By studying the insects in museum collections, these specimens come back to life.

In Britain and Ireland there is a wonderful network of specialist curators and collection managers working with insect collections. The *Insect Collection Managers Group* meets annually to exchange knowledge and provide entomological collections advice. If you are in need of collections-based guidance, are seeking specimens to support your current research or are making plans for your personal collection, the ICMG is here to help. Further details can be found on the webpage (https://www.natsca.org/icmg) and you can also follow the ICMG on Twitter (@InsectManagers).

References

Barnes, K.M. *et al.* (2019) *Journal of Archaeological Science: Reports* **25**, 600–609.

Côté, I.M. *et al.* (2018) *FACETS* **3**, 682–694.

Hulcr, J. *et al.* (2019) *American Entomologist* **65**, 92–96.

Lane, S.A. *et al.* (2020) The Histeridae, Sphaeritidae and Silphidae of Britain and Ireland. Field Studies Publications, Telford, UK.

Lessard, B. *et al.* (2017) *Annals of the Entomological Society of America* **110**, 467–479.

Making Twitter a fabulous place to be

Fig. 1: Simon Leather's Twitter profile highlighting his longstanding interest in the biodiversity of urban roundabouts.

Twitter isn't for everyone. It can be a horrible place, where horrible people say horrible things. But it can be also a fabulous place, where like-minded people share everyday joy, life-changing news and, well, just gossip. Simon was one of the people that made Twitter a fabulous place. His feed, the stream of short messages (tweets) that tweeters post, was a constant source of information, joy, insight and inspiration for the 10,000 or so followers of his @EntoProf account (Fig. 1). He is deeply and frequently missed.

We both joined Twitter at around the same time, back in 2012 when Twitter was already well-established. I had come across Simon a little through my involvement with the RES, and from some interactions with him wearing his journal editing hat. I first knew him as a kind, patient editor who had helped me as a PhD student shepherd a tricky, but ultimately worthwhile, manuscript through the publication process. But, once on Twitter, I got to know Simon in a wholly different way. He always tweeted as "himself", sharing his Sunday lunches and his trips to France (often with some level of travel-related jeopardy to his followers on tenterhooks), as well as his entomological and ecological thoughts, both trivial and profound.

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His blog, *Don't Forget the Roundabouts* (Fig. 2), was an anchor for the more profound of Simon's Twitter outputs but, as the very many followers of his blog will know, even the profound was delivered with gentle humour and an openness of mind often missing from academics on social media. His last post, "The most difficult thing I have ever had to write – *Insects, A Very Short Introduction*" details his trials and tribulations producing what turned out to be the last, as well as the most difficult, thing he wrote. His followers were often treated to updates on the progress of the book and on the challenges of producing such a short work on such a large group. I lost track of the various word count goals that Simon reached and breached; usually his problem was having too much to say, especially about aphids! Either way, the updates were always welcome.

When Simon died it hit me far harder than I would have imagined. In part, of course, it was because he was someone I admired and respected. His contribution to entomology was great, and his wise counsel was incredibly important over the past few years of change at the RES. But the far greater reason was that, through his tweets, I had come to know and care about Simon in ways that, on examination and reflection, surprise me. I realise that for much of the past 9 years of our mutual time on Twitter I had interacted with Simon several times a week, often several times a day. Whenever a tricky specimen was presented, or some entomological puzzle unearthed I'd be sure to turn to Twitter secure in the knowledge that, like some Batman of insect science, Simon would come to my rescue once the "@EntoProf" tag was activated. And sure enough, Simon would invariably swoop in with an ID, a suggestion of someone who could help, or a head-scratching post of solidarity.

Yes, Twitter isn't for everyone. But it was certainly for Simon. I'll miss his daily presence, his inspiring posts, his help, assistance and advice. And his Sunday lunches – they always sounded great.

Fig. 2: One of Simon Leather's very popular blogs in the Entomological Classics series.

Obituary

Professor Simon R. Leather

13th March 1955 – 27th September 2021

Allan Watt

My long time friend and colleague Simon Leather was the most influential British entomologist of his generation. His passion for writing about insects not only resulted in over 200 research papers, books and articles but also involved editorial roles in several journals. His research was curiosity-driven, notably his work on the insect communities found on roundabouts, but he was a strong advocate of applied research and made significant contributions to both pest management and insect conservation. He was a voracious reader, not just of the entomological literature. He found the perfect opportunity for sharing his entomological knowledge through university teaching and then found a much bigger audience through social media.

After a degree in agricultural zoology at Leeds University, Simon joined Tony Dixon's large group of PhD students at the University of East Anglia (UEA), most of whom were working on aphids. Simon's was on the Bird cherry–oat aphid, a species that would occupy his attention for many years to come and which triggered a life-long love of aphids. Tony Dixon's enthusiasm for all aspects of aphid ecology and his very active approach to encouraging new ideas led Simon to work on many topics, another life-long trait. The first example of Simon's broadening research interest was on the relationship between aphid ovariole number and fecundity. He later referred to the importance of "side projects" such as this, driven by a "satiable curiosity". Simon's sense of fun and mischief also became evident during his years in Norwich, although the snowballs, carefully set aside one winter for use (now frozen hard) in a lab in the summer, were not fully appreciated by the University hierarchy.

Cereal aphid field work, Norfolk 1978. (Photo: Allan Watt.)

Simon next went to Finland to continue his research, now focusing even more on the Bird cherry–oat aphid's life on its overwintering host. Simon also became interested in another insect on the same tree, the Bird cherry ermine moth, and developed a long-term fascination with the tree and its insect community. Later he wrote on Bird cherry in the *Biological Flora of the British Isles* series, co-authored a book on insects on cherry trees and planted several Bird cherry at Silwood Park. One has been planted beside his grave.

After a second post-doc at UEA, in 1982 Simon moved to the Northern Research Station of the Forestry Commission on the Bush Estate outside Edinburgh to work on the Pine beauty moth, which was having a devastating impact on Lodgepole pine plantations in Scotland, particularly in Speyside and Sutherland. This research sought to understand and prevent such outbreaks, which were happening despite it being an innocuous insect on Scots pine. The notion that stressful growing conditions were the cause of the problem was prevalent within the forestry community but in the most ambitious experiment on a forest pest ever established in the UK, Simon showed clearly that site selection or forest management could prevent outbreaks. Working with three of his first PhD students, Paddy Walsh, Maureen Docherty and James Aegerter, Simon provided convincing evidence for the alternative hypothesis that natural enemies were playing the major role in defining where outbreaks occurred.

Pine beauty moth was arguably the most significant insect threat to Scottish forestry but for entomologists it was an exciting and inspiring time, not just because of the vast numbers of adult moths and larvae witnessed at the peaks of the outbreaks but also because of the potential relevance of the new ideas about the relationship between plants and insects that were emerging elsewhere, particularly in the US and in Finland, where Simon had recently worked. The research was demanding at times, particularly in the Scottish winter and, paradoxically, it was often difficult to find evidence of Pine beauty moth, particularly of the egg stage, after the outbreaks subsided. The study locations, nearby hotels and distilleries, and teams of students and visiting researchers, made the experience much easier! One of the most challenging experiments of the many that we did together took place in Poulary forest, Lochaber, to see whether tree defences were stimulated by previous attacks. This required caging insects on mature trees in this isolated forest, waiting for a phone call to say the forest was about to be sprayed with insecticide, rushing back to protect the cages with plastic bags, returning a few days later to remove the covers, and finally taking down the cages when the larvae were full-grown. Despite frequently working at height, often with secateurs, the experiment was completed successfully, and medical assistance was only required once!

Simon continued to publish his research at an exceptional rate but also looked for other ways to communicate his growing knowledge of forest pests and other insects. He started to contribute to *Entopath News*, a Forestry Commission newsletter read by forest practitioners as well as researchers, and later became its editor. The importance of the Pine beauty moth research was such that when Simon and I co-organised a conference on forest insects in Edinburgh in 1989, many of the major forest entomologists from North America and Europe came, including Peter Price, Alan Berryman, Jack Schultz and Erkki Haukioja.

Pine beauty moth monitoring team, Sutherland 1989. (Photo: Alan Thomson)

Simon used his time in Scotland to continue to work on the Bird cherry–oat aphid and on aphid ecology generally. He also developed general perspectives on the relationships between insect herbivores and their hosts. His two most cited papers are on host-plant quality, insect size and fecundity, and are clearly informed by his experience of working on two very different insect herbivores, aphids and Lepidoptera.

In 1992, Simon fulfilled a long-held ambition to return to academia and teaching. He joined Imperial College, working at Silwood Park for 20 years then, in 2012, moved with his team (Tilly Collins and Tom Pope) to Harper Adams University. He supervised about 55 PhD students, ran entomology MSc courses and continued his research, which expanded to include several aphid species, various forest pests including the Pine weevil, and agricultural pest management. His important syntheses on, for example, insect overwintering and sampling forest insects, are highly regarded.

Simon's interest in the insect communities of trees continued, growing from a focus on cherry to a broader re-evaluation of the relationship between the size of insect communities on rosaceous species and, for example, the area occupied by the plant species. The original inspiration for this work is, of course, Macarthur and Wilson's species–area research, which has had a profound influence on ecology. Although many people, including Simon, had already applied this theory in several different contexts, Simon, inspired by the road system in places such as Bracknell, took it in a very novel direction – the insect communities of roundabouts. Simon and Alvin Helden showed that roundabouts behaved similarly to biogeographical islands: the larger and more diverse their habitats, the more diverse their fauna. They also realised their potential as teaching aids and many entomologists now look at roundabouts in a very different way.

Roundabouts were also the inspiration for Simon's blog. Perhaps it was unsurprising that having already spread the word about insects in so many media, Simon would turn to social media so naturally and so effectively. He took to Twitter as @EntoProf in 2012, and to his blog *Don't Forget the Roundabouts* in 2013. In the blog, he describes how his growing concern about the public's ignorance of entomology first took him into schools and then, finally convinced by Fran Sconce, one of his PhD students, took to social media. Simon's written legacy takes many forms and although we will greatly miss the wonderful conversations that rapidly and unpredictably moved from topic to topic, many traces of these conversations can be found in his blog. His enormously diverse interests shine through

Setting up a Pine beauty moth experiment, Poulary 1987. (Photo: Allan Watt)

but also his modesty, describing himself as a "competent field entomologist" and suggesting that his research career was launched by a variety of wheat particularly susceptible to aphids. His blog on this variety, Maris Huntsman, is a wonderful example of how Simon could weave a tale from seemingly insignificant, random elements. It is also, typically, beautifully written, with an enticing title and a thought-provoking conclusion. Simon had a love of the (properly) written word and returned time and time again to the theme of writing and publishing. He wrote from the perspective of the author, the editor, and the reviewer, all of which is well worth reading by anyone interested in the publication process. These reflections on writing and publication are unique, certainly in the entomological world. They include thoughts on passive and active voices in writing, notable not just for the historical perspectives but also for an openness about his change of views. Scientists rarely write about their motivations for particular work or the challenges they face but Simon did. He wrote about particular aspects of science writing, such as the crucial aspect of writing paper titles, and shared practical thoughts on scientific presentations, including recommendations on what to wear, and cautious advice on the use of humour in talks based on his own experiences of getting it right – and wrong! He also wrote about the papers that influenced him and why, and about his own papers, both the highly cited ones and those that were relatively ignored. Regarding one of the latter, on aphid cannibalism, Simon suggested that it was too original to be highly cited, as not many other people were working, or writing, about aphid cannibalism. Impact, of course, takes many forms and although Simon's papers on Pine beauty moth are not among his most cited, they certainly had an impact on Scottish forestry by questioning the wisdom of growing large plantations of Lodgepole pine.

Simon also wrote about his experiences of being an editor, why he did it, and the changing world of publishing. Some of his strongest writing on the publication process was reserved for reviewers. He wrote about selecting reviewers, responding to reviewers, and, most significantly, highlighted their importance: "Referees, or reviewers as we now tend to call them, are the life-blood of a successful journal; … good reviewers are worth their weight in gold and should be treasured and encouraged." As in many things, Simon led by example both as a reviewer himself and in his defence of reviewers, on one occasion asking whether journals that use bullying tactics to speed up their review process should be boycotted.

More than anything else, however, Simon's contributions to social media gave voice to his championing of all things entomological and of the people who study insects. He, of course, used aphids as examples of the intriguing world of insects, whether that be their complex life cycles and why they have evolved them, their common names (such as the wheat dolphin) or their cultural significance (from postage stamps to HMS Aphis). He also wrote about vampire moths, the way that insects such as caddisflies are named across the world, coming across snow fleas at the end of a 2 hour walk in deep snow to a field site, and much more.

Simon's writing often stemmed from curiosity, no more so than when writing about entomological mysteries such as the dorsal tubercle (or shark's fin as Simon described it) of the Giant willow aphid. His writing, in his blog and elsewhere, stimulated more curiosity in the reader and has, undoubtedly, led many people to find out more about insects and to become entomologists, amateur and professional. He saw the amateur entomologist as "the backbone of entomology", wrote of always being in "awe of the taxonomic expert", and valued the contribution of all scientists, whether they were, in his words, groundbreakers or bricklayers. Simon's blogs on the work of particular entomologists and of the methods they used provide further evidence that his interest in, and support for, entomologists and the process of entomological study was as great as his interest in entomology itself. Simon was very much the entomologists' entomologist.

Simon was never unkind about other disciplines but his advocacy for insects and their study was often outspoken. He criticised journals that claimed to publish research on animals but neglected insects, and bemoaned the conservation emphasis on the so-called charismatic mega-fauna: "They suck away much-needed funds and bright capable students into an area that is vastly over-supplied with resources that could be much more profitably used elsewhere, *i.e.*, the study of our planet's dominant animal inhabitants, the invertebrates." Simon fought hard for more funding for entomology, not only on social media but also in journal articles, pointing out that the relative neglect of insect science – *institutional vertebratism* as he defined it – threatened both insect conservation and food security. The ability to keep pursuing the message on Twitter, however, made it the best medium for Simon's unrelenting campaign for more attention for insects.

Simon played a major role in traditional publishing too. He was editor of *Antenna* and *Ecological Entomology*, a senior editor of *Annals of Applied Biology*, and an Associate Editor of *Agricultural and Forest Entomology*, where the breadth of his knowledge of applied entomology made him the go-to person for difficult manuscripts. In 2006 he helped to launch and became Editor-in-Chief of *Insect Conservation and Diversity*, and it is perhaps particularly fitting that this journal and so much of his passionate writing about insect decline and insect conservation occupied so much of his last years.

Apart from his editorial roles, Simon contributed to the Society as a trustee (1993-1996 and 2011-2014), chair of the library committee, and regular contributor to its conferences and other meetings, including joining a working group on the Society's new strategy last year. Simon viewed the Society's Postgraduate Forum as being particularly important for the future of entomology and played a very active role in the outreach initiatives of the Society and other organisations. A Fellow since 1978, he was appointed an Honorary Fellow in 2015. He was delighted to be a member of the Entomological Club, and as Secretary of the Verrall Association from 2013 organised the annual Verrall Supper until 2020. Simon was also an active member of the British Ecological Society, including the BES Summer Schools, and the Association of Applied Biologists.

Taking a rest from field work, Poulary 1987. (Photo: Allan Watt.)

Simon leaves a remarkable written legacy and, had he lived, he would have added to this through, for example, his planned books on aphids. He had reached the stage of wishing to synthesise and disseminate his knowledge rather than adding to it with new research. We still have one book to look forward to, however, *Insects – A Very Short Introduction* – to be published this year.

Perhaps, however, the greatest professional legacy is his students, particularly the Master's and PhD students whom he taught and supervised from his time at the Forestry Commission, through generations of Silwood Park alumni and on in his years at Harper Adams. Judging by the comments on social media after he died, even Simon's words of encouragement to those he met only briefly, or 'met' only on social media, had an impact. I am not convinced that Simon fully appreciated the impact he had: he once wrote "I have been content with adding bricks to the scientific edifice, grouting in between entomological and ecological tiles and adding pieces to the vast jigsaw of life." Simon certainly added many important pieces and, perhaps even more significantly, he gave many others the tools and the inspiration to make their own contributions.

Royal Entomological Society

Society News

Soldier beetle on sentry duty. Credit Greg Hitchcock

News from Council

Meetings of Council

Council met on 9th February 2022. Following approval of the Royal Entomological Society strategy by trustees in the autumn of 2021, this meeting focussed on arrangements for the implementation of the strategy over the next three years. Discussion focussed on further development of the Society including a review of all committees and their structure, diversity and inclusivity and revised trustee policies. The following is a summary of the main points.

CEO Report

A review of the Society's activities since the previous meeting in December was presented. A draft of the final RES strategy document was shared in preparation for the launch at the start of March. There was also an update on the planning of the strategy launch event to be held at the Garden Museum in London. Following this, there was a review of the recent changes to staffing.

There was an update on the garden design work being undertaken by the RES, and the Mansion House building works, including the recent completion of significant asbestos removal. Finally, assessments of RES publishing and the launch of the new website were given.

Strategic Implementation Plan, Financial Plan and Annual Business Plan

Having previously agreed the Vision and Strategic Priorities, the Senior Leadership Team presented the various projects and programmes for the upcoming three years that had been shared with committees. Each project or programme had been mapped to link to the Strategic Priorities and Vision as well as various impacts, outcomes and risks. Alongside this, a comprehensive financial plan was discussed to ensure a sustainable future for the Society. Finally, the Annual Business Plan, detailing activities for the 2022–2023 year, was presented. The final plans were agreed for the next strategic period.

Diversity & Inclusion

The existing Diversity & Inclusion Policy for the RES was shared, alongside a proposed external statement that was presented for discussion. It was felt that the RES was making good progress and that the next steps would be to have a new working group that could further develop the diversity and inclusivity strategy and targets for the Society. An audit of the Society practices would be instigated and a working group would be brought together to continue developments in this area.

Committee Review & Trustee Policies

Following the Society's governance review in 2020 and 2021, it was felt that the committees now needed to be appraised to ensure that they could best function to support implementation of the strategy. Therefore, a review was agreed looking at the current structure and terms of reference. Any changes would be proposed later in the year and agreed at a future Council meeting.

It was also felt that it may be good to develop a governance handbook or suite of trustee policies. This would provide additional guidelines that support the bye-laws of the Society. These would be further developed over the coming months.

Committee Reports

Minutes of the Finance Committee were reported.

Grand Challenges Project

The manuscript of the Grand Challenges project is being finalised ready for submission in the coming weeks.

Verrall Lecture

An update on the Verrall Lecture being given this year by Camille Parmesan was given. The 2022 lecture was now to be online only.

Simon Ward
Chief Executive Officer

Ento22

13-16 September 2022

UNIVERSITY OF LINCOLN

Plenary speakers

Dr Sylvain Pincebourde
Université de Tours

Dr Jessica Ware
American Museum of Natural History

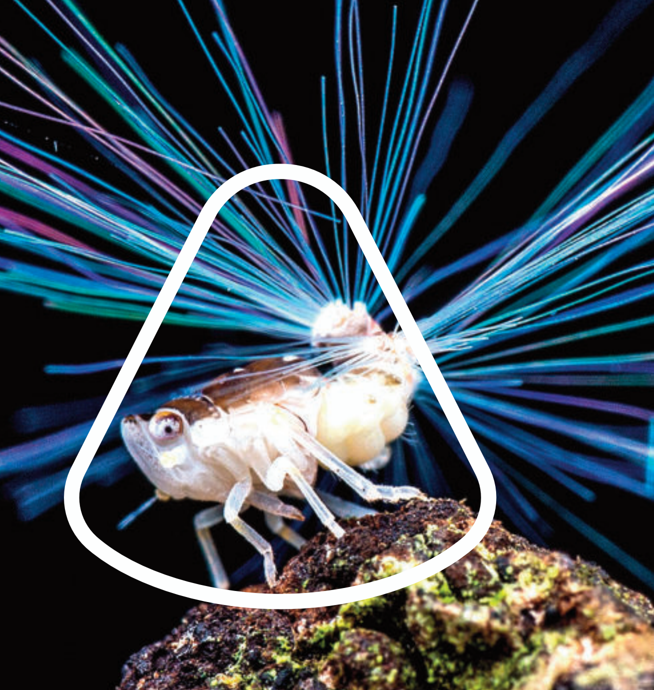
Dr Nalini Puniamoorthy
National University of Singapore

Our annual insect science meeting taking place at the University of Lincoln, UK

In the current climate and biodiversity crises, insects are being increasingly recognised for their value as service providers, indicators of biodiversity loss and models for understanding ourselves and other animals. The RES recently recognised a series of 'Grand Challenges in Entomology', and at Ento22, our first annual meeting in person for two years, we will provide a platform for the key themes.

Ento22 will be a hybrid meeting for those unable to attend in-person.

The meeting will include three plenary speakers, one each morning, followed by relevant 'Grand Challenges' sessions.



Royal Entomological Society

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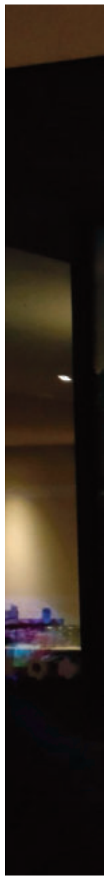
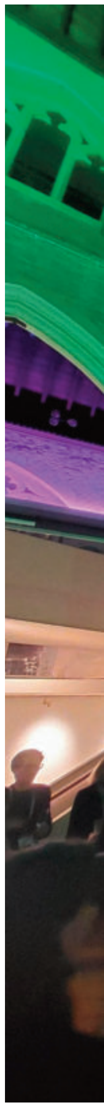
RES Strategy Launch



Enrich the world with insect science



Over the last year, the Royal Entomological Society has been developing its inaugural strategy. With a clear vision to ***enrich the world with insect science***, the strategy has been evolved at a time when we want to increase our impact and relevance as well as ensure a sustainable future for the Society.

On 10th March we launched the strategy at the Garden Museum in London. This was an occasion to invite representatives from other learned societies, charities, businesses, scientific organisations, decision-makers and government departments to share our plans.

During the evening the winning photography of the 2021 Insect Week competition was illuminated in the courtyard garden of the museum. There were also visual presentations and stands showcasing our publishing partnerships with Wiley and the Field Studies Council as well as other areas including the library, outreach and the Grand Challenges programme.

Our president, Professor Helen Roy, gave a warm welcome and this was followed by speeches that set out the four key strategic priorities that will focus our work until 2025. The speeches can be viewed on our website and YouTube channel.

The event was a great success and feedback has been extremely positive. There was a real excitement with many looking to strengthen their ties with the Society, which will have a positive impact for all of our membership. My thanks to all those who made the event such a success.

The 2022–2025 Royal Entomological Society vision and strategy can be downloaded from the Royal Entomological Society website. Alongside the strategy is a short explanatory video.

Simon Ward
Chief Executive Officer

Meet the RES team

Simon Ward Mem.RES
Chief Executive Officer

Simon leads the Society and has significant experience in the charitable and environmental sector. He studied for an MRes in Ecology and Environmental Management at the University of York and a BSc in Environmental Biology at the University of the West of England. Simon was previously the Head of Field Studies Council East Region and Education Lead.

He is a trustee of the Council for Learning Outside the Classroom and a Fellow of both the Royal Society of Biology and the Royal Geographical Society.

Robert Spencer Mem.RES
Director of Finance & Operations

Robert is an experienced finance director with detailed knowledge of operating within the charity and commercial sectors.

Robert has a BSc in Engineering from the University of London, holds a Diploma in Company Direction from the Institute of Directors and is a Fellow of the Chartered Institute of Management Accountants. He was previously Director of Finance at two professional membership organisations: the Royal College of Physicians and the Chartered Institute of Management Accountants.

Dr Luke Tilley FRES
Director of Communications & Engagement

Luke is an experienced charity executive and science communicator. He heads the engagement team at the Society, supporting conferences, Special Interest Groups, membership services, press and media, and outreach activities. Luke completed a PhD on parasitoids in horticultural biocontrol at the University of York and a BSc in Biology at the University of Sheffield. He is also a Fellow of the Royal Society of Arts and a trustee of a mediation and community cohesion charity in his hometown of Sheffield, UK.

Emilie Aimé Mem.RES
Head of Publishing

Emilie has many years' experience in academic publishing, mainly in STEM journals. She has held previous roles at the British Ecological Society, the Royal Society and BioMed Central (part of SpringerNature). She is responsible for the overall success of the RES publications portfolio, including journals, handbooks and *Antenna*. Emilie is also responsible for the Society's much-loved and internationally important library. She has a BSc in Zoology from the University of Liverpool.

Prof. Jim Hardie Hon.FRES
Resident Entomologist

Jim has been a Fellow of the RES for over 40 years. He has been President, Vice-President, Treasurer, a trustee and was an editor of *Physiological Entomology* for over ten years. He is now resident entomologist at the Society and answers entomological questions from the press and public. Jim has a BSc from Brunel University London, a PhD from the University of Birmingham and a DSc from the University of London. Jim is Professor Emeritus at Imperial College London.

Francisca Sconce Mem.RES
Senior Outreach & Learning Officer

Fran coordinates the Society's outreach and learning activities, including Insect Week. She studied a BSc in Ecology & Environmental Biology and a Masters of Entomology at Imperial College London, then did postgraduate research at Harper Adams University looking at springtails in agroecosystems. Fran is a STEM Ambassador and an Associate Fellow of the Higher Education Academy.

Gulam Hussain Mem.RES
Membership & Events Officer

Gulam has wide experience in the membership sector and has previously worked at the Chartered Institute of Linguists, as well as the trade union Prospect/BECTU. He is first contact for any membership queries, as well as supporting the development of RES membership services and events.

Jemma Gannon Mem.RES
Finance & Governance Administrator

Jemma has experience of operational support and office administration for various organisations in Hertfordshire, UK. She supports RES members with their payments and enquiries, and provides operational support at RES headquarters. Jemma also helps with Council and committee administration at the Society.

Bianca Saccone Mem.RES
Digital & Media Officer

Bianca has a background in analytics, research administration and data reporting. She maintains the RES and Insect Week websites and the Society's social media channels. Bianca is also responsible for online and virtual participation at RES events. She takes an active role in improving promotion and reach online of all RES activities.

Rose Pearson Mem.RES
Librarian and Archivist

Rose runs the Society's world-famous library. She was previously the librarian for Bird College Conservatoire of Dance and Musical Theatre, and an assistant librarian at Christie's Education. Rose graduated from University College London with an MA in Library and Information Studies.

Kate Watkiss Mem.RES
Facilities Officer

Kate ensures the smooth and efficient running of RES headquarters, making sure the Society's buildings comply with current legislation. Kate also helps members with their enquiries and ensures that visitors to HQ have everything they need.

David Simcox Mem.RES
Conservation Project Manager

David graduated with a BSc hons in Ecology at Royal Holloway College. Part of his role with RES is to advise on the management at Daneway Banks, underpinned by the evidence he collects on the impacts of extreme weather events brought about by climate change.

Sarah Meredith Mem.RES
Conservation Officer

Sarah is undertaking research to help advise the conservation work at Daneway Banks. She studied for a BSc in Countryside Management at the University of Lincoln and a MSc in Wildlife Management and Conservation at University of Reading.

Journals and Library

Insect Molecular Biology: an introduction to the journal

Jenn Brisson[1], Mark J. I. Paine[2], and Zhijian Jake Tu[3]
co-Editors-in-Chief

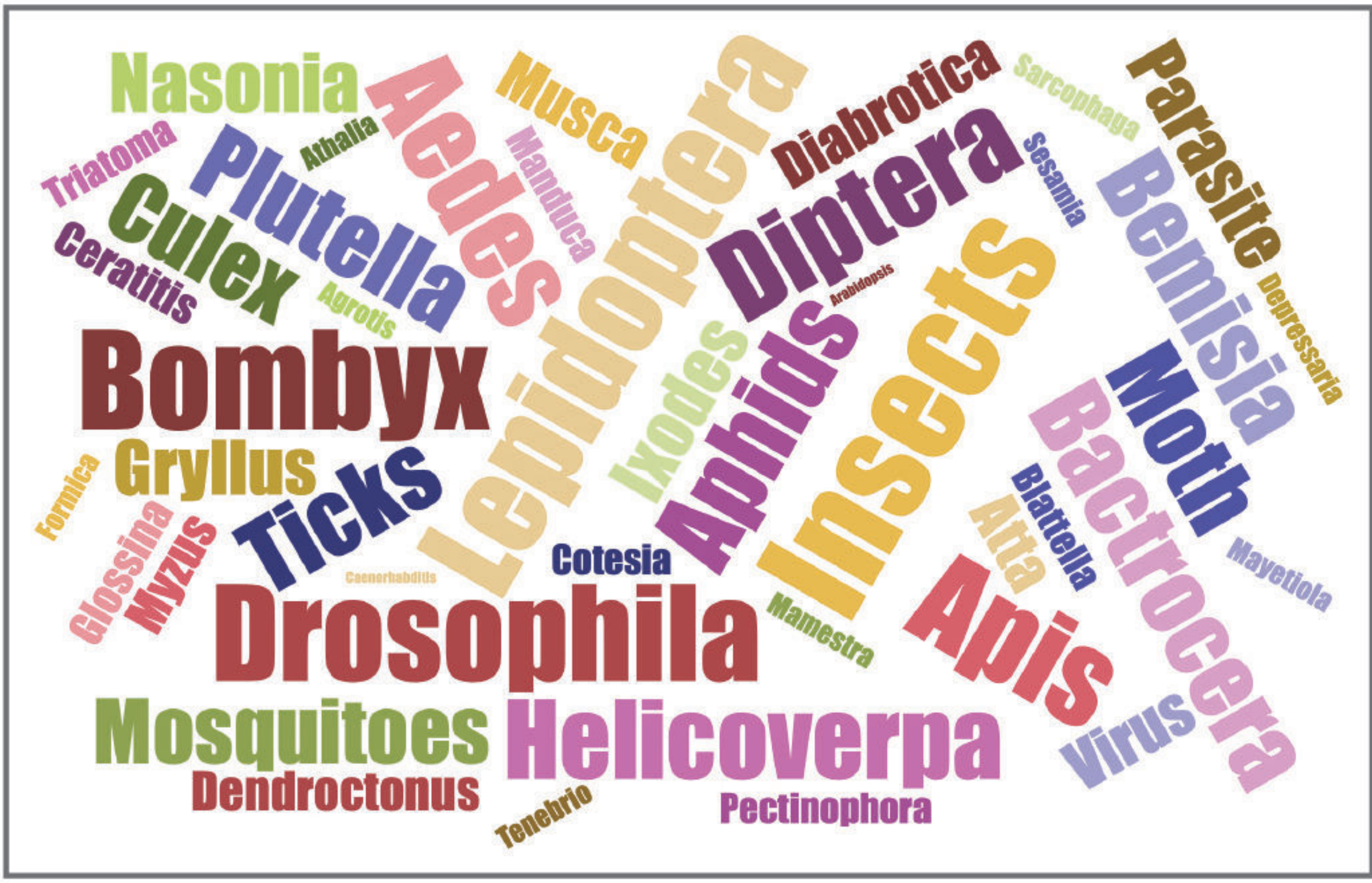
[1] Jenn Brisson, Department of Biology, Hutchison 310, University of Rochester. jennifer.brisson@rochester.edu. 585-275-8392. www.brissonlab.org

[2] Dr Mark J I Paine, FRES, Dept of Vector Biology, Liverpool School of Tropical Medicine, Pembroke Place, Liverpool L3 5QA, UK. mark.paine@lstmed.ac.uk. @MarkJIPaine1

[3] Zhijian Jake Tu, Department of Biochemistry and Fralin Life Sciences Institute, Virginia Tech, Blacksburg, VA 24061. jaketu@vt.edu.

Overview

Insect Molecular Biology (IMB) publishes high quality original research on topics broadly related to both fundamental and applied aspects of insect molecular biology. This Royal Entomological Society journal was launched in August 1992 by Anthony (Tony) James and Julian Crampton, who sadly passed away in 2019. They were the inaugural Editors-in-Chief, to be followed over the years by Lin Field, David O'Brochta and Paul Eggleston. 1992 was an exciting time, with rapid expansion in genomic and molecular biology research, and IMB was the first journal to provide a focus for research on insect molecular biology. The scope remains as it was in Julian and Tony's first editorial: to be "intentionally broad to serve both the fundamental and applied aspects of insect molecular biology with papers relating to the agricultural and medical sectors being equally welcome". The current co-Editors-in-Chief are Mark Paine (Liverpool School of Tropical Medicine), Zhijian Jake Tu (Virginia Tech) and Jenn Brisson (University of Rochester). They lead the journal with the invaluable support of 24 Associate Editors, who handle the day-to-day business of reviewing manuscripts, and a Review Editor, George Dimoupoulos. IMB receives approximately 175 manuscripts a year, with about a 30% acceptance rate. Almost all are research articles, although we do



Word clouds depicting the study organisms (left) and study area (right) for all articles published in IMB from 2011-2021.

have an occasional review and would welcome more. The current impact factor is 3.585 and has been growing over the last couple of years.

A look at the keywords gathered from the last decade of IMB publications provides a birds-eye view of the types of science that we publish. Notice that many different types of insects show up: bees, moths, flies, beetles – ranging from established models to models currently being developed. Often the focus is on pest species. Also notice that articles generally focus on the RNA and/or protein level. The molecular biology subjects are diverse, including the molecular genetics of odour detection, insecticide resistance, behaviour and reproduction. Articles often focus on a single gene or multiple genes involved in a process, and study how those genes function using tools like RNA interference or CRISPR/Cas9 knockout. Our overall goal with each article is to add a bit of generalisable knowledge to the broader field of insect molecular biology.

A global journal

Approximately half of the submissions come from authors in China, with the United States, India and Brazil being runners up. This is consistent with increases in investment in both fundamental and applied research on diverse insect species in China. As we expand our global reach, we would also like to take this opportunity to encourage submissions from RES members in the United Kingdom.

Looking to the future

IMB is looking to make several changes. The journal transitioned in 2019 from an Editorial Board system to a system of Associate Editors who invite reviews and help evaluate the manuscripts. To facilitate the transition and create a stronger community, we organised a successful Associate Editors' meeting in 2021 and plan to continue the practice. We would also like to expand our board of Associate Editors and are particularly interested in increasing the number of women Associate Editors and Associate Editors from Europe, Asia and Central/South America. We added five AEs at the end of 2021 and we are continuously open to applications from talented and service-oriented candidates.

As we maintain our focus on publishing high-quality, original, hypothesis-testing research on topics broadly related to the molecular biology of insects, we are also interested in serving as a venue for the rapid dissemination of genome assemblies and well-curated -omics datasets to encourage resource sharing and facilitate the development of data sciences for insects. We are also looking to increase the number of reviews that we publish. Reviews can be a valuable addition to the literature and reviews that capture the rapidly expanding topic areas or disciplines are especially helpful.

IMB is a strong supporter of transparency, scientific rigour and reproducibility in our publications. In the near future, we look to formalise and standardise guidelines on these important topics. Finally, we are looking into starting a series of special issues. Please contact one of the Editors-in-Chief if you are interested in becoming an Associate Editor for IMB, have an idea for a review article or would like to lead a special issue.

Student Forum, Cardiff, 17th–18th February 2022

Max Tercel, Charlie Woodrow, Manuela Carnaghi

The RES has a reputation for providing accessible and productive scientific meetings at every career-stage for entomologists. For students, the RES Postgraduate Forum has been a cornerstone in the entomological calendar. With the success of *EntoCareers* last year (*Antenna* **45**(2) 86–87), it was clear that we could still connect in meaningful, useful and fun ways even when physical gatherings were not possible. But it also highlighted just how important in-person meetings can be. With that in mind, we (the student reps) aimed to host the annual Student Forum both in-person and online using a blended approach, renamed from the *Postgraduate Forum* to be more inclusive of advanced students passionate about entomology who may not have their Bachelor's degree yet.

After much planning and several stressful COVID rule-changes for Wales in the 10 weeks before the event, it was held in the Temple of Peace (Fig. 1), Cardiff, and simultaneously beamed to dozens of online participants across the UK and abroad. The first day kicked off with Cardiff's own Dr Hefin Jones, a long-standing friend of the RES and Editor of *Agricultural and Forest Entomology*, who delivered a wonderful "retrospective" look at his epic scientific career in-person, which received huge praise from the delegates. The next invited talk came from Dr Natasha Mhatre from the University of Western Ontario, and she discussed her personal journey through science and how entomology is not a constraint on the type and mode of science you are able to do – quite the opposite. Natasha explained how studying tree crickets has allowed her to diversify her research from structural acoustics to biophysics, behaviour, neurobiology and even cognition. The student talks on day one were also fantastic and ranged widely in subject area

Fig. 1. The Temple of Peace, Cardiff.

from the conservation of the *Stethophyma grossum* (Large marsh grasshopper) to the effects of non-neonicotinoid pesticides on bumblebee behaviour. However, once student talks were wrapping up and we were preparing for the poster and evening networking session, *the bad news struck*. In what can only be described as titanically unlucky, storm Eunice swept in, and with it a "RISK TO LIFE" weather warning. Given that the RES values the safety and general aliveness of its members, it was clear we needed to move the second day online. This was particularly unfortunate because the Student Forum represented the first in-person meeting held by the RES in over two years due to COVID! Nevertheless, the delegates were in good spirits and we were able to continue the poster and networking session with wine and pizza in the Temple of Peace, later moving to the Pen & Wig pub to finish off the day.

On day two, after a very calm start, the weather picked up just as the talks began, causing significant damage in various parts of Cardiff (Fig. 2), confirming it was the right decision to move everything online. Dr Amoret Whitaker from the University of Winchester began the second day talking about 'CSI: Crime Scene Insects' and gave a comprehensive view of forensic entomology and its application, also discussing her career and working with police authorities as an entomologist. After the first session, we moved onto the Careers Session, where we were very lucky to hear from Dr Hefin Jones (Cardiff University, again!), Dr Chris Jeffs (British Ecological Society) and Dr Manpreet Kohli (American Museum of Natural History). These talks were particularly thought-provoking for many of the attendees because they covered a wide range of avenues to practice entomology and science generally, within or outside of academia, and from a range of backgrounds. The delegates did an excellent job of adjusting to the last-minute online format, many of whom attended virtually from their hotels (Fig. 3)! The Careers Session was the most interactive of the whole conference, and the digital format lent itself well to

Fig. 2. Damage caused by storm Eunice in the immediate vicinity of Cardiff University. Photo credits: Rebecca Young and Isa Pais.

speakers being able to answer questions in the Zoom chat whilst other talks were ongoing. The final invited talk of the event was from Dr Leonidas-Romanos Davranoglou, a postdoc at Oxford University Museum of Natural History, where he shared tips on starting an entomological career applicable to schoolchildren and postdoctoral researchers alike. He also discussed the various challenges entomologists face and provided his view on how to push the field forward significantly. The student talks of the day were, again, very varied: from the function of spider web stabilimenta to the control of the dreaded *Psylliodes chrysocephala* (Cabbage stem flea beetle).

The adaptability of student delegates who were set to deliver these talks in-person was excellent, and delegates generally were positive despite the difficulties. We rounded off the day with the student prizes. The 2nd place poster prize went to Charlie Woodrow (University of Lincoln) for his poster 'Reviving the sound of a 150-year-old insect: the bioacoustics of *Prophalangopsis obscura*', with the 1st place poster awarded to Dawn Morgan (University of Wolverhampton) for her poster titled 'Overview of forensic entomology teaching and research in the United Kingdom'. The 2nd place talk prize went to Hannah Fenton (Fera Science Ltd & University of Newcastle) for her talk 'Combatting pesticide resistance in insects using botanical bio-synergists', with the first prize talk going to Harry Fishlock (University of Cambridge) for his talk 'Function of the stabilimenta'. Massive congratulations to the winners and to everyone who presented over the course of the conference – competition was fierce this year.

Despite the storm-induced chaos, it was fantastic to be back to in-person meetings with fellow entomologists, and we look forward to seeing you all again in the future, online or physically. A huge thanks to Luke Tilley and Fran Sconce who supported us through all of these difficulties and in the planning stages of the conference, as well as the support for adapting and evolving the meeting into a 'blended' approach.

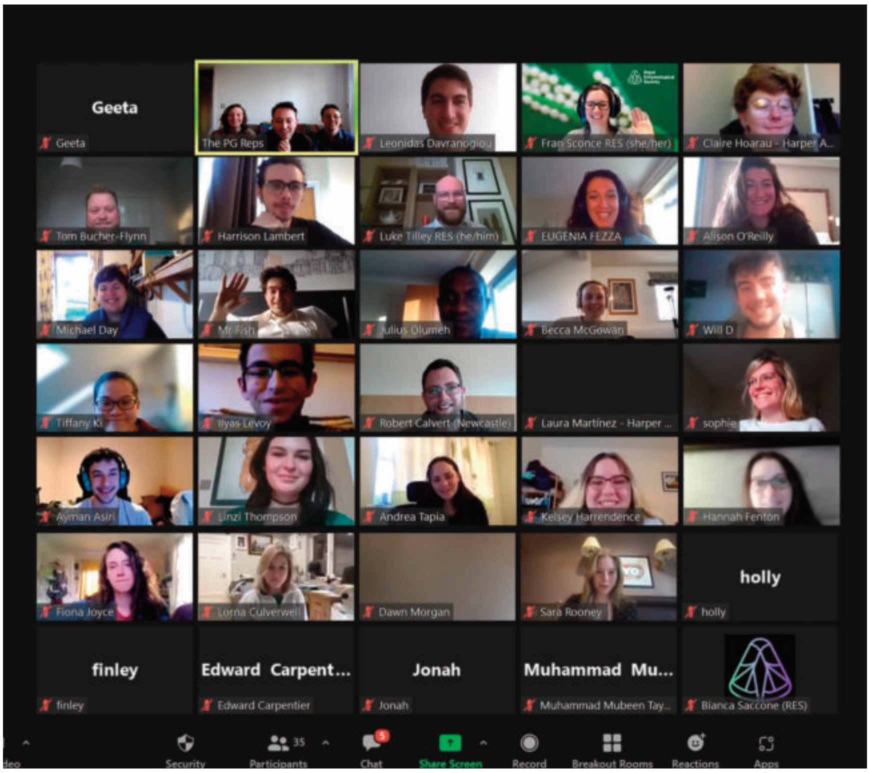


Fig. 3. The second day participants all attended via Zoom due to storm Eunice.

The Verrall and Young Verrall Lectures

2nd and 5th March 2022 (online)

Speaker: Professor Camille Parmesan Hon.FRES
Theoretical and Experimental Ecology (SETE), CNRS, Moulis, France
School of Biological and Marine Sciences, Plymouth University, UK
Department of Geological Sciences, University of Texas at Austin, USA

Hot off the press from IPCC: Insects in a warming world

Report by Richard Harrington

Camille Parmesan taken at Wembury beach near Plymouth.

Speakers for the Society's most prestigious lecture, the Verrall Lecture, are booked a year ahead. At that point, we had no idea of the timeliness of the lecture, for it came just two days after the publication of the Intergovernmental Panel on Climate Change (IPCC) Working Group II contribution to the Sixth Assessment Report, *Climate Change 2022: Impacts, Adaptation and Vulnerability* (www.ipcc.ch/report/ar6/wg2/) of which Camille Parmesan was a Coordinating Lead Author dealing with terrestrial and freshwater ecosystems. Had she known of the timing, I'm not sure that she'd have agreed to speak, as the workload involved in the build-up to, and aftermath of, the report's publication was extremely intensive and challenging. Perhaps it was a good thing that our event was online and thus avoided the need for Camille to travel from France, much though we missed her in-person presence, as indeed we missed again enjoying a Verrall Supper.

First, a bit about Camille's impressive achievements. She is Director of Research at the CNRS Station for Experimental and Theoretical Ecology (SETE, in Moulis, France) as a French "Make Our Planet Great Again" Laureate. Her research focuses on the impacts of climate change on wild plants and animals, and spans field-based work on butterflies to synthetic analyses of global impacts on a broad range of species across terrestrial and marine biomes. She has authored numerous assessments of impacts of climate change on agricultural pests, and on human health through changes in disease risk. Her 2003 paper in *Nature* was ranked the most highly cited paper on climate change (Carbon Brief, 2015). Her scientific awards include being the 2nd highest-cited author in "climate change" (T Reuters) and being named the "2013 Distinguished Scientist" by the Texas Academy of Sciences. She has been elected Fellow of the European Academy of Sciences, Fellow of the Ecological Society of America and Honorary Fellow of our own Society. She received the Conservation Achievement Award from the National Wildlife Federation and was named "Outstanding Woman Working on Climate Change" by the IUCN. She has worked with the IPCC for more than 20 years, and was an official Contributor to its Nobel Peace Prize in 2007.

Camille first outlined the process for producing the IPCC report. It involved 270 lead authors and 675 contributing authors (59% male, 43% female) from 67 countries (57% "developed", 43% "developing"). 34,000 scientific papers were reviewed and there

Camille and husband Mike. Note former President Dame Miriam Rothschild with parasol.

were 62,418 reviewer comments, all of which required a response. There is no doubt that the report received considerably greater scrutiny than any peer-reviewed paper, which was essential for its credibility.

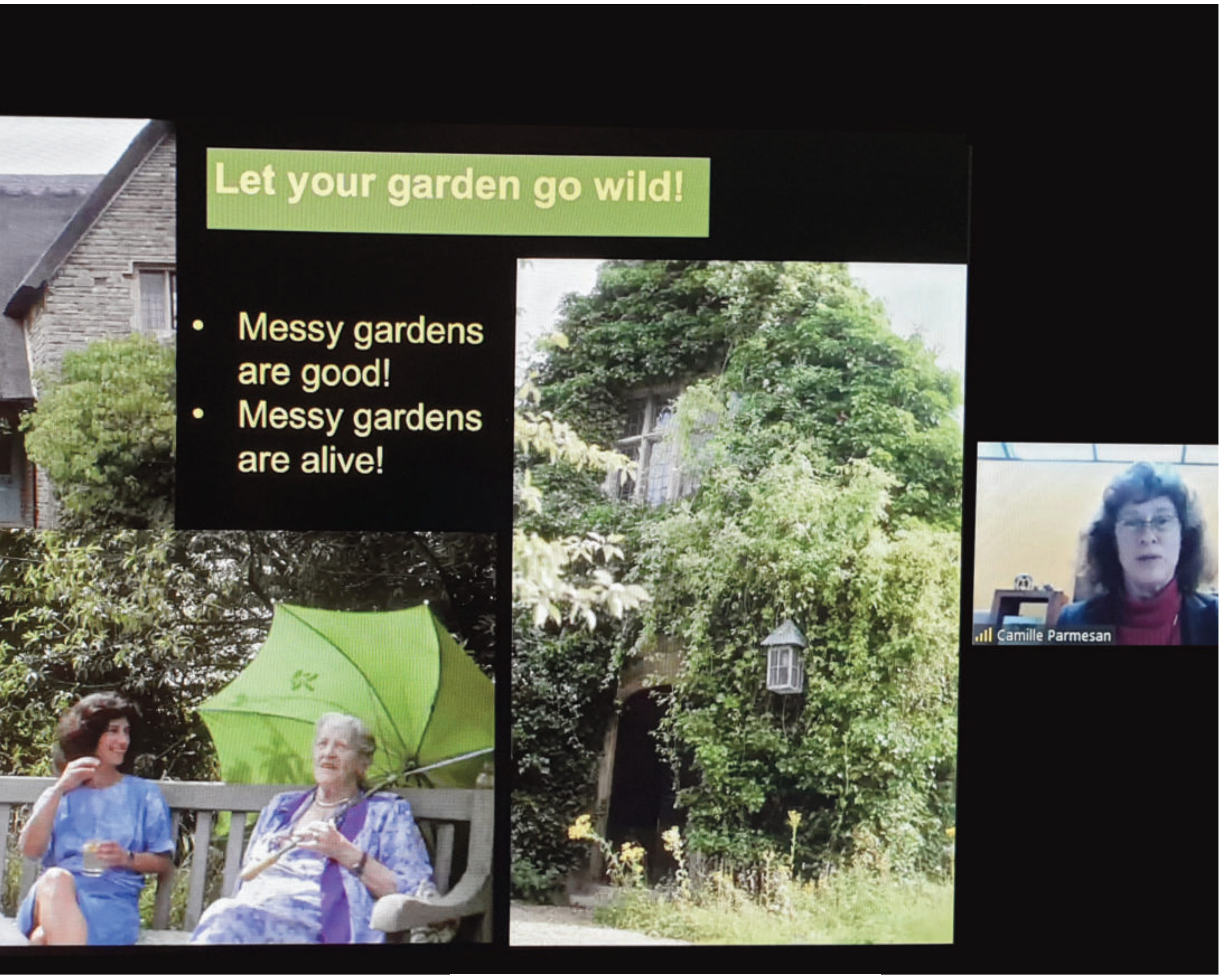
The Working Group I Report, published in 2021, predicted that global temperature will continue to rise until 2050 under all emissions scenarios and that global warming will exceed 2°C unless there are steep reductions in emissions. Ocean and land carbon sinks are weakening, and warming has happened almost everywhere, although it has been greatest at higher northern latitudes due to changing albedo (reduced reflection of sunlight by snow). This is leading to movement of disease-carrying insects and other vectors. For example, Nepal has seen six new vector-borne diseases involving three genera of mosquitoes since the publication of the last assessment five years ago. There is also an increase in the rate of emergence of new diseases in the High Arctic, involving ticks, mosquitoes, biting flies, deer flies, horse flies, blackflies and other vectors.

In spite of their vital function, there are no clear data on the impacts of climate change on pollinators as a group, as reported declines have multiple causes that are very difficult to disentangle, but the increasing frequency of temperatures exceeding historically-observed upper tolerances helps explain widespread bumblebee species declines.

There is no hiding Camille's love of butterflies which, she explained, are fabulous indicators of climate change with excellent data. *Euphydryas editha* (Edith's chequerspot), Camille's signature species, is going extinct as a result of climate change throughout its range, not just at its range edge. Eggs are being laid higher up plants as the ground gets hotter (ground temperatures can reach 48°C at elevations of 2,500 m). There is hope, though. Colonisation of new sites releases new genetic variation, facilitating host-plant switching, for example. Camille predicts that this butterfly will survive climate change. You heard it here first.

The IPCC report showed that forest insect pests have expanded northward and that the severity and extent of outbreaks has increased, due particularly to warmer winters.

There is less certainty attached to changes in precipitation than there is to changes in temperature. Britain's drying appears to be slow, but soil



moisture is what matters and the UK will experience increased soil drying with a concomitant threat to peatland carbon sinks, which currently cover 12% of UK land and store two billion tonnes of carbon, more than all the forests in the UK, Germany and France put together. They also support a wealth of insect species. Fire seasons have lengthened and there are projected increases in fires in arctic, boreal, mediterranean, tropical forest and savannah ecotones.

There is an impending risk of irreversible impacts such as species extinctions. Two species are known to have been lost as a direct result of climate change and ninety more in combination with disease. The proportion of species at risk is rising. Hundreds of populations have gone extinct, resulting in localised losses.

Camille's main message is that nature remains the best way to remove carbon from the atmosphere and we must save and restore useful ecosystems. Greening up cities has great potential for both cooling cities and absorbing carbon. We must avoid maladaptation. Planting trees is not useful in, for example, natural grasslands and peatlands. There is a window of opportunity to limit global warming, but it is small and rapidly shrinking.

Tradition has it that the Verrall Lecturer is awarded The President's Medal, which was passed miraculously again this year from Helen to Camille via the ether.

One hundred and thirty-one members and guests from 14 countries enjoyed the lecture, which was modified and repeated the following Saturday as The Young Verrall Lecture, with more focus on actions that humans can take to mitigate the effects of climate change, and a bit more about Camille's career journey. This was hosted jointly with the Amateur Entomologists' Society, and attended online by 33 enthusiastic young entomologists from eight countries, and six panellists.

Key points from an excellent and wide-ranging question and answer session were:

- land-use change trumps climate change in relation to species declines, as it can prevent the dispersal expected as a result of climate change;
- volunteer and other long-term datasets are incredibly useful;
- much literature is not solid enough to blame climate change, and such literature was not included in the IPCC report;
- a loss of 75% of species would lead to ecosystem collapse, as has already been shown with corals;
- organic farming has a useful role to play as it uses less pesticide and artificial fertiliser, which are major sources of greenhouse gases (40 to 60% of nitrogen put on to plants comes off as nitrous oxide or is washed into streams causing eutrophication. Farmyard manure is better);
- diversification and interspersed crops are good for resilience, but are probably more costly and more labour intensive.

Camille with French President Emmanuel Macron.

insect WEEK

21 to 27 JUNE 2021

2021 Photography Competition

We're pleased to highlight the fantastic winning entries from the 2021 Insect Week photography competition. We had a fantastic number of entries this year from 58 countries around the world. The overall winner was Ángel Plata Sánchez with a beautiful image of a *Chrysolina banksii* beetle, and the winner of the under 18 category was Adam Lawson with an incredibly detailed photo of a Carder Bee. Well done to both of you, and to all our commended photographers too.

If this has inspired you, our 2022 competition opens on 20 June 2022. Check out the Insect Week website for more details, and to see more great photos from previous competitions. We look forward to seeing your entries!

Judges

Tim Cockerill, Falmouth University (Head Judge)

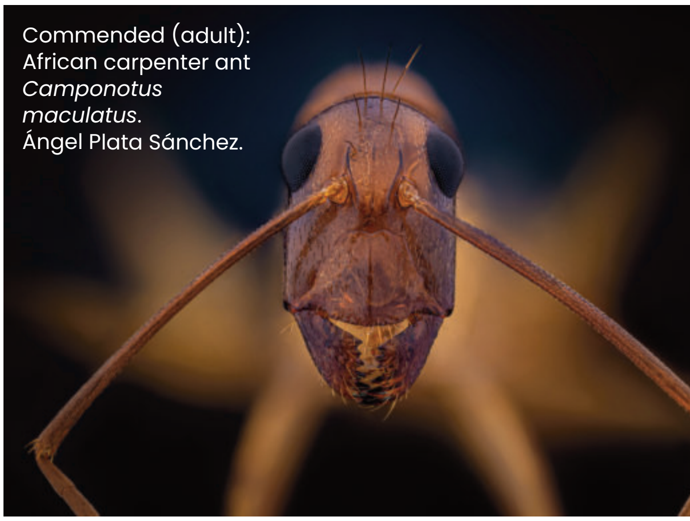
Ashleigh Whiffin, National Museums Scotland

Nick Baker, Naturalist and presenter

Lucia Chmurová, Plantlife

1st (adult): *Chrysolina banksii*. Ángel Plata Sánchez.

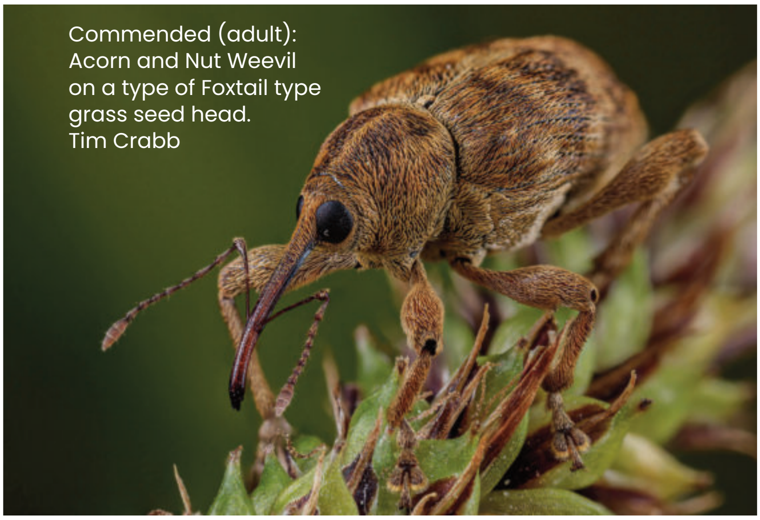
Commended (adult): Ruby-tailed Wasp. Dorothy Mathews.



Commended (adult): African carpenter ant *Camponotus maculatus*. Ángel Plata Sánchez.

Ashleigh Whiffin (judge):

"I think that the standard this year was incredibly high, with a brilliant range of subjects. I was particularly pleased to see more entries featuring beetles this year! These images provide us with a detailed glimpse into the beauty of the insect world, and I hope they will inspire people to take a closer look at these incredible animals."



Commended (adult):
Acorn and Nut Weevil
on a type of Foxtail type
grass seed head.
Tim Crabb

Commended (adult):
Small emerald moth.
Glenn McNeil

1st (Under 18): Carder Bee. Adam Lawson.

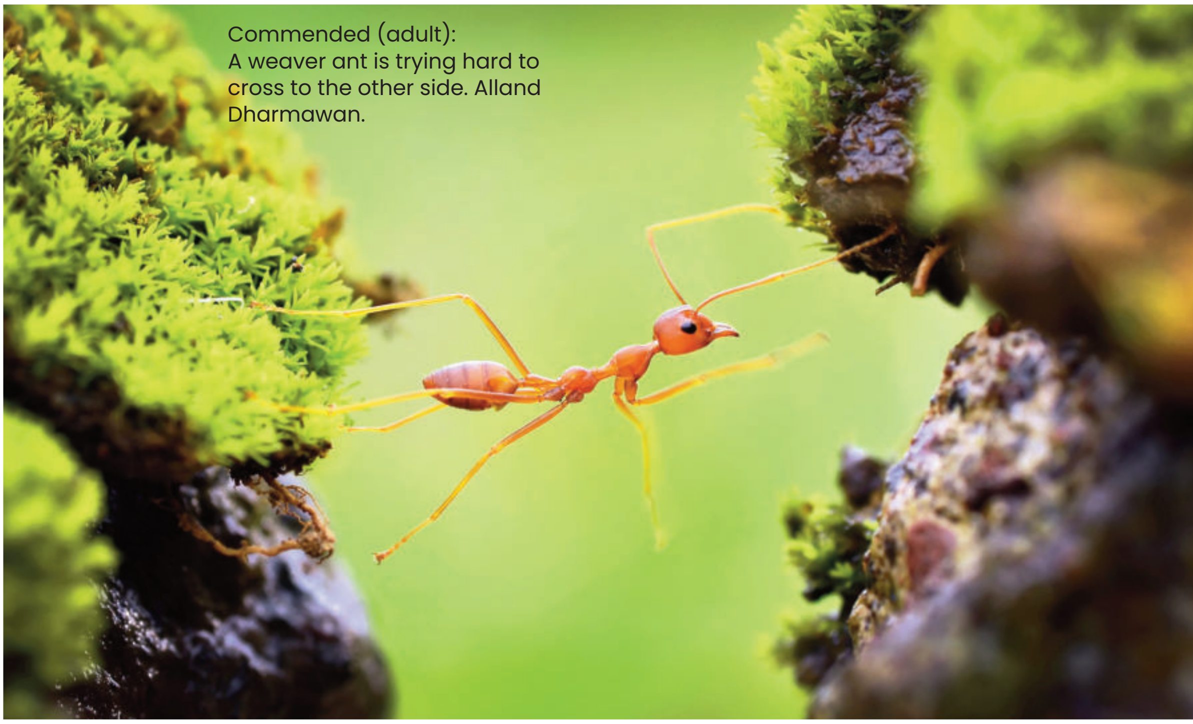
Tim Cockerill (Head Judge) quote:
" Macrophotography reveals so much about the miniature world of insects. High-quality images from the Insect Week Competition play an important outreach role revealing the fascinating lives of insects to people that would normally not take a closer look. I would like to congratulate all our shortlisted winners, and every photographer who submitted an entry in 2021"

Commended (adult):
Mole cricket foreleg.
Ángel Plata Sánchez.

Commended (adult):
Familiar Colours.
Bailey Carswell-Morris

Commended (adult): Babies it’s your lunch time. Dibakar Roy

Commended (adult): Lovers in the Meadow. Rory Lewis



Commended (adult): A weaver ant is trying hard to cross to the other side. Alland Dharmawan.

Commended (adult): Pearl-bordered Fritillaries. Katarzyna Bukowska.

Commended (adult): Sawfly larvae. Jamie Spensley.

Commended (adult): Silver-studded Blue. Katarzyna Bukowska.

Commended (adult): Extreme close-up of a female Blue-tailed Damselfly. Tim Crabb

Commended (under 18): In search of lunch. William Hunter.

Commended (under 18): *Pseudochorthippus parallelus* (Meadow Grasshopper). Will Scarratt

All winning entries can be viewed at:
insectweek.co.uk/photography

INSECT ODYSSEY: INSECTS, BOOKS AND THE ARTISTIC IMAGINATION

Saturday 25 June to Sunday 25 September, 2022

The Salisbury Museum, The Kings House, 65 The Close, Salisbury SP1 2EN
www.salisburymuseum.org.uk/

This exhibition offers an insight into the insect world through the visual responses and interpretations of contemporary artists and makers to the entomological publications which, since the 17th Century, have recorded and illustrated these intriguing creatures. The selected artists working in different disciplines and media mirror the rich diversity of the insect world. Through the varied scales and materials employed in the new works, and through the narratives embedded in them, the aim is to draw attention not only to the myriad physical and behavioural characteristics of insect populations, but also to the historical, cultural, and social associations they evoke. *Insect Odyssey* celebrates contemporary artistic practice, champions the relationship between art and science, and highlights the crucial role played by insects in the environment.

JULIE AYTON / BRIDGET BAILEY / NICOLA BEALING / SU BLACKWELL / HENNY BURNETT / TRACEY BUSH / TESS CHODAN / LOUISA CRISPIN / RUTH DRESMAN / ARLETTE ESS / TESSA FARMER / SUSAN FRANCIS / SARAH GILLESPIE / KATY HARRALD / KATE HOLLAND / SUSAN HORTH / KATE KATO / NOEMI KISS / PATRICIA LOW / JAMES MORTON-EVANS / LINN O'CARROLL / PETER RANDALL-PAGE / LOUISE RICHARDSON / LOU ROTA / KT ROTHE / RHEA THIERSTEIN / JULIEANN WORRALL-HOOD

Curated by Dr ELISABETH DARBY and PRUDENCE MALTBY, with Dr MICHAEL DARBY, Entomologist.

Supported by a Goodman Award from the Royal Entomological Society

Royal Entomological Society

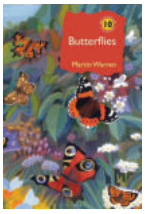
Royal Entomological Society

Antenna Reviews

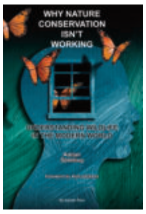
If you wish to recommend a book for review, please contact Richard Jones: antenna@royensoc.co.uk.

The following reviews have been added to the *Antenna* website:
https://www.royensoc.co.uk/publications/book-reviews/

Bumblebees of Europe and Neighbouring Regions
Pierre Rasmont, Guillaume Ghisbain and Michaël Terzo
Published by N.A.P. Editions.
ISBN 978-2-913-68838-4. £69.00.
Reviewed by Steven Falk.

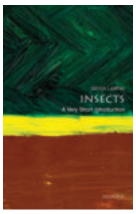


Butterflies: A Natural History
British Wildlife Collection Volume 10
Martin Warren.
Published by Bloomsbury Publishing.
ISBN 978-1-472-97525-6. £34.99.
Reviewed by Richard Jones.

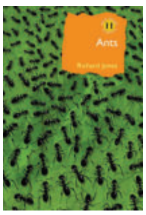


Why Nature Conservation isn't Working: Understanding wildlife in the modern world
Adrian Spalding.
Published by Siri Scientific Press.
ISBN 978-1-838-15284-0. £14.99.
Reviewed by Alan Stewart.

Insects: The Hidden Treasures of Mahausakande
Jayanthi Edirisinghe, Inoka Karunaratne and Roman Prokhorov. Edited by Sriyanie Miththapala.
Published by Ellawala Foundation Trust.
ISBN 9789-5-534-51002. £37.00.
Reviewed by Andy Austin.



Insects – A Very Short Introduction
Simon Leather.
Published by Oxford University Press.
ISBN 978-0-198-84704-5. £8.99.
Reviewed by M. G. Leonard.



Ants: The Ultimate Social Insects
British Wildlife Collection Volume 11
Richard Jones.
Published by Bloomsbury Publishing.
ISBN 978-1-472-96486-1. £32.99.
Reviewed by Seirian Sumner.

Insects – A Very Short Introduction

Simon Leather
Published by Oxford University Press, 2022
ISBN 9780198847045

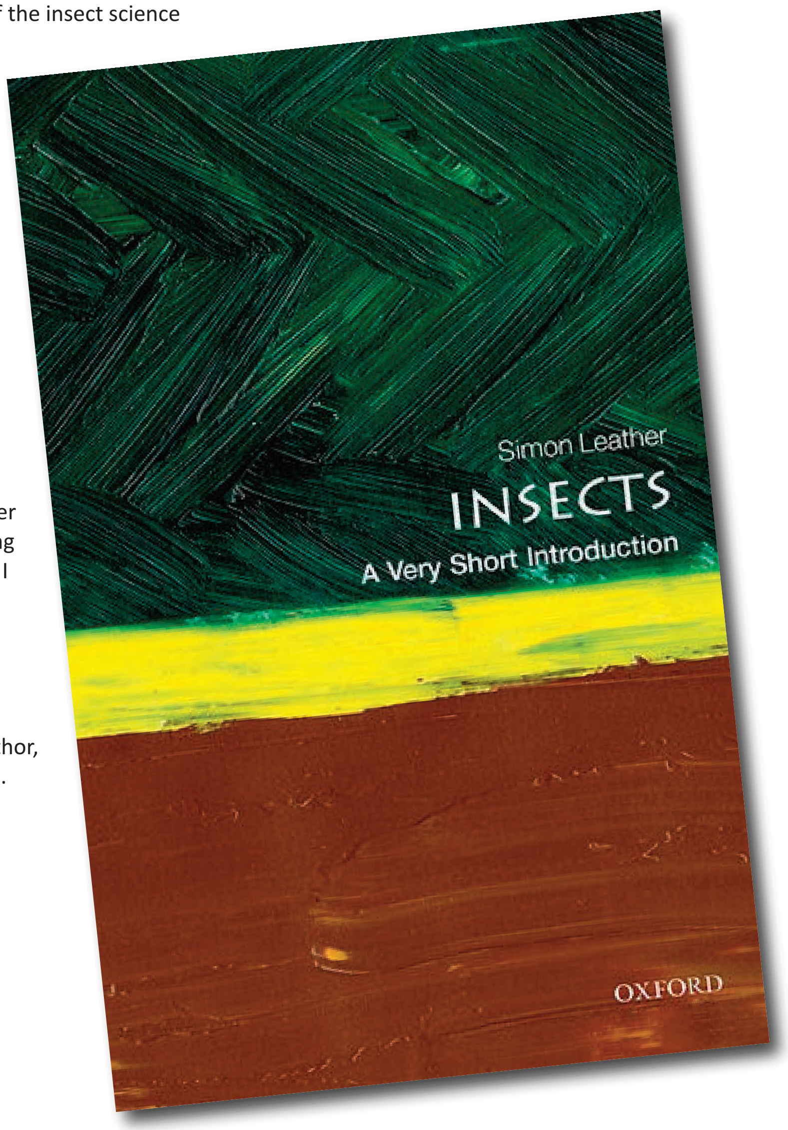
Reviewed by M. G. Leonard

It takes a daunting amount of knowledge, countless years of communicating, and the glimmer of genius to refine an inexhaustible and complex subject, such as the insect, into a readable, clear, engaging, concentrated and comprehensive short volume. This is precisely what Simon Leather has done in *Insects – A Very Short Introduction*.

The central argument of this book, that insects are worthy of study, understanding and enthusiasm, is one that most readers of this review have already subscribed to. However, the ambition of this introduction is to amplify the message, communicating it to the wider world. It is a cheerful ringmaster's cry to come and see the weird and wonderful creatures in the Earth's incredible circus of invertebrates. Once the reader has opened the book, Simon powerfully impresses upon them the importance of learning about our invertebrate friends: "Insects are the bedrock on which human civilisation rests; without them there would almost certainly be no humans." In his preface he explains he is telling, "a story that conveys the wonder and awe that insects have inspired in me", and a fabulous story it is.

In barely more than a hundred small pages the reader: travels though time, learning about the evolution and taxonomy of insects (one of the simplest most concise explanations I have ever read); considers behaviour, use of pheromones and reproduction; examines the way insects travel, flight, migration, and their search for food; visits their living quarters, habitats, relationships and social structures; takes a boat trip to see the aquatic insects; admires the ways in which insects avoid death and put on displays, using mimicry and camouflage; marvels at how insects cope with the challenge of weather, overwintering, and their innovative ways of responding to temperature and light; reviews the reputations of insects as good or bad, pests or pollinators, predators and parasites, underlining their essential role in the Earth's ecosystem; and touches on the distressing fact that the planet's populations of insects are in decline.

Insects – A Very Short Introduction is a powerful argument for the importance of understanding insects and the delight to be found in doing so, tackling the problem of cultural "insect blindness" and the idiocy of this when they "are part of the very fabric of existence." As a lay person, who paddles at the edges of the insect science ocean, I found this book to be readable, interesting and, at times, surprising. Each paragraph begins with a summary sentence that any level of reader will comprehend, then expands with interesting examples, anecdotes and studies, only employing scientific language where necessary, not exhaustively, and with humour. As someone who was lucky enough to have known him, it was lovely to hear Simon Leather's voice through his words, and it made me smile to see his passion and specialism in aphids woven through the narrative.



Simon Leather is someone whom I admire, respect, and had the pleasure, for a short time, of calling a friend. When my debut children's novel, *Beetle Boy*, was published in 2016, he invited me to speak at an entomology conference at Harper Adams University. I protested that I wasn't a scientist and would be of little interest to attendees, but he argued that it was precisely because I was an enthusiast, communicating the wonder of Coleoptera to children, that he wanted me there. I went, taking my first steps into the entomological community and I'm so glad I did. Simon and I talked at length about insects in children's literature — a subject he was incredibly knowledgeable and passionate about — and he made me feel like a welcome and useful addition to the community. He was the embodiment of positive outreach, a champion of the insect underdog, and his absence is a great loss. He turned me from being a children's author, into an amateur entomologist, and for that I'll always be grateful.

EVENTS

Details of the meetings programme can be viewed on the Society website (www.royensoc.co.uk/events) and include a registration form, which usually must be completed in advance.

Offers to convene meetings on an entomological topic are very welcome and can be discussed with the Chair of the Meetings Committee (richard@royensoc.co.uk).

June 2022

Mon 20
20 June - 26 June
Insect Week 2022

Tue 21
21 June
Perceptions of insects: Philias and Phobias (online discussion)

Wed 22
22 June
The Big Bang Fair 2022

Tue 28
28 June
CONNECTED (online Conference)

July 2022

Tue 5
5July
Insects: RADAR detection and threats to aircraft (online meeting with the Royal Aeronautical Society)

Sun 17
17 July - 22 July
XXVI International Congress of Entomology (ICE)

September 2022

Tue 6
6 September - 8 September
Pollinators in Agriculture (residential conference with the AAB and BES)

Tue 13
13 September - 15 September
ENTO '22 (hybrid event)

Wed 14
14 September
Annual General Meeting (hybrid event)

November 2022

Wed 2
6 November
Orthoptera Special Interest Group

March 2023

Wed 1
1 March
Verrall Lecture

Sat 4
4 March
Young Verrall Lecture

April 2023

Wed 26
26 April
Behaviour Special Interest Group (hybrid event)

October 2023

Wed 2
16 October - 20 October 2023
XII European Congress of Entomology (ECE)

For full details on all RES meetings please visit www.royensoc.co.uk/events

Pearl-bordered Fritillaries.
Katarzyna Bukowska.

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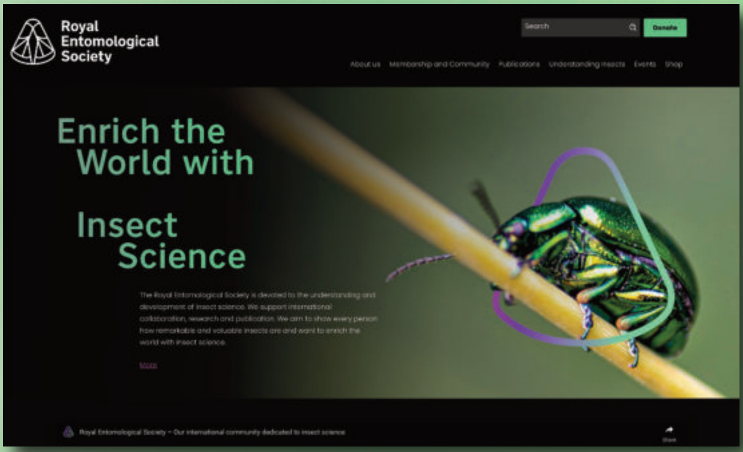

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