ecologies

Perspective

Positive and Negative Ecology, a Conceptual Overview

Hugh D. Loxdale

School of Biosciences, Cardiff University, The Sir Martin Evans Building, Museum Avenue,
Cardiff, Wales CF10 3AX, UK; loxdaleh@cardiff.ac.uk

Abstract: Animal populations, even among common species, often exhibit demographic heterogeneity. This is particularly evident in species with metapopulation structures, where geographically distinct subpopulations experience varying degrees of inbreeding due to limited interbreeding. A phenomenon termed 'negative ecology' highlights cases where species, despite suitable habitat availability, display fragmented distributions within small geographic areas (<20 km^2). These subpopulations, however, do not conform to classic metapopulation dynamics, as even vagile species such as birds can theoretically move freely between them. Similar patterns emerge at larger scales (>100 km^2) in birds and butterflies, suggesting ecological constraints—either abiotic or biotic—underpin these structured distributions. Understanding these constraints is essential, particularly in conservation efforts. The principles of positive (extant) and negative (locally absent/extinct) ecology have profound implications for species re-introductions, as historical occupancy does not guarantee successful re-establishment. Abiotic and biotic factors may hinder the recolonization of previously inhabited or entirely new habitats. This article primarily explores the ecological forces shaping such fragmented distributions in birds and butterflies, two especially well-studied taxa in the UK and mainland Europe, in the hope that such a new perspective may thereby contribute to broader conservation and ecological restoration strategies.

Keywords: biodiversity; birds; butterflies; demography; ecosystems; lacunae; population heterogeneity; vagility

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1. Introduction

Natural populations are rarely homogeneous in their distribution, either at small or large geographic spatial scales [1–3]. Indeed, even with species populations that appear to be homogeneous, application of high-resolution molecular (DNA) markers can show that in fact the studied populations comprise genetically distinct cryptic populations, which may occur either sympatrically, parapatrically, or allopatrically [4,5]. In the case of sympatric populations of a genetically heterogeneous species population, the initiation and maintenance of the genetically different forms, which may show large-scale karyotypic differences, is ultimately due to some genetic incompatibility or other, perhaps ultimately leading to the differentiation of the population into ecologically specialised sub-populations [6], e.g., roe deer, *Capreolus* spp. and sub-spp. (cf. https://en.wikipedia.org/wiki/Roe_deer; accessed 6 April 2025). Such differentiation could be initiated and reinforced by habitat preferences of one form or another, including in the case of herbivores, plant-based mechanisms. It could also be due to lower-level genomic changes, including incompatible regions of the genome itself, e.g., [7]. All such changes are ultimately caused by mutations, including genomic re-arrangements such as inversion polymorphisms or larger-scale karyotypic changes like translocations, fissions, and fusions, as well as hybridisation/introgression events between species [8]. Over time, these genetic alterations may drive speciation events that, certainly initially perhaps, result in the formation of cryptic entities, everything from strains and biotypes through to ethospecies and races, sibling, sister, and sub-species, and ultimately, full species [6,8,9]. All of these entities may develop during the course of evolutionary changes, governed by ecologically specialised adaptations, leading to levels of reproductive isolation between sub-specific populations.

Ecological specialisation with concomitant adaptation is at the cutting edge of the evolutionary process, and various so-called 'good' species populations may be actively changing, not just over evolutionary time scales, but, depending on the selective pressures involved and the speed of reproduction of the organism concerned, over much shorter historical time scales, as found in some fast-breeding insect species [10]. Ultimately, when we view a 'good' species population, we may well not know what we are actually looking at, certainly at the genetic/genomic level, that is, until this is rigorously investigated using molecular techniques [5].

Even assuming that a particular species is 'good' in terms of genetic identity, that is to say, there are no *obvious* micro– or macro changes in terms of genetic variation occurring within and between geographical sub-populations, demographic homogeneity is not a given. In the case of animals known to display metapopulation structuring, for example, butterflies with low vagility, this leads to heterogeneous population structuring, as is now well-demonstrated empirically [11,12]. But what about those species populations that are not known to show such structuring and, indeed, are considered to be ubiquitous demographically over a particular region or regions? Here, I briefly describe and discuss the concept of what I term 'negative ecology' and its ramifications, based on observations of certain wild bird species inhabiting the Exmoor region in North Devon, UK and in Germany, notably the states of Thuringia and Bavaria, and certain British butterfly species. For this purpose, I define negative ecology as follows:

> *A discontinuity or disruption in the perceived homogeneous population structure of a species over a given area or region due to one or more as yet unrecognised biotic or abiotic governing factors.*

By extension, extant species populations able to fill such habitats show 'positive ecology'.

2. Ecological Specialisation

In the 1950s, George Evelyn Hutchinson (1903–1991) showed theoretically that the distribution of a given species in time and space is governed by a multifactorial array of axes or vectors, each relating to particular critical selective element maintaining or constraining the organism within the confines of its niche [13,14]. This could be either a novel niche which the organism has evolved to fill, or a vacant niche, once occupied by an organism with a seemingly similar lifestyle and ecology and hence ecological requirements. If this is true, which there is no reason to doubt, then the niche each living organism occupies may perhaps be described graphically as a point in space from which radiate a number of such axes, each representing a selective force (Figure 1). Such axes include abiotic factors, including climate and weather, and biotic ones, including diet and diet breadth, predation and parasitism risk, longevity, reproductive span, the probability of finding a mate and reproducing, fecundity, etc. [3,15–18], cf. also [19]. In this way, each individual species and, indeed, every individual within that species, is defined by its own unique set of life-limiting ecological–genetic vectors.

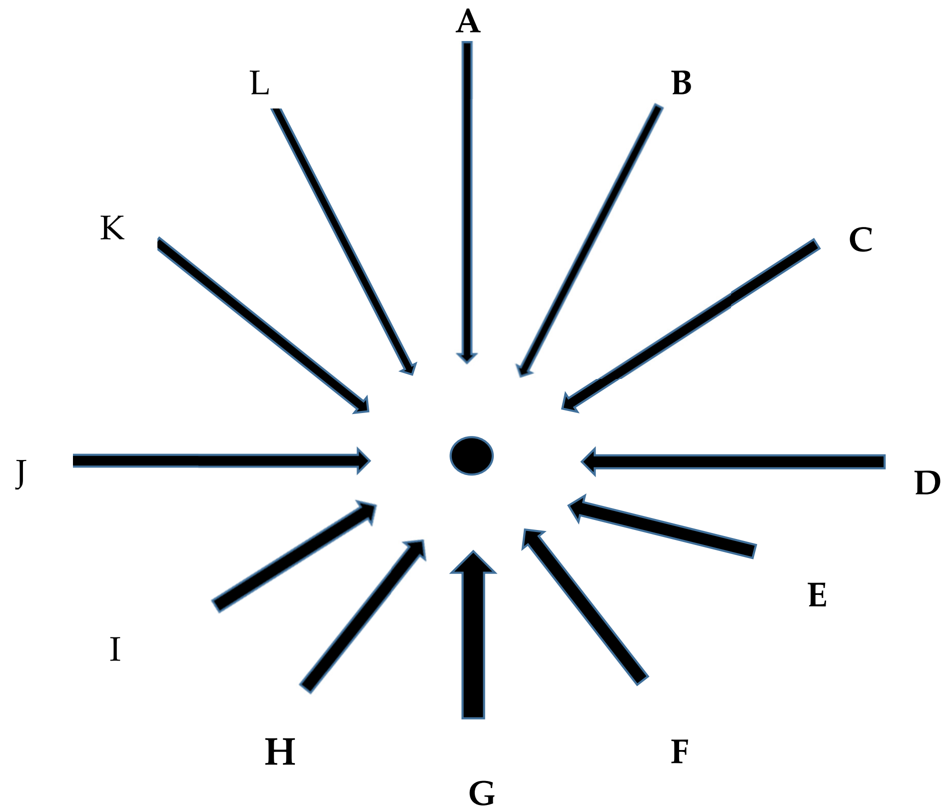

Figure 1. Three-dimensional diagram showing the main influences affecting an individual within a given species population (black central dot), which impinge on its survival, including reproduction survival, within its niche and hence also act as constraints on its diet/dietary breadth. Key: A = Climate; B = Weather; C = Age/fitness, including 'bad genes' à la Raup [20]; D = Predation; E = Parasitism; F = Pathogens; G = Mutational changes/cancers; H = Food availability, especially preferred food, including during reproduction; I = Cost/benefits in terms of ease in acquiring that particular food item/s; J = Nest/roosting site availability; K = Intraspecific competition for food resources and nesting/roosting sites; L = Interspecific competition for food resources and nesting/roosting sites.

Of course, the lifestyle of the organism concerned, including chemistry/biochemistry, chemical ecology, physiology, genetics, and behaviour, is also crucial in defining the life-history parameters of the species [21]. Hence, each species is indeed a unique entity within the pantheon of life on Earth. And here, I do not just mean extant species but also the vast array of now extinct species that formerly inhabited the planet. In their day, to perhaps state the obvious, each of these species had its own unique geometric/topological vector diagram of constraints, limiting its demography and, ultimately, as the ecology around it changed, its species lifespan. Some species seemingly lasted but a short time in the geological record, whilst others prospered (for whatever reasons, including prey availability) and became ubiquitous across the face of the Earth, lasting for many millions of years.

In the following, I provide case scenarios of the distribution of certain living organisms (here, birds and butterflies), which one assumes should be demographically ubiquitous over large geographic regions, such as in Europe (e.g., the UK and Germany), but are not. Some of these perceived differences are doubtless due to strict habitat requirements in terms of abiotic and biotic factors, and/or competition of one form or another, but clearly not all.

3. The Case of Birds: Observations from Nature

3.1. Small Spatial Scales, UK

Study area: The small village of Heasley Mill, situated in a valley on the edge of Exmoor in North Devon, UK (51°04′31.8″ N 3°48′15.5″ W). The area is very largely pastureland grazed by livestock, mainly sheep, and interspersed with mixed native woodlands as well as conifer plantations. Over a two-year period (2021–2022), 38 bird species have been recorded by my wife and I in our garden in the village, especially visiting a range of bird feeders, or flying over it, including residents and migrants, amounting to some 6% of the UK national total [22]. In addition, some birds have been seen or heard within a two-kilometre radius of our house and garden, including the Eurasian kingfisher, *Alcedo atthis* on the River Mole, which runs through the village, Eurasian jay, *Garrulus glandarius*, mistle thrush, *Turdus viscivorus*, willow warbler, *Phylloscopus trochilus*, goldcrest, *Regulus regulus*, western yellow wagtail, *Motacilla flava*, and Eurasian tree creeper, *Certhia familiaris*. The European dipper, *Cinclus cinclus* has been seen on the river here, and a common redpoll, *Acanthis flammea* was recently observed visiting a bird feeder (Gibson Teasdale; Katie Blackmore, pers. comm.). So, the area is fairly rich in terms of avian diversity, in large part due to the heterogeneity of the local environment.

However, and interestingly, whilst carrion crow, *Corvus corone* are abundant in the nearby towns of North Molton and South Molton, about 2.2 and 6.6 km south of Heasley Mill, respectively, they have never been seen in the village or immediate surroundings by us. They even nest amidst trees on the side of the roads locally, including the nearby A road (A361). According to the British Trust for Ornithology (BTO) map, they are widespread over much of Britain, except the northwest of Scotland and the Western Isles. Their local absence could be due to competition for food with the abundant Eurasian jackdaw, *Coloeus monedula* population, or less likely, common raven, *Corvus corax*, which also occur in the Exmoor region. However, since carrion crow, jackdaw, and raven have different nesting site preferences, such competition cannot be a cause of the former species absence in the village.

The area is subject to shooting in the autumn and winter period, notably for common pheasant, *Phasianus colchicus* and red-legged partridge, *Alectoris rufa*, both reared locally and released, and thus it is possible that carrion crows have been persecuted over the years and, being highly intelligent birds, have learnt to avoid the area, their nests being especially vulnerable to disturbance and shooting by game keepers. Ditto the Eurasian magpie, *Pica pica*, which is abundant along the A361 from Barnstaple to Tiverton, feeding on road kills, of which there are many, but is largely absent from Heasley Mill (I have only seen one in the valley since June 2021 to the present). Great spotted woodpecker, *Dendrocopos major* are abundant locally, whereas the European green woodpecker, *Picus viridis* is seemingly absent (HDL, pers. obs.), yet they are known to occur within a few kilometres north of us (Jim Starr, pers. comm.). Their apparent absence could be due to competition with the great spotted woodpecker, but then again, these species have slightly different dietary breadths. For example, the green woodpecker is a notable ground feeder, feeding on ants, whereas the great spotted woodpecker is not.

Another bird of interest in relation to the concept of negative ecology is the common swift, *Apus apus*. This arrives in our area in late April–early May, as it does elsewhere over the UK. It is abundant over South Molton and occurs in North Molton too, but is seemingly absent over Heasley Mill. I have personally only seen one pair fly over the village in four years of observation, effectively four summers. As the speed of the swift in straight flight is calculated to be maximally around 110 kph (www.rspb.org.uk/birds-and-wildlife/swift/; accessed 6 April 2025), then it should take the birds just over a minute flying time to reach here from North Molton. There are common house martins, *Delichon urbicum* and barn swallows, *Hirundo rustica* nesting in the village, but not swifts. There are only some

11 houses in the village, the former hotel (Heasley House) taller than the rest, and maybe the fact that they do not nest here is because of the lack of suitable nesting sites or competition with the house martins and swallows, although this is unlikely as they have rather different nesting preferences, or maybe it is linked to the available food, i.e., small, flying insects.

3.2. Larger Spatial Scales: UK and Germany

In a recent paper discussing the improbability of so-called generalism in nature over large spatial scales (>50 km) [23], we present maps from the BTO records of observations, including, in one case, breeding records for the years 1970–2007 for three species, the European pied flycatcher, *Ficedula hypoleuca*, a spring and summer migrant species, and two resident species, the Eurasian nuthatch, *Sitta europaea* and Eurasian magpie, *P. pica*, the last with site as well as breeding records. The conclusion drawn from these data is that for whatever ecological reasons, the demography of these three species is constrained. In the case of the magpie, although it is widespread over most of the UK landmass, this is not true of the breeding data, which show a clear concentration of the bird at certain sites, mainly urban, in mainland Britain, but not so in Northern Ireland. This is probably associated with the availability of nesting sites, reduction in persecution by gamekeepers, availability of food put out by humans for other wildlife and, as a consequence, the increased number of small birds and their eggs which it can predate [23].

In relation to another migrant species, the common nightingale, *Luscinia megarhynchos*, this species is very abundant in and around the city of Jena, Thuringia, Germany during the spring and summer months, especially along the banks of the River Saale, as I have observed over a five-year period (2006–2011). However, in Bavaria, certainly in and around the village of Utting on the western bank of the Lake of Ammersee, and along the River Wertach, flowing though the city of Augsburg, it appears absent, as I have witnessed over an extended period (1993–2024). The Dachverband Deutscher Avifaunisten (DDA) distribution maps of the birds of Germany (https://www.ornitho.de/; accessed 6 April 2025) confirm this finding and reveal that this species has a rather patchy distribution throughout Germany, being more common in mid- and northern Germany. This is also true for other birds in Germany, including the European pied flycatcher, which displays a more mid to northerly distribution.

Many common European birds also show a patchy or non-homogeneous pattern of distribution in Germany, including the European robin, *Erithacus rubecula*, Dunnock, *Prunella modularis*, bullfinch, *Pyrrhula pyrrhula*, and chaffinch, *Fringilla coelebs*. The Eurasian siskin, *Spinus spinus* is interesting in this respect as it, opposite to the pied flycatcher in the UK, shows a more easterly distribution, here perhaps due to the preference for conifer forests, which are more prevalent in the eastern regions of Germany, such as Thuringia. Some of the gaps in the otherwise widespread patterning could be due to ecological constraints of which we are not conversant, as in the case of the clear westerly distribution of the pied flycatcher in the UK, or due to sampling effects, such that the distribution to some extent represents the distribution of the recorders involved in the sampling rather than the birds themselves.

This is a common criticism of distribution maps of insects in the UK, especially for orders like fleas (Siphonaptera) with relatively few species (62) [24] and for some plants, like orchids with around 55 species [25]. In the case of birds, butterflies, and moths (Lepidoptera), due to public involvement in recording schemes to monitor the distribution and abundance of species, probably the maps shown in contemporary atlases such as those provided, for example, by the BTO in the UK and DDA in Germany and for Lepidoptera (butterflies and macro-moths) in the UK (*Atlas of the UK Butterflies, 2015–2019*; *The State of Britain's Larger Moths 2021*; https://butterfly-conservation.org/sites/default/files/2021-0

3/StateofMothsReport2021.pdf; accessed 6 April 2025), are pretty robust, and are updated on a regular basis, often annually.

In terms of conservation concerns, the cases of the corncrake, *Crex crex*, red-backed shrike, *Lanius collurio*, northern lapwing, *Vanellus vanellus*, and Eurasian bittern, *Botaurus stellaris*, all vagrant species, have been much debated in the recent literature and discussion thereof can be found on Wikipedia and BTO websites (https://www.bto.org/understanding-birds/birdfacts/; accessed 6 April 2025). Sterling attempts have been made to increase numbers of corncrake and bittern in the UK especially, the latter species being extinct since the late 1800s, and have been successful (e.g., https://en.wikipedia.org/wiki/Corn_crake; accessed 6 April 2025). This has been achieved by re-creating a suitable breeding habitat, protected from negative forces such as hunters and agricultural machinery, e.g., combine harvesters. With red-backed shrikes and lapwings, their decline may be due to a combination of land usage/management changes, climate change, and predation pressures. The red-backed shrike is on the north-westerly limit of its European range (https://en.wikipedia.org/wiki/Red-backed_shrike; accessed 6 April 2025). The bird became effectively extinct in the UK in 1989, but since then, only a few pairs have successfully bred. In relation to the bittern population recovery, according to Wikipedia:

> *After extensive reedbed restoration, nesting and breeding was observed in north Wales, while in 2020, two pairs successfully bred at Newport Wetlands in Gwent, south Wales. These were the first bitterns to breed in the county in some 250 years.*

Clearly, in the case of some bird species in the UK (641 spp. including residents, vagrants, and migrants, according to the Wikipedia entry https://en.wikipedia.org/wiki/List_of_birds_of_Great_Britain; accessed 6 April 2025), the cause of their population decline is clear. Often as not this has been as a consequence of extensive hunting, effectively 'predation', as shown in Figure 1, i.e., the Victorian and Edwardian (19th and early 20th century) passion for taxidermy (Figure 2a) and the hat trade, especially detrimental to certain birds with flamboyant plumage, as well as raptorial birds due to the past and present actions of gamekeepers, along with egg collecting of rare and endangered species, less so perhaps for food, leading some species to near or actual extinction. This has fortunately been halted or populations successfully restored in the case of certain species (thanks to the actions of conservation groups, especially the RSPB, in purchasing and maintaining habitats and actually protecting the birds therein). However, with some other species, as with the aforementioned red-backed shrike, the species' demise is not so obvious, either here or in mainland Europe.

(**a**) (**b**)

(**c**)

Figure 2. (**a**) Stuffed birds collected around Earlham in North Norfolk in the 1880s, the victims of the Victorian and Edwardian obsession with taxidermy and somehow trying to 'own' or at the very least 'capture' the essence of the natural world. Photo: © David Tipling (Alamy). (**b**) A collector's case of British butterflies There are 59 breeding butterflies in the UK and four former breeding species, as well as rare migrants such as the monarch butterfly *Danaus plexippus* from North America and Mexico (middle right). Photo: © Paul D Stewart (Nature Picture Library). (**c**) Male and female specimens of the extinct British subspecies of the Large Copper butterfly, *Lycaena dispar dispar*. Photo: Katherine Child, © Oxford University Museum of Natural History.

4. The Case of Butterflies

Butterflies as a group, especially European and North American species, have been studied extensively for the past 150 years or so. Hence, one might assume that we know a great deal or indeed most there is to know, certainly the main details, about their biology, including ecology. However, in truth, they remain rather mysterious creatures in many respects and there is still much we can learn by researching them, especially on a case-by-case basis. Of the 59 recorded species in the British Isles, and here I concentrate only on certain of them, some species are largely resident with a limited vagility, or, as aforementioned, have a metapopulation structure, whilst other species are much more dynamic, and some species still are vagrants or even renowned international migrants, annually traversing great distances, like the Nymphalids, the monarch, *Danaus plexippus* [26], and the painted lady, *Vanessa cardui* [27].

Some species are widely distributed geographically and have well-established, thriving populations, while others, including those with metapopulation structuring, e.g., the Glanville fritillary, *Melitaea cinxia* (Nymphalidae), show fluctuating local populations with frequent extinction and re-establishment of local demes [28] (see below). Even with the celebrated migrants *D. plexippus* and *V. cardui*, these have boom and bust years, which are only partially understood [29].

And this is the crux of the matter, as with the multifactorial diagram (Figure 1) showing the factors impinging on and constraining individuals within species, and hence the factors allowing for population growth and expansion, not all such factors are appreciated, let alone known. It is unknown why, for example, some species are thriving and expanding, like the speckled wood butterfly in the UK, *Pararge aegeria* (Satyridae) [30], whilst others are contracting and heading for extinction, like the wall butterfly, *Lasiommata megera* (Satyridae), both in the UK and some parts of mainland Europe [31–33]. In this light, it is very difficult to generalise on the multifarious factors responsible for the increasing abundance or decline of various butterfly species, and in this section of the paper, due to the vastness of the subject and associated literature, all I can hope to do is to give a few examples and suggest the reasons as to the main factors influencing the ecology of these animals, both positive and negative. Here, I concentrate on examples of British species.

It is now often stated that environmental changes, especially that anthropogenically induced, involving degradation of habitats, e.g., deforestation, building, and land usage for other reasons such as agriculture, horticulture, and forestry using non-native trees, plus of course overzealous usage of a range of synthetic pesticides and herbicides in the last 80 years or so, have led to catastrophic climate effects and habitat loss with concomitant loss of native flora and fauna, especially including birds and butterflies, during the so-called Anthropocene period, e.g., [34–39]. Yet despite the negative aspects of human interference within the ecosystem, due to a plethora of conservation initiatives and programmes, many rare and endangered species have been rescued from oblivion in many parts of the world, often involving individual researchers or small groups of interested people, government-run and -funded bodies, and learned scientific societies or other organisations (e.g., Rothamsted Research, UK; Butterfly Conservation, UK) and sometimes involving public participation, i.e., 'citizen science', especially in terms of surveying butterfly and moth populations, both spatially and temporally [40].

Some butterfly species, such as the black-veined white, *Aporia crataegi*, whose larvae feed on hawthorn and blackthorn and occasionally on cultivated fruit trees (Rosaceae), show classic boom and bust cycles, having been immensely common in some years, rarer in others, and ultimately declining to near or total extinction, as happened in the UK in the early 1920s. Such fluctuations are not that well-understood [41,42]. Of interest is the fact that such populations can decline to extremely low numbers and highly restricted distribution, before recovering, seemingly naturally, or via vagrants from mainland Europe (or due to re-introduction by human agency from foreign sources, which cannot be ruled out), as has recently happened with *A. crataegi* in southeast London, after an absence of around a century [43]. It is also possible that as the species became rarer, collecting also hastened its last population strongholds, although considering how common it was prior to its demise in the period 1918–1925, this seems improbable (but see below in relation to other rare and endangered species).

Besides climate-related and parasitoid-related factors involved in its eventual demise and extinction in the UK, perhaps the small effective population size, leading to concomitant inbreeding depression, may have also played a role (cf. [42] for further discussion of these possibilities). Lastly, its extinction in the UK in the mid-1920s may have been more apparent than real, with its disappearance actually a sampling effect rather than true extinction; in other words, not enough people were suitably trained or observant to differentiate this butterfly in flight from, for example, the female brimstone butterfly, *Gonepteryx rhamni* and the large white, *Pieris brassicae* [44], even though their flight behaviour is markedly different, *A. crataegi* being a stronger, more determined flier than both these other species

(HDL, pers. obs.), and hence it went unnoticed until very recently when the army of citizen scientists and other interested persons (especially those performing butterfly transects for Butterfly Conservation) finally marked its 'return' 100 years later.

Other examples of natural butterfly population recovery, in addition to the aforementioned speckled wood, once confined mainly to the southwest of England, but now having naturally spread throughout the entire UK, including into Scotland, where it had been absent for decades, seems to be due to long-term climatic trends [30], although it is a larval grass-feeding butterfly, preferring sun-dappled, otherwise shady woodland rides and hitherto residing in the damper regions of the country, prior to its extraordinary spread starting in the 1940s onwards.

Another example of regional spread is that of the white admiral butterfly, *Limenitis camilla* (Nymphalidae). According to E.B. Ford [45], this butterfly was mainly found in the southern counties of England, especially in the area around the New Forest. But at some time starting in the 1920s, it began to spread outwards. As Ford recounts, a certain vicar tried to introduce the butterfly, whose larvae feed on common honeysuckle, *Lonicera periclymenum*, into woods in Kent without success. Later, the butterfly naturally expanded its range, came to even occupy the said woods, and by 1934, was prolific there. Ford suggests that the climate may have had a part in its eventual return to the region in which it had formerly frequented, but genetic factors are also a strong possibility (e.g., inbreeding depression).

A similar story concerns that of the Comma butterfly, *Polygonia c-album*, also a Nymphalid, the larvae of which fed mainly on hops, *Humulus lupulus* and as such were largely confined to the hop-growing areas of Kent and Herefordshire. By around 1903, for whatever reason/s, the butterfly had contracted its range to a few areas of Herefordshire and surrounding counties and Wales, and it seemed to be facing extinction.

According to Colin Pratt [46], there were large fluctuations in the numbers of this insect in various counties over the 19th and early 20th centuries, including extinctions and revivals (probably the extinctions were actually due to sampling effects, i.e., not enough recorders to prove whether this was actually true or not). Thereafter, it unexpectedly expanded its range after around 1914, now feeding mainly on common stinging nettle, *Urtica dioica*, and within a few years, had spread all around England and Wales, including to regions in northern Britain that it had been absent from for decades [46]. This expansion apparently involved a switch of host plant, hop to stinging nettle [47], and as such, may well have had a genetic basis, i.e., transcriptional and physiological plasticity [48] (cf. also [41,44] for further details concerning the demise and recovery of the butterfly in the UK). Possibly some of the re-establishment and revival of the fortunes of this butterfly were due to immigration from the continent of Europe, although this is debatable [46].

With butterflies showing boom and bust cycles, that of the holly blue, *Celastrina argiolus* (Lycaenidae), whose larvae feed on holly, *Ilex aquifolium* and ivy, *Hedera helix*, and which occurs mainly in southern Britain, is well-known to have peak years of great abundance, such as 1998 and 2002, followed by intervening years of relative scarcity [49]. This is known to be due to the depredations of a specific ichneumonid wasp parasitoid, *Listrodomus nycthemerus*, which tracks its host in a typical predator–prey cycle [50,51], as with the classic scenario of the snowshoe hare and lynx in North America [52]. The nowadays rare and local marsh fritillary butterfly, *Euphydryas aurinia* (Nymphalidae), the larvae of which feed on devil's-bit scabious, *Succisa pratensis*, is confined in the British Isles to a few localities in Dorset, Somerset, Devon, Wales, as well as certain of the Scottish Isles and Ireland, inhabiting a wide range of habitat types [44], and also shows dramatic boom and bust cycles. Ford [45] recounts how, earlier in the late 19th and early 20th centuries, the larvae in some regions of north-west England (Cumberland) showed great fluctuations in number (cf. also [44]). The exact cause of such abundance in these isolated and vulnerable colonies followed by scarcity is not known, but may be due to climatic and other natural factors, food plant shortage, or predation/parasitism, e.g., by the specialist wasp parasitoid, *Cotesia bignellii* (Braconidae) in the south of England [41,44,53], or a combination of these factors.

With other butterflies, the cause of their decline is certain, but the factors preventing their re-introduction much less so. Hence, we are uncertain as to the exact nature of the positive followed by negative ecological factors determining the species' success and later demise, and remain so. A classic example is that of the English subspecies of the large copper, *Lycaena dispar dispar* (Lycaenidae). The butterfly formerly flourished in the fens of East Anglia, the larvae feeding on great water dock, *Rumex hydrolapathum*, but as these were drained in the 17th to 19th centuries to turn this area into farmland suitable for grazing livestock and growing crops, the butterfly became increasingly localised and rare, thereby attracting collectors who sought specimens of this very colourful butterfly for the display cabinet (as in Figure 2b), which exacerbated the decline of the species, resulting in its extinction in the period 1845–1864 (Figure 2c) [41,44].

In the First World War period, a very similar subspecies was discovered in the fens of northeastern Holland, *L. d. batavus*. Subsequent attempts to introduce this subspecies, morphologically almost identical to the original native English subspecies *L. d. dispar*, into the original haunts of this subspecies, as well as introduction of the subspecies *L. d. rutilus* (widespread in central and southern Europe) in similar habitats in southern Ireland (Greenfields, Tipperary) ([54]; https://en.wikipedia.org/wiki/Large_copper; accessed 6 April 2025), have so far met with failure, suggesting that the ecological requirements/constraints between the three subspecies are not exactly comparable, and as yet, remain unresolved These may well relate to the genetics of the butterfly (e.g., inbreeding depression) or that of the host plant on which the larvae feed, i.e., in terms of the chemotype suitability for the larvae ([4]; cf. also [54] for other plausible ecological reasons why the large copper populations introduced into England and southern Ireland ultimately failed).

Whilst some localised butterfly species in the British Islas have headed—or are still heading—for extinction, some have been rescued from this fate or have recovered naturally, for whatever reason/s. The classic case of extinction followed by restoration is the large blue butterfly, *Maculinea (Phengaris) arion* (Lycaenidae) ([41,44]; https://en.wikipedia.org/wiki/Large_blue; accessed 6 April 2025). This butterfly used to be common in former times on the chalk downs grazed by sheep, its life cycle being intimately associated with wild thyme, *Thymus polytrichus*, as well as red ants, *Myrmica* spp. As such, in its larval form, it may be described as a serial herbivore, brood parasite and carnivore. Hence, on completion of its herbivorous stage (4th instar), and on leaving the host plant, the larva wanders around and, upon coming across an ant of the appropriate species, exudes droplets of honeydew to entice the ant to carry it back to its nest. There, it employs semiochemical mimicry to feed undetected and unmolested on the ant larvae, whilst at the time, using acoustic mimicry to dupe the host ants into preferentially feeding it [55], before pupating in the ants' nest to complete its life cycle [41]. Interestingly, it continues to use chemical and acoustic mimicry for protection even in the pupal stage [55].

On emergence as the adult butterfly a year later, it passes through the hosts' galleries before emerging into the world above. It then climbs up a stem of foliage to dry its wings in the sunshine, before taking flight to find a mate, whereafter, following mating, the female lays eggs on *T. polystrichus*, on which the larvae feed [44]. The butterfly preferentially parasitizes the common red ant, *Myrmica sabuleti*, in the UK, on which it does better compared with other related *Myrmica* hosts such as *M. scabrinodis* ([41]; https://butterfly-conservation.org/butterflies/large-blue; accessed 6 April 2025).

Various reasons, notably the fact that the sward of grass in its habitat was no longer maintained at a precise length preferred by the nesting ants due to the reduction in sheep farming and the decline of rabbit populations following the myxomatosis outbreak of the early 1950s, allowing the nest to reach a certain temperature as heated by the sun, and the role of butterfly collectors as the species became rarer, led to severe population decline [41]. At this point, the insect inexorably headed for extinction, its last stronghold being along the northern coastline of Cornwall in south-west England, before its final demise in 1979 ([41,44]; https://en.wikipedia.org/wiki/Large_blue for details, accessed 6 April 2025). Thanks to the discovery of morphologically very similar populations of *M. arion* in Sweden and following considerable research on the ecology and ecological requirements of the insect, the butterfly was successfully re-introduced into several sites in southern England following rigorous preparation of these regarding their suitability to support the species, which is now thriving and indeed yearly increasing in numbers [44,56–58].

Incidentally and interestingly, it was found during this research that different species of large blue in mainland Europe are tended by different species of *Myrmica* ants, emphasising the close-knit ecological as well as semiochemical associations involved in such complex interactions (cf. [59,60] for further details). It also seems that there are rare, morphologically similar cryptic entities amongst the blue butterflies and some may be—or are—cryptic species, thereby adding to difficulties in conservation strategies to enhance populations of the butterfly and its ant host/s in Europe and elsewhere [61]. The butterfly may be considered parasitic as well as herbivorous and later carnivorous, due to the fact that the host insect, the ant, derives little from hosting the butterfly larva and pupa, and indeed the association is wholly *negative* as far as the ants are concerned [59–61].

Mention has already been made of the wall butterfly, *L. megera* in Britain, a grass-feeding species [31,41,44,62]. Its continuing decline over the past 50 years or so, 'coinciding with four wet summers' in the mid-1980s [41], has resulted in it being now mainly confined to coastal sites in England and Scotland in addition to the Isle of Man and the Channel Isles ([44]; https://www.ukbutterflies.co.uk/species.php?species=megera/; accessed 6 April 2025). This decline appears to be due to the requirement of the larva for a particular level of solar intensity during development, i.e., microclimatic conditions at overwintering larval sites, as well as to the excessive use of nitrogen fertiliser application to cultivated grasslands in both Britain and mainland Europe, e.g., the Netherlands, where the butterfly has also retracted its former range [33]. According to these authors:

> *In comparison with larval sites of P. aegeria, those of L. megera showed higher temperatures at the mesoscale and less plant cover and more dead plant material at the microscale. L. megera caterpillars were also found closer to the shelter of vertical structures. The greater dependence on warm microclimates suggests that microclimatic cooling through excess nitrogen contributes to the recent decline of L. megera.*

Due to climate change as well as the excessive use of nitrogen fertilisers in grassland, the microclimatic conditions are apparently no longer suitable further inland and so the butterfly has retreated from these areas towards the coast, where the ecological requirements are still met. Alas, the butterfly has shown no recent signs of long-term population recovery, despite having done so in the past (e.g., 1988 in some sites in southern England [41]), so that its future in this country seems unsure, and as I write this, is seemingly extinct over large areas of the country. (*Nb. I have personally not seen a wall butterfly in the UK since the 1960s, when they used to be common in the area I grew up in the west of Hertfordshire*).

The small heath butterfly, *Coenonympha pamphilus*, another grass-feeding Satyrid species, has also declined in population size and distribution in the UK over roughly the same time span as the wall butterfly, i.e., since the 1970s [31,44], which may well also be connected to long-term climate change and/or habitat changes, such as those affecting the wall butterfly.

In the case of two species showing localised metapopulation structuring, the silver-spotted skipper, *Hesperia comma* (Hesperiidae) and the Glanville fritillary, the former species is now very rare and localised in the UK, being restricted *'to close-grazed chalk downland in the south-eastern corner of England as far west as Dorset'* [44]. This author states that south-facing slopes are usually preferred, with the females opting for egg-laying areas with sparse vegetation *'where the food plant grows on [i.e., sheep's fescue grass, Festuca ovina], or adjacent to patches of bare earth. Crumbling slopes, animal tracks and rabbit scrapes often provide these relatively warm microhabitats'* (cf. also [63,64]).

Hence, this butterfly has very specific habitat requirements and is only found on cropped grasslands where these criteria are met. The butterfly is reluctant to travel far from its isolated downlands, but does show considerable mixing in terms of local sites on the same escarpment, e.g., the North Downs west of Dorking, Surrey and southeast England, according to Thomas and Lewington [41], p. 20). These last authors also state the need of the butterfly for the warmth of close-cropped turf, as supported by the finding that in southern France, the insect thrives in much more overgrown turf.

As of the early 1990s, over 50 colonies are known, some of low population size, others thriving ([41], p. 22). With the recovery of rabbits after the myxomatosis outbreak of the early 1950s [63], hopefully colonies will continue to grow and expand, which they appear to have done since 1980 (https://butterfly-conservation.org/, accessed 6 April 2025). However, having said that, Thomas and Jones [63] employing logistic equations for the fragmented colonies, predict no significant spread over the next 100 years, except in East Sussex. These authors posit the following:

> *The dynamics of H. comma over 100 years demonstrate (i) the importance of environmental events that are correlated over large areas, (ii) the importance of refuges during adverse periods, and (iii) the potential for alternative, stable regional distributions, depending on the locations of refuges and barriers to dispersal.*

With reference to the other butterfly showing clear metapopulation structuring, *M. cinxia*, the larvae of which feed mainly on ribwort plantain, *Plantago lanceolata*, its current day restricted distribution is probably due to a combination of both climatic as well as land usage changes, it being at the edge of its northern range in Europe and in the UK, and is confined to the undercliffs of the southern coast of the Isle of Wight, e.g., Ventnor (50.5955° N, 1.2061° W), and Guernsey and Alderney in the Channel Isles [44]. According to Adrian Riley [44], there is a single vulnerable population in southern Hampshire on the mainland and an introduced colony in northern Somerset.

The fact that the butterfly occurs much further north in Europe, including the Åland Islands in Finland (60°07′00.0″ N 19°54′00.0″ E), on which Hanski and co-workers [28] have studied the metapopulation dynamics of the butterfly, strongly suggests that climate in not the only factor affecting the insect's distribution and colony stability. According to Hanski [28]:

> *The landscape [of the islands] consists of a very large network of dry meadows with the pooled habitat area covering about 1% of the landscape. Here, we analyse data for 22 years, comprising 66,527 records of the presence or absence of the butterfly in 4415 habitat patches distributed among 125 semi-independent networks.*

The authors show the following:

> *The majority of the habitat networks of the butterfly are below the extinction threshold. Metapopulation persistence and sizes of the networks above the extinction threshold can be predicted by spatial configuration, habitat quality and Pgi genotypes.*

[SNP allelic variation in the gene coding for the enzyme phosphoglucose isomerase, *Pgi.* Variation at this particular locus accounts for ~30% of variation in metapopulation size, the *Pgi* genotypes being associated with dispersal rate and hence with colonisations and extinctions]. The authors conclude by stating the following:

> *Our results demonstrate how a large heterogeneous landscape is a mosaic of 'hot' and 'cold' sections in the sense that parts of the landscape harbour networks with viable metapopulations (viable networks for short), while the rest consists of non-viable networks in which the species is not expected to persist on the long term. In our case, 39% of the 4415 habitat patches, and 29% of the pooled habitat area, are located in the cold sections, in networks below the extinction threshold. These networks may be temporarily occupied due to dispersal from the more favourable parts of the landscape, and these networks may thereby function as temporary stepping stones and facilitate the spread of a species across large areas. Classifying heterogeneous landscapes into hot and cold sections is helpful for practical conservation, as knowing the structure of the landscape helps direct conservation measures in a meaningful manner.*

Thus, it seems that even in this broadly suitable habitat for the butterfly, the persistence of colonies is precarious, and these are likely to become extinct (the so-called 'cold' sections where the colonies are not expected to persist, in effect showing 'negative ecology'), unless reinforced by migrants from larger colonies, especially adjacent ones, that is, the more favourable 'hot' sections of the landscape, within the overall metapopulation structure [28]. Factors likely to cause such extinctions include unfavourable climatic change, especially drought, predation by birds and arthropod predators, parasitism by hymenopterous parasitoids (the butterfly is attacked by a range of ten wasp parasitoids, including two specialists, *Cotesia melitaearum* (Braconidae: Microgastrinae) and *Hyposoter horticola* (Ichneumonidae: Campopleginae), which attack the larvae and egg and larvae of the butterfly, respectively [65,66], and inbreeding depression [67]. Since the Glanville fritillary in Finland has a flight range of <<500 m [68,69], its specialist parasitoid *C. melitaearum* can only persist in well-connected populations, as found in other insects showing metapopulation structure and attacked by specialist parasitic wasps, e.g., certain tansy-feeding aphids [70], whereas the other *M. cinxia* specialist, *H. horticola*, because of its comparatively greater flight capacity and hence range, can access even far-flung host butterfly colonies [69].

Similarly, in the case of the heath fritillary, *Melitaea athalia*, the butterfly, whilst widespread and more common on mainland Europe, is now very rare and localised in the UK, being largely confined to sites in North Devon, the Cornwall/Devon border, Essex, and Kent ([44]; https://butterfly-conservation.org/butterflies/heath-fritillary; accessed 6 April 2025). Attempts to conserve the species here and indeed enhance these local populations have concentrated on reducing the canopy in the woodlands that it still occurs in, as once happened when such woods were regularly coppiced to provide small, straight timber for fencing, etc., which, at the same time, has encouraged the growth and spread of the larval food plants, especially cow-wheat, *Melampyrum pratense*. This approach has been largely successful in halting the extinction of this species following ecological studies of the butterfly involving mark–recapture experiments at several sites in S.W. England and Kent [71].

From this pioneering study, the author suggests the following:

> *The conservation of M. athalia within large woodland complexes can be assisted by encouraging migration and rapid colonization by (i) reducing the distance between source colonies and potential new sites; (ii) providing interconnecting rides to encourage movement between potential sites; (iii) encouraging large, thriving colonies which can*

> *act as good sources of migrating adults; and (iv) creating numerous, highly suitable receiving sites.*

From this same study, it also appears that collecting of the butterfly by collectors could have a deleterious effect on populations of this rare and endangered insect, but only in the case of small populations, and presumably only in terms of adult butterflies during the flight season and in relation to the number of specimens actually taken.

Other UK butterflies which have undergone considerable population declines in recent years, verging on near extinction or actual extinction with recent successful attempts at re-establishment of certain species populations in their original strongholds, include the small tortoiseshell, *Aglais urticae*, large tortoiseshell, *Nymphalis polychloros*, high brown fritillary, *Fabriciana adippe* (all Nymphalidae), Duke of Burgundy, *Hamearis lucina* (Riodinidae), and the chequered skipper, *Carterocephalus palaemon* (Hesperiidae) [37]. Of these, perhaps the decline of the small tortoiseshell is the most bizarre. Once a very common butterfly, with the larvae feeding on stinging nettles, *U. dioica* and the adults being a common sight in the countryside, as well as regularly visiting gardens and garden flowers such as buddleia bushes, it drastically declined nationally, and in Western Europe generally, in the period 1990–2000, and sharply between 2003 and 2008 [72], only starting to make a definite recovery from about 2010 onwards.

According to the Wikipedia entry (https://en.wikipedia.org/wiki/Small_tortoiseshell, accessed 6 April 2025):

> *Scientific evidence shows that the summer drought is a cause of declining populations, because larvae grow normally on drenched leaves (but hatchlings were even rarer the wet summers of 2007 and 2008). However, before 2000, according to data from an English butterfly monitoring programme, there was a good correlation between reproductive success, the abundance of populations of this species and the host plant moisture stress. From 1976 to 1995, the butterfly had more success in summers that were cool and wet at the beginning of summer than when it was hot and dry. This butterfly may then be sensitive to global warming.*

It is certainly more regularly seen nowadays, but has perhaps still not yet recovered to levels seen prior to the onset of its dramatic population decline. The reason/s for this fluctuation are currently unknown, despite the above-mentioned speculation about climate/weather influences on the success of the butterfly's lifecycle. Parasitism by a relatively new dipteran parasitic fly, *Sturmia bella* (Diptera: Tachinidae) to Britain was at one time suspected [72], but then it was noted that the butterfly has declined in Europe, where this particular specialist parasitoid of Vanessids is resident (http://tachinidae.org.uk/blog/the-parasitoids-of-small-tortoishell-aglais-urticae/; accessed 6 April 2025). As revealed in this online article, other specialist and polyphagous dipterous parasitoids are also implicated in the decline of the small tortoiseshell:

> *In the light of the available data, concluding that S. bella is the main driver of the recent declines of A. urticae would be premature. The fact that host numbers have also—though to a lesser extent—been declining in continental Europe* [73]*, where S. bella has been present for a long time, suggests that other explanations for the decline need to be considered* [72].

So, it is not certain that *S. bella* is the culprit responsible for the rapid decline of the butterfly in the UK, more especially since the peacock butterfly, *Aglais io*, also parasitized by this parasitoid fly, has not declined over the same period as the small tortoiseshell [72].

In the case of the chequered skipper, according to Ravenscroft [74,75] who studied the ecology of the butterfly, an ideal site comprises the following:

> *Open woodland, usually dominated by [Sessile] Oak Quercus petraea or [Downy] Birch Betula pubescens, on gently sloping hillsides, often by the side of lochs, in sheltered clearings that catch the sun.*
>
> (cited in [76])

Clearly, if this ecological requirement is not met, the butterfly cannot flourish, as proved to be the case in the English colonies of this butterfly that died out in its last Nottinghamshire stronghold in 1976 (incidentally a very hot year with prolonged drought conditions; [77]. It has now been successfully introduced from continental stock [78]. The butterfly also occurs in Scotland [45]. The ten core Scottish populations seem to be flourishing...so far (https://butterfly-conservation.org/butterflies/chequered-skipper; accessed 6 April 2025).

There was no obvious difference in terms of shared haplotypes in the genetics of butterflies in England and Scotland and in other parts of its European range (Belgium and Norway) when tested using a small selection of mitochondrial DNA sequence markers (CO I, CO II, and Cyt b) [79]. Why the butterfly should have persisted in Scotland but died out in England may perhaps be due to weather-related issues associated with the intense heat and drought experienced in England in the very hot summer of 1976. (cf. also [78] for further details of the attempts to re-introduce this butterfly into England again).

The decline and disappearance of the high brown fritillary from its former strongholds in southern England and Wales seems also to be a bit of a mystery, but suitable woodland conditions, including a plenitude of the larval food plant violet, e.g., common dog-violet, *Viola riviniana* and hairy violet, *V. hirta*, seems to be most probable [41,44]. According to Bulman et al. [80] of Butterfly Conservation:

> *The High Brown Fritillary was once widespread in coppiced woodlands and grazed Bracken habitats. Its decline since the 1950s has been sudden and severe with an 82% loss over the last 20 years. The butterfly is now restricted to around 50 sites, principally on Dartmoor and the Morecambe Bay Limestones. Sadly, only a few colonies are still present in Wales and on the Malvern Hills.*
>
> In relation to habitat, the authors state the following:
>
> *Bracken habitats suitable for Fritillary butterflies are those where the ground flora consists of a mixture of woodland plants (e.g., violets, Wood Anemone, Wood Sage, Bugle and Primrose) and acid grassland plants (e.g., Tormentil and Wavy Hair-grass). Bracken containing these plant communities can occur on hillsides, in woodland clearings or at woodland edges. Fritillaries are most commonly found when these communities occur on neutral to slightly acidic soils....For example, High Brown and Pearl-bordered Fritillaries require Bracken on warm, dry slopes where the dark-coloured caterpillars bask on dead Bracken to raise their body temperatures enough to develop in the cool spring weather.*

As for conservation efforts, which are critical if this species is to be conserved, they claim the following:

> *Many colonies have been lost due to changes in woodland management practice, such as the abandonment of coppicing, and these species have become increasingly restricted to areas of rough grassland and Bracken habitats. ...Overgrazing causes an increase in grass cover, which is particularly detrimental to the High Brown Fritillary.*

Alas, without such dedicated and persistent efforts, especially including understanding of the fundamental ecology and ecological requisites of this species, it seems that the butterfly is still heading inexorably for extinction.

The large tortoiseshell actually became extinct in the UK in the late 1940s after a decline over many years, having once been widely distributed in the UK [44]. The favoured larval food plant is elm, *Ulmus* ssp., but the gregarious larvae will also feed on aspen, *Populus tremula*, birch, *Betula* spp., poplars *Populus* spp., and Willows, *Salix* spp. (https://butterfly-conservation.org/butterflies/large-tortoiseshell; accessed 6 April 2025). The species still occurs in mainland Europe and is abundant in some areas but scarce in others. In Jena, Thuringia, Germany, I saw one live specimen and two dead specimens in the period 2006–11, and one live specimen in Herssching by the eastern side of the Lake of Ammersee, Bavaria in about 2010 (HDL, pers. obs.).

The reasons for this decline in the UK and elsewhere in Europe are not precisely known, as with the black-veined white butterfly earlier mentioned, but climatic and parasite attack by dipterous and hymenopterous parasitoids are likely [81]. It is certainly attacked by the dipterous parasitoid *Drino inconspicua* (Tachinidae) on mainland Europe [82]. In Britain, the decline of many species of elm in the mid-1970s, especially *U. procera*, exacerbated by the heatwave of 1976, probably prevented any re-establishment of the species in its former range by vagrants crossing the Channel and North Sea from mainland Europe. In recent years, some sightings of adults of this impressive butterfly have been made in southern England, e.g., the Poole area of Dorset (Richard Harrington, pers, comm.), undoubtedly vagrants. With the recovery of elms in the UK [83], it is possible that the butterfly may make a comeback here in the longer term, just as the black-veined white is apparently doing (cf. [84]).

According to the analyses performed by [73] [16 years (1992–2007) of butterfly transect count data studying butterfly population levels, i.e., '*the annual incidence and relative abundance of 20 species that have been considered common and of no conservation interest*'] in urban, semi-urban, and rural landscapes in the Netherlands:

> *Our analyses clearly showed declining patterns in several common species, but they do not directly reveal the causes of these patterns. Reasons for the negative trends are most probably multiple and complex. Nevertheless, on the basis of other case studies, we hypothesize that 3 general factors are significant contributors, all symptoms of ongoing intensification of land use* [85]*: nitrogen pollution level, declining nectar supply, and the rapid ecological changes in the wider landscape.*

So here, as described and discussed, the factors (single or multiple) responsible for the decline of some hitherto common butterfly species are still unresolved and their descent from a positive to a negative ecological condition will require more research to fathom, most probably on a case-by-case basis.

5. Discussion

The main take-home message of this article is that even for common and widespread organisms like many birds species in Britain and mainland Europe, both migrants and residents, demographic homogeneity cannot be assumed, especially over large spatial scales, and when distribution maps are inspected, the distributions are found to be patchy, sometimes with a latitudinal or longitudinal bias, for whatever ecological reason/s. We do not necessarily know why the birds are absent from particular geographic regions, as in the case of the nightingale, more especially considering that the habitat appears suitable for them, e.g., has lots of mixed deciduous woodlands and rivers and streams with bramble thickets (*Rubus fruticosus* agg.) along their banks.

But clearly it is not. If true, this statement reflects our lack of knowledge of the ecology of many species of living organism, here generally well-studied ones (birds and butterflies), and that the ecology of each species has to be considered in a case-specific manner. In addition, it is not just the homogeneity/heterogeneity of the distributions, but the broad distribution of the various species as displayed at a large geographic scale in field guides of birds or on dedicated websites like that of the BTO and DDA, which is worthy of our attention and critical appraisal and comment. If we could answer such questions, we would surely know much more about ecological processes, both specifically and more broadly, than at present.

At a much smaller spatial scale, a local scale, we also observe a lack of homogeneity, sometime within a few kilometres of known breeding populations of a given species, as with the common crow, green woodpecker, and swifts, as alluded to above. Besides local biotic and abiotic constraints, of which we know every little, behaviour of the species concerned is also important, one imagines, since behaviour is a driving force in ecological and evolutionary processes [86]. This seems to be so in the case of the common crow and its reluctance to nest and breed in Heasley Mill, whilst breeding nearby at other local sites.

6. Conclusions

In conclusion, examination of the distribution of living organisms, here birds and butterflies as way of exemplars, at various spatial scales, local or at large national spatial scales, shows that populations are not necessarily homogeneous, even of common species. Rather, a patchy, heterogeneous distribution is observed, leading to negative ecological patterns. The exact ecological causes of this patterning may be unknown but presumably can be resolved in time on a case-by-case basis. What this realisation does bring to the fore is that homogeneity of a species population—and here I primarily refer to common species—cannot be take for granted. This is also true for many species in terms of genetic identity, as revealed using high-resolution molecular markers. From this view of nature, it is clear that collectively as ecologists, we have some way to go before we understand all the factors, the ecological axes, that constrain species and allow them to thrive in one area, but not in another, sometimes a very geographically near locality. Of course, in order to conserve endangered animals or plants, or re-introduce them into areas they once occupied or into new areas, such knowledge relating to their exact ecological requisites is essential for success to be achieved in the longer term.

Most important amongst these is surely the concept of the ecological niche and how living organisms are maintained and constrained by this (cf. https://en.wikipedia.org/wiki/Ecological_niche for details; accessed 6 April 2025). If, for whatever reason/s, the niche becomes unsuitable or untenable, then the organism filling that niche is liable to become extinct, or must evolve and undergo ecological specialisation to allow it to adapt and fill a new niche, different from the one it originally stemmed from. Because we do not necessarily know what the 'fine-grained' ecological requirements for any given animal species are that enable it to fill a new niche, let alone one that it hitherto occupied (as in the case of the British subspecies of the large copper butterfly), then multi-faceted research may well be necessary to determine these requirements for any particular species. These include molecular ecological/genetic studies to establish the level of genetic variation within the population under study, its vagility and habitat fidelity, and level of dietary specialisation, including its chemotype preference when specialised herbivores feed on one or a few plants [5]. In the last instance, this is governed by the ability of the organism to digest particular food items, which often relates to its biochemical ability to deal with toxic secondary plant compounds evolved by plants to deter such attacks. In this way, animals are not free agents and are constrained in what they eat, leading to co-evolution, such that food webs may become highly structured depending on what a given animal species can or cannot consume. Animals are of course constrained in terms of their spatial—and sometimes temporal—distribution by the distribution of their prey in the case of predators and parasites (such as winged parasitic insects), and plants in the case of herbivores, e.g., aphids [87] and giraffes [88].

On larger geographical and temporal (geological) scales, as is well-known, living organisms have been undergoing extinction events ever since life evolved some 3.5 billion years ago [89]. Famous extinction events include the Permian, Triassic, and Cretaceous mass extinctions, affecting life globally, both terrestrially and within aquatic environments (marine and freshwater), largely caused by, as is generally accepted, volcanic eruptions, and in the case of the last event, a meteorite strike on the Yucatan Peninsula in Mexico (Chicxulub crater) some 66 million years ago, leading to the demise of the non-avian dinosaurs [90–93] (but cf. also [94]). There have also been large-scale global extinctions since then, including in the Eocene/Oligocene Transition and Pleistocene epochs (cf. [91] and references therein).

Charles Darwin was well-aware of extinction as a necessary force in evolution [95] and also coined the term 'Utter Extinction', when a lineage or particular taxa become irrevocably extinct with no living descendants whatsoever [96]. Besides cataclysmic extinctions occurring over a wide area due to geological or astronomical reasons, a variety of causes are usually posited for the loss of such lineages, *viz.* climate change leading to radical habitat change, fragmentation of populations so that these are more susceptible to disease events, predation/parasitism, *intra-* and *inter*specific competition and damaging genetic effects, more especially inbreeding depression due to the accumulation of deleterious homozygous mutations of one sort and another [97], and disruption of established food webs, often involving close, long co-evolved associations [98]. The importance of the robustness of food webs in the face of changes in species composition, loss of species, and their trophic interactions, and how these are likely to—or do—affect ecosystem functioning and hence the stability of ecosystems and the taxa inhabiting these, is discussed in a recent article by Ståhl et al. [99].

Finally, as aforementioned, during our present Anthropocene epoch, loss of species diversity globally due to human-induced climate change, human deprivations on habitats and ecosystems [35,36,100], the international illegal trade in wildlife, especially endangered wildlife [101], and pollution, including synthetic pesticides, heavy metal poisoning, and micro-plastics, are sadly collectively having a negative worldwide effect on biodiversity, leading to a new threat to the diversity and well-being of life on Earth. Thus, a plethora of negative ecological forces, some relatively new, are impacting the world's wildlife and it seems that, what with the human population continuing to grow and expand, and hence likely to outstrip the available natural resources of the world, especially food and the land necessary to grow this [102], the future for species other than ourselves and those exploited by us does not seem too rosy. And indeed, can we long survive in a world where biodiversity has itself been drastically curtailed? This may then be thought of as the ultimate chapter in the ongoing round of extinction events that has already led to an estimated loss of 99% of all the living organisms that have ever existed on this planet [103,104], a vast number dying out in the Permian-Triassic (cf. https://en.wikipedia.org/wiki/Permian%E2%80%93Triassic_extinction_event; accessed 6 April 2025) and Cretaceous-Paleogene extinctions especially (cf. https://en.wikipedia.org/wiki/Cretaceous%E2%80%93Paleogene_extinction_event; accessed 6 April 2025). And of course, this raises the topic of bad genes or bad luck, as originally expounded by David Raup (1933–2015) in a seminal paper [20] and later discussed further at length in a book of the same name [105] (cf. also [106]).

Since then, it has been proposed from the fossil record that species only last on average some 0.5–13 million years, depending on the taxa concerned (cf. https://en.wikipedia.org/wiki/Background_extinction_rate; accessed 6 April 2025). This may be due to a processes similar or analogous to so-called 'mutational meltdown', as first discovered experimentally in asexual lineages of water fleas, *Daphnia pulex* (Leydig) (Crustacea: Cladocera) [107–109], and no doubt involving the intervention of transposons (see below), leading to smaller population sizes with inbreeding, genetic drift, concomitant fitness loss, and eventual extinction, e.g., [110].

This is the ultimate lot of all species, as it indeed is of individuals within populations of a given species of living organism, the complex, multifactorial result of selection caused by one or more random actions: disease, predation and parasitism, competition for resources of one form or another, including sexual selection in sexually reproducing animals, and population genetic influences, including effects on the individual and populations via mutations of one kind and another, e.g., cancers (mutational load), transposable elements (TEs or transposons) [111,112], and chromosome telomere effects as well as other repetitive elements along the genome itself [112–114], and lastly, but very importantly, random stochastic actions, i.e., bad luck, when life forms indulge in the great race of life, à la Darwin's (1859) theory of evolution by mean of natural selection [95]. In other words, and at a finer level, since ecology is the first step on the ladder of evolutionary change, species populations adapt and subsequently evolve–or not as the case may be–due to the processes inherent in positive *versus* negative ecology.

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