Towards an understanding of the development and constitution of the Irish postglacial syrphid fauna (Diptera, Syrphidae)

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It is most unlikely that direct evidence of the constitution of European postglacial syrphid faunas will become available from remains of the insects derived from postglacial deposits. So any attempt at understanding the postglacial development of the syrphid fauna of any part of Europe will have to rely on indirect information. Such indirect information is provided by habitat data derived, in particular, from palaeobotanical studies. From a knowledge of the habitat array present in Ireland at different times during the postglacial, an attempt is made here to gain some understanding of the origins of the island's present-day syrphid fauna, using the habitat-association data coded into the Syrph the Net (StN) database.

It is concluded that all of the species comprising the present fauna would be predicted to occur in Ireland and should have been in place by 5,000BP, but that the entire present-day fauna is unlikely to have been present more than 7,000 years ago. From this starting point the probable geographical origin and degree of completeness of the existing syrphid fauna of Ireland are explored, resulting in the conclusion that, although derived from the Atlantic Region, the Irish syrphid fauna is a sub-set of the Atlantic Region fauna that has been "filtered" by the land mass of Great Britain, i.e. species predicted to be present will not be, unless also present in Great Britain. It is further concluded that the Irish fauna is to a noticeable extent incomplete, in comparison with the predicted fauna, even when it is assumed that the Irish fauna is derived from the restricted British fauna.

Comparing microhabitat occupancy levels in Ireland and Britain, within the present-day Irish habitat array, demonstrates that a concentration of "missing" species occurs in particular groups of microhabitats, an effect identified with the impact of human activity on the Irish landscape during the postglacial. Modification of remaining forest habitats by man's activities is highlighted, manifested in an absence of syrphids associated with overmature/senescent trees that is so complete that overmature forest habitat can essentially be regarded as missing from the island. However, man's activities can be identified as probably responsible for the absence of only some 50% of the "missing" British species.

An alternative explanation for the absence of the rest of the "missing" species is sought, by assessing the potential contribution of levels of syrphid inventory activity in Ireland, from which it is concluded that all species with a localised distribution in Ireland are as yet unlikely to have been recorded. Similarly, predicting the presence in Ireland, now, of species that have supposedly arrived in Britain only during the last 50 years is identified as unrealistic. Bringing all of these various factors into consideration would reduce to 10-15 the number of British species inexplicably absent from the Irish syrphid fauna, from an initial total of some 60 species. It is concluded that the known syrphid fauna of present-day Ireland is largely the product of the interaction between available habitats and the adjacent British species pool over the last 5,000 years, modified by the impact of man's activities throughout that period and by the amount of inventory work that has now been carried out on the Irish fauna. Modifications to the fauna introduced by human activities appear to be largely in the form of species losses, caused by replacement of naturally occurring forest by farmed grassland that is dependent upon man's management for its survival. There seems to be little evidence of faunal accretion resulting from the presence of these grasslands. In particular, British species associated with well-drained grassland microhabitats are conspicuously lacking from the Irish syrphid fauna.

Keywords: Syrphidae, Ireland, postglacial development of fauna.

Zusammenfassung

Es ist wenig wahrscheinlich, dass die postglaziale Entwicklung der europäischen Syrphidenfauna direkt aus (sub)fossilen Insektenresten des Postglazials rekonstruiert werden kann. Wir sind deshalb auf indirekte Informationen angewiesen. Solche verdanken wir insbesondere paläobotanischen Studien, die Aussagen über Habitate und ihre geografische Verbreitung zulassen.

Ausgehend von den Kenntnissen der Vegetation Irlands während verschiedener Abschnitte des Postglazials und den in Syrph the Net (StN) codierten Habitatansprüchen von Schwebfliegen-Arten wird ein Versuch unternommen, die Herkunft und Entwicklung der heutigen Syrphidenfauna der Insel nachzuvollziehen.

Dabei wird davon ausgegangen, dass das Vorkommen sämtlicher Arten der heutigen Fauna in Irland zu erwarten sei und diese seit etwa 5000 Jahren heimisch sind, dass es aber sehr unwahrscheinlich ist, dass die gesamte heutige Fauna bereits vor 7000 Jahren bestand. Ausgegehend von diesem "Startpunkt" wird die vermutliche geografische Herkunft und der Grad der Vervollständigung der heutigen irischen Syrphidenfauna untersucht.

Die irische Fauna gehört zur Fauna der Atlantischen Region. Allerdings fehlen manche Arten, deren Vorkommen hier eigentlich zu erwarten ist. Die große Landmasse Großbritanniens (wo viele dieser Arten vorkommen) wirkte hier offenbar als "Filter". Verglichen mit den Vorhersagen, die sich aus den Habitatansprüchen ergeben, erweist sich die irische Fauna als zu einem erheblichen Anteil unvollständig, selbst wenn davon ausgegangen wird, dass sie von der Fauna Großbritanniens abstammt, die ebenfalls schon durch eine eingeschränkte Artenvielfalt ausgezeichnet ist.

Der Vergleich des Vorkommens von Mikrohabitaten in Großbritannien und Irland (ausgehend von der heutigen Habitatausstattung) zeigt, dass "fehlende Arten" an ganz bestimmte Gruppen von Mikrohabitaten gebunden sind, die in Irland aufgrund menschlicher Einflüsse im Postglazial fehlen. Gezeigt wird das insbesondere an den durch menschliche Aktivitäten beeinflussten verbleibenden Wälder, die so weit gehen, dass reife Waldlebensräume praktisch vollständig fehlen. Dem entsprechend fehlen auch Schwebfliegenarten, die an überreife Bäume gebunden sind.

Menschliche Aktivitäten lassen sich allerdings nur für etwa 50% der "fehlenden" britischen Arten verantwortlich machen. Für die restlichen Arten sind verschiedene Erklärungen denkbar. Die Intensität der Erfassung der Schwebfliegenfauna Irlands lässt darauf schließen, dass Arten mit sehr eingeschränkter Verbreitung nicht vollständig nachgewiesen sind. Ähnliches gilt für Arten, von denen angenommen wird, dass sie sich erst innerhalb der letzten 50 Jahre nach Großbritannien ausgebreitet haben. Berücksichtigt man das, reduziert sich die Zahl der in Großbritannien vorkommenden und in Irland "unerklärlicherweise" fehlenden Arten von ungefähr 60 auf 10-15.

Die (bekannte) heutige Schwebfliegenfauna Irlands hängt also weitgehend einerseits von den vorhandenen Habitaten, andererseits vom Arteninventar des benachbarten Großbritanniens im Verlauf der letzten 5000 Jahre ab. Sie wurde während dieser Zeit auch durch menschliche Aktivitäten beeinflusst – wobei diese in der Regel den Verlust von Arten bedeuteten, in erster Linie als Folge der Umwandlung von Wäldern in bewirtschaftetes Grünland, das seine Existenz dauernder Bearbeitung verdankt. Für einen Zuwachs an Arten als Folge der Schaffung dieser offener Graslandhabitate gibt es kaum Hinweise. Auffallend ist insbesondere, dass der irischen Fauna britische Arten, die an (Halb-)Trockenrasen gebunden sind, fehlen.

Introduction

Postglacial, palaeoecological studies have not incorporated determination of fragments of syrphids (if any!) found in postglacial deposits, so there is no direct evidence of which species occurred in Ireland following the retreat of the ice at the end of the last glaciation.

All known Irish syrphid species occur also elsewhere in Europe (a significant proportion of the present Irish syrphid fauna is also found in N America). Similarly, there are no known endemic Irish varieties of syrphid species. This situation provides no grounds for assuming that the Irish syrphid fauna has been isolated from that of the rest of Europe for very long, if at all. The adults of European syrphid species are fully-winged and, so far as is known, all of them can, and do, use their wings for flight. Not only do they fly, but they are well-recognised as capable of flying long distances, some of them being regarded as "migrants" (Aubert et al. 1976, Gatter & Schmid 1990). The syrphids found on groups of islands much distant from continental Europe, such as the Canaries (Marcos-Garcia et al. 2002), Iceland (Ólafsson 1991) and the Faroes (Jensen 2001) attest to the ability of European species to traverse salt water, as well as land or freshwater bodies. When considered together, these points make it extremely difficult to construct an *a priori* case for claiming either that being geographically an island would have prevented immigration of syrphid species to Ireland during the post-glacial, or that the existing fauna somehow survived glacial periods in Ireland in situ.

Given that syrphids can be expected to have arrived in Ireland under their own volition, it becomes possible to consider the probable constitution of the Irish syrphid fauna at different times during the post-glacial, from a knowledge of which syrphid habitats were present in Ireland at different times in the post-glacial and which syrphid species are associated with each of those habitats in Europe today. There is evidence of the types of habitat occurring in Ireland at various stages in the postglacial, derived primarily from palaeobotanical and palaeogeomorphological studies. A review is provided by Mitchell (1986) and various papers have been published more recently, adding, in particular, valuable insights into the habitat array present at various times during the last 6,000 years – when man has been active in the postglacial Irish landscape. Using these habitat data in conjunction with the Syrph the Net (StN) database Part 1 of this text investigates when, during the postglacial, habitat suitable for each species in the present syrphid fauna first became available, and whether suitable habitats have subsequently been continuously available up to the present day. In Part 2, by again using the database to examine the representation in adjacent parts of Europe of syrphid species associated with the habitats today represented in Ireland, the extent to which the observed Irish syrphid fauna coincides with the syrphid fauna predicted for the island is considered. In parts 3-5 possible explanations are sought for differences between the observed and predicted faunas. These various exercises have been conducted to gain some understanding of how long the existing syrphid fauna may have inhabited Ireland, what changes have probably occurred in that fauna and to what extent such changes are open to explanation.

Part1: the post-glacial development of the fauna

Methods

In conducting this review it has been necessary to both marshal information on habitats represented in Ireland during the postglacial and to subdivide the post-glacial into a number of time periods, corresponding with phases in the evolution of environmental conditions indicated from the literature. These phases are briefly described and referenced in Appendix 1. Any such compilation has to be regarded as approximate, particularly in respect of the time at which a particular habitat appeared or disappeared. Equally, it is inevitably based on generalising about the condition of the entire island from pieces of information derived from individual sites, and does not allow for much regional variation.

Once the array of habitats for a particular time period has been assembled, a list of the European species associated with those habitats can be derived, using the Macrohabitats file of StN (Speight et al. 2003). Sorting that list with the species list for Ireland then shows which of the Irish species could occur in association with that habitat array.

Results

The species in the present syrphid list for Ireland expected to occur in association with each time period of the Irish post-glacial are shown in Table 1.

Tab. 1: The present-day syrphid list for Ireland, showing which of the species would be expected to occur in association with the habitats present in Ireland in different time periods in the post-glacial. BP = before present.

	Approximate time period BP (in thousands of years)						
PRESENT-DAY IRISH SPECIES	11 to10	10 to 9	9 to 7	7 to 5	5 to 2	2-0.2	0.2 to now
Anasimyia contracta		1	1	1	1	1	1
Anasimyia lineata		1	1	1	1	1	1
Anasimyia lunulata		1	1	1	1	1	1
Anasimyia transfuga		1	1	1	1	1	1
Arctophila superbiens		1	1	1	1	1	1
Baccha elongata		1	1	1	1	1	1
Brachyopa insensilis			1	1	1	1	1
Brachyopa scutellaris			1	1	1	1	1
Brachypalpoides lentus			1	1	1	1	1
Brachypalpus laphriformis			1	1	1	1	1
Chalcosyrphus nemorum		1	1	1	1	1	1
Cheilosia ahenea		1			1	1	1
Cheilosia albipila		1	1	1	1	1	1
Cheilosia albitarsis		1	1	1	1	1	1
Cheilosia antiqua		1			1	1	1
Cheilosia bergenstammi		1	1	1	1	1	1
Cheilosia chrysocoma		1	1	1	1	1	1
Cheilosia grossa					1	1	1
Cheilosia illustrata			1	1	1	1	1
Cheilosia impressa		1	1	1	1	1	1
Cheilosia latifrons		1	1	1	1	1	1
Cheilosia longula	1	1	1	1	1	1	1
Cheilosia nebulosa		1	1	1	1	1	1
Cheilosia pagana		1	1	1	1	1	1
Cheilosia psilophthalma		1	1	1	1	1	1
Cheilosia pubera	1	1	1	1	1	1	1
Cheilosia scutellata			1	1	1	1	1
Cheilosia semifasciata	1	1	1	1	1	1	1
Cheilosia uviformis		1	1	1	1	1	1
Cheilosia variabilis			1	1	1	1	1
Cheilosia velutina			1	1	1	1	1
Cheilosia vernalis		1	1	1	1	1	1
Cheilosia vicina		1			1	1	1
Chrysogaster coemiteriorum		1	1	1	1	1	1
Chrysogaster solstitialis		1	1	1	1	1	1
Chrysogaster virescens		1	1	1	1	1	1
Chrysotoxum arcuatum			1	1	1	1	1
Chrysotoxum bicinctum	1	1	1	1	1	1	1
Chrysotoxum cautum					1	1	1

Chrysotoxum fasciatum	1	1	1	1	1	1	1
Criorhina berberina		1	1	1	1	1	1
Criorhina floccosa			1	1	1	1	1
Criorhina ranunculi	1	1	1	1	1	1	1
Dasysyrphus albostriatus			1	1	1	1	1
Dasysyrphus hilaris		1	1	1	1	1	1
Dasysyrphus pinastri	1	1	1	1	1	1	1
Dasysyrphus tricinctus	1	1	1	1	1	1	1
Dasysyrphus venustus	1	1	1	1	1	1	1
Didea alneti			1	1	1	1	1
Didea fasciata			1	1	1	1	1
Doros profuges			1	1	1	1	1
Epistrophe eligans			1	1	1	1	1
Epistrophe grossulariae		1	1	1	1	1	1
Epistrophe nitidicollis		1	1	1	1	1	1
Episyrphus balteatus	1	1	1	1	1	1	1
Eriozona erratica			1	1	1		1
Eriozona syrphoides							1
Eristalinus aeneus		1	1	1	1	1	1
Eristalinus sepulchralis		1	1	1	1	1	1
Eristalis abusivus		1	1	1	1	1	1
Eristalis arbustorum		1	1	1	1	1	1
Eristalis cryptarum	1	1	1	1	1	1	1
Eristalis horticola	1	1	1	1	1	1	1
Eristalis interruptus		1	1	1	1	1	1
Eristalis intricarius		1	1	1	1	1	1
Eristalis pertinax		1	1	1	1	1	1
Eristalis tenax		1	1	1	1	1	1
Eumerus funeralis					1	1	1
Eumerus strigatus		1	1	1	1	1	1
Eupeodes bucculatus		1	1	1	1	1	1
Eupeodes corollae		1	1	1	1	1	1
Eupeodes latifasciatus		1	1	1	1	1	1
Eupeodes luniger		1	1	1	1	1	1
Ferdinandea cuprea	1	1	1	1	1	1	1
Helophilus hybridus	1	1	1	1	1	1	1
Helophilus pendulus	1	1	1	1	1	1	1
Helophilus trivittatus		1	1	1	1	1	1
Heringia heringi			1	1	1	1	1
Heringia vitripennis		1	1	1	1	1	1
Lejogaster metallina		1	1	1	1	1	1
Lejogaster tarsata		1	1	1	1	1	1
Leucozona glaucia			1	1	1	1	1
Leucozona laternaria		1	1	1	1	1	1
Leucozona lucorum			1	1	1	1	1
Melangyna arctica	1	1	1	1	1	1	1
Melangyna compositarum			1	1	1		1
Melangyna lasiophthalma	1	1	1	1	1	1	1
Melangyna quadrimaculata			1	1	1	1	1
Melangyna umbellatarum		1	1	1	1	1	1
Melanogaster aerosa		1	1	1	1	1	1
Melanogaster hirtella		1	1	1	1	1	1
Melanostoma mellinum	1	1	1	1	1	1	1
Melanostoma scalare	1	1	1	1	1	1	1
Meligramma cincta			1	1	1	1	1
Meligramma guttata		1	1	1	1	1	1
Meliscaeva auricollis			1	1	1	1	1
Meliscaeva cinctella		1	1	1	1	1	1
Merodon equestris							1
Microdon analis					1	1	1

Microdon mutabilis		1	1	1	1	1	1
Microdon myrmicae			1	1	1	1	1
Myathropa florea	1	1	1	1	1	1	1
Neoascia geniculata		1	1	1	1	1	1
Neoascia meticulosa		1	1	1	1	1	1
Neoascia obliqua		1	1	1	1	1	1
Neoascia podagrica		1	1	1	1	1	1
Neoascia tenur	1	1	1	1	1	1	1
Orthonevra geniculata		1	1	1	1	1	1
Orthonevra nobilis		1	1	1	1	1	1
Paragus constrictus		1			1	1	1
Paragus haemorrhous		1	1	1	1	1	1
Parasyrphus annulatus			1	1	1		1
Parasyrphus lineolus			1	1	1		1
Parasyrphus malinellus			1	1	1		1
Parasyrphus nigritarsis		1	1	1	1	1	1
Parasyrphus punctulatus			1	1	1	1	1
Parasyrphus vittiger			1	1	1		1
Parhelophilus consimilis		1	1	1	1	1	1
Parhelophilus versicolor		1	1	1	1	1	1
Pipiza austriaca			1	1	1	1	1
Pipiza bimaculata		1	1	1	1	1	1
Pipiza luteitarsis			1	1	1	1	1
Pipiza noctiluca		1	1	1	1	1	1
Pipizella viduata			1	1	1	1	1
Platycheirus albimanus	1	1	1	1	1	1	1
Platycheirus ambiguus					1	1	1
Platycheirus amplus		1	1	1	1	1	1
Platycheirus angustatus		1	1	1	1	1	1
Platycheirus aurolateralis			1	1	1	1	1
Platycheirus clypeatus		1	1	1	1	1	1
Platycheirus discimanus		1	1	1	1	1	1
Platycheirus fulviventris		1	1	1	1	1	1
Platycheirus granditarsus		1	1	1	1	1	1
Platycheirus immarginatus		1	1	1	1	1	1
Platycheirus manicatus	1	1	1	1	1	1	1
Platycheirus nielseni	1	1	1	1	1	1	1
Platycheirus occultus		1	1	1	1	1	1
Platycheirus peltatus		1	1	1	1	1	1
Platycheirus perpallidus		1	1	1	1	1	1
Platycheirus podagratus	1	1	1	1	1	1	1
Platycheirus ramsarensis	1	1	1	1	1	1	1
Platycheirus rosarum		1	1	1	1	1	1
Platycheirus scambus		1	1	1	1	1	1
Platycheirus scutatus			1	1	1	1	1
Platycheirus splendidus			1	1	1	1	1
Platycheirus sticticus			1	1	1	1	1
Portevinia maculata		1	1	1	1	1	1
Rhingia campestris			1	1	1	1	1
Riponnensia splendens		1	1	1	1	1	1
Scaeva pyrastri		1	1	1	1	1	1
Scaeva selenitica			1	1	1	1	1
Sericomyia lappona	1	1	1	1	1	1	1
Sericomyia silentis	1	1	1	1	1	1	1
Sphaerophoria batava		1	1	1	1	1	1
Sphaerophoria fatarum		1			1	1	1
Sphaerophoria interrupta		1	1	1	1	1	1
Sphaerophoria loewi		1	1	1	1	1	1
Sphaerophoria philantha	1	1	1	1	1	1	1
Sphaerophoria rueppelli						1	1

Sphaerophoria scripta		1	1	1	1	1	1
Sphegina clunipes		1	1	1	1	1	1
Sphegina elegans			1	1	1	1	1
Syritta pipiens		1	1	1	1	1	1
Syrphus rectus					1	1	1
Syrphus ribesii	1	1	1	1	1	1	1
Syrphus torvus	1	1	1	1	1	1	1
Syrphus vitripennis	1	1	1	1	1	1	1
Trichopsomyia flavitarsis		1	1	1	1	1	1
Tropidia scita		1	1	1	1	1	1
Volucella bombylans		1	1	1	1	1	1
Volucella pellucens			1	1	1	1	1
Xanthandrus comtus			1	1	1	1	1
Xanthogramma festivum					1	1	1
Xylota abiens		1	1	1	1	1	1
Xylota florum			1	1	1	1	1
Xylota jakutorum		1	1	1	1		1
Xylota segnis		1	1	1	1	1	1
Xylota sylvarum			1	1	1	1	1
Xylota tarda			1	1	1	1	1
	32	124	164	164	176	170	179

Table 1 shows that while little more than 15% of today's syrphid fauna is likely to have been in Ireland under tundra conditions and remained present in Ireland right through from then to now, more than half of the existing fauna could have been in place by approximately 10,000BP and all but 10% of the present-day Irish syrphid fauna could apparently have found appropriate habitat in Ireland by 7,000BP. The remaining species could nearly all of them have been provided for by the addition of Atlantic scrub and limestone pavement habitats, by 5,000BP, leaving only 7 species unaccounted for. Of these, four would be expected to colonise grassy areas developed within forest, caused by the grazing of livestock, following the localised forest clearance activities which were underway from 5,500BP onwards, 1 would be anticipated to arrive following introduction of cultivation and the remaining 2 would be predicted to have arrived only recently, one in association with suburban gardens and the other with plantations of introduced conifers. In other words, the presence in Ireland 5,000 years ago, of nearly all the syrphid species known from Ireland today, would be predicted from the habitats judged to have been present then. That fauna would also be predicted to occur in Ireland now, on the basis of the habitats represented today.

Discussion and conclusions

Is there any necessity to consider the period prior to 5,000BP, in exploring the origins of the present Irish syrphid fauna? Is there reason to suppose that any of the syrphids occurring in Ireland today must have been present in Ireland earlier in the postglacial than 5,000BP, in order to explain their occurrence in Ireland now? If all the Irish species also occur now in other parts of Europe easily accessible to Ireland, the syrphid fauna of Ireland prior to 5,000BP would seem of little relevance to an understanding of the present fauna, since the species would have been readily available to colonise Ireland more recently. Certainly, all but one of the Irish species (*Paragus constrictus*) are known to occur today on the island of Great Britain, the closest land mass to Ireland. Of more relevance would seem to be whether the present Irish fauna could have colonised the island *at all times* during the last 5,000 years. The Irish climate in the period from 5,000BP to the present-day has been characterised by Atlantic conditions sufficiently similar to those occurring now that this period can realistically be taken as a unit, in terms of potential impacts of climate upon fauna. In other words, the syrphid species occurring in adjacent parts of Europe have had a 5,000 year period in which the influence of climate, on the habitats available for colonisation in Ireland, has remained essentially the same, providing plenty of time in which to ensure that the fauna reached a maximal diversity, within the limits imposed by habitat availability. An exception to this generalisation would be the species dependent upon conifer forest habitats, which would be predicted to have been largely lost from Ireland with the disappearance of indigenous *Pinus sylvestris* forest during the last 2000 years, and only able to recolonise the island within the last 200 years, when conifer plantations were established. Table 1 shows that 8 species in the existing Irish syrphid fauna would be predicted to have been affected by this phenomenon.

It can be concluded that there is no need to invoke the existence of glacial refugia or post-glacial land bridges to explain the Irish syrphid fauna, since it could have arrived during the last 5,000 years but is unlikely to have been in place more than 7,000 years ago, long after the refugia or land bridges relied upon by some authors to explain odd components of the Irish flora and fauna (see Mitchell 1986) would have disappeared. But what has happened during the last 5,000 years? Is the prediction procedure used here so insensitive that is cannot differentiate between species that could have arrived 5,000 years ago and others that could only have arrived more recently? It hardly seems realistic to conclude that habitat change occurring in Ireland during the last 5,000 years has not made possible colonisation of the island, by more than a handful of species for which appropriate habitats were absent from the island 5,000 years ago.

Part 2: the degree of similarity between the species lists of Ireland and other parts of Europe

Introduction

The simplistic view of the development of the Irish syrphid fauna during the post-glacial, presented in Pt 1 of this text, omits at least one relevant issue from consideration. Namely, if the existing Irish syrphid fauna can be predicted on the basis of habitat representation and would seem to have had adequate time (the last 5,000 years) in which to colonise the island, are there species associated with those same habitats, and occurring in adjacent parts of Europe, whose presence would also be predicted for Ireland, but which are absent from Ireland. Also, if such species can be identified, how might their absence from Ireland be explained? The first of these two issues is addressed here, in Pt 2 of the text.

Methods

Species lists for many parts of Europe are incorporated into the Range and Status file (Speight et al. 2003) of the StN database. Comparison between these lists and the species list for Ireland (updated to include *Platycheirus aurolateralis* and *P.splendidus*: see Speight et al. 2004) shows how many of the species occurring in Ireland are shared with other parts of Europe. For purposes of the current exercise comparisons have been made between the number of Irish species occurring in each of the various Regions of Europe and in each of several States in the Atlantic Region.

Results

Comparison between species lists, as in Table 2, shows that the present Irish syrphid fauna is shared, almost in its entirety, with other parts of the Atlantic Region and with the Continental Region of Europe. Elsewhere in Europe somewhat smaller numbers of species are shared with Ireland, the smallest numbers of Irish species being shared with the Macaronesian and Meditrerranean Regions. Now that *Cheilosia ahenea* has been discovered to occur on islands offshore of Scotland (Parker 2001), there are no syrphid species known to occur in Ireland that are unknown elsewhere in the Atlantic Region. The one Irish species, *Platycheirus ramsarensis*, missing from the Continental Region, is shared with other parts of the Atlantic Region. And all but one of the Irish species (*Paragus constrictus*) are known from the island of Great Britain.

Discussion and conclusions

Taking number of shared species as a measure of relationship between faunas, the Irish syrphid fauna could as easily have been derived from the Continental Region of Europe as from the Atlantic Region. But, since the Atlantic Region lies, geographically, between Ireland and the Continental Region, it would seem logical to suggest that, for Continental Region species to reach Ireland during the postglacial, they should also have been established somewhere in the Atlantic Region at some point during the

Part of Europe	No IRL spp
Alpine region	163
Atlantic region	179
Continental region	178
Macaronesian region	24
Mediterranean region	110
Northern region	164
Belgium	168
Britain	178
Denmark	165
France NW	145
Netherlands	166
Schleswig-Holstein	150

Tab. 2: the number of syrphid species shared by Ireland and various parts of Europe. – France NW = north-western France, as defined in Speight and Castella (2003); IRL = the island of Ireland.

post-glacial, *en-route*, as it were, to Ireland. This could well provide explanation for the presence in Ireland of the one Continental Region species, *Cheilosia ahenea*, not at present known from other parts of the Atlantic Region except for islands offshore of Scotland. This is an unimproved grassland insect occurring at altitudes of 1000-2000m or more (Speight 2003), in central Europe, which survives in western Ireland today in calcareous dune grassland and limestone pavement areas. Perhaps *C.ahenea* is, indeed, a survivor of early post-glacial range expansion of alpine grassland insects through the Atlantic Region, before forests re-established themselves, remaining in dune grassland in the West of Ireland during the period 9,000 - 5,000BP, while grassland was otherwise largely absent from the island.

A second Irish species that is an exception in terms of its current distribution is *Platycheirus ramsarensis*. This insect is not known from the Continental Region of Europe, or from the Atlantic Region other than in Ireland and Great Britain. Elsewhere it occurs today in the Northern Region, in Scandinavia and the Faroes. Whether *P.ramsarensis* occurs in Siberia or N America is at present unknown – it was described too recently (Goeldlin, Maibach and Speight 1990) to be incorporated into relevant regional faunal revisions. This is an insect of tundra, streamsides and flushes in transition mire, blanket bog and moorland, oligotrophic *Molinia* grassland and open, wet areas within Caledonian forest. It is arguable that *P. ramsarensis* could be a survivor of an early postglacial phase of colonisation of Ireland which, having reached the island from adjacent parts of the Atlantic Region whilst tundra was present, survived in Ireland in a succession of different habitats to the present day, but disappeared from both the rest of the Atlantic Region (except Great Britain) and the Contintal Region during the intervening period. A less exotic explanation for its presence would be that, since it is present in Great Britain (where it is known from Scotland, northern England and Wales), it could have arrived in Ireland at any time during the postglacial that the species was present in Great Britain. Habitat appropriate for *P. ramsarensis* would seem to have been present in Great Britain throughout the post-glacial, so this species could have arrived there early in the post-glacial from some adjacent part of continental Europe now in the Atlantic Region (and now without *P. ramsarensis*), or somewhat later in the post-glacial directly from the Northern Region – its presence in the Faroes indicates it is well able to survive a salt-water crossing without need for any land bridge. So *P. ramsarensis* may have colonised Ireland from Britain at any time during the last 10,000 years – including the last 5,000 years, during which extensive areas of appropriate secondary habitat would have become available to it in both Britain and Ireland, in the form of moorland.

Essentially, then, all but one of the species in the present-day Irish syrphid fauna could be expected to colonise Ireland from adjacent parts of the Atlantic Region of Europe at any time during the last 5,000 years, leaving but one species, *Cheilosia ahenea*, more likely to have arrived earlier in the post-glacial. But whatever may be the explanation for the presence of *C.ahenea* in Ireland it is clear that this species represents an exception. Scenarios developed to explain its presence have to be compatible with scenarios generated to explain the presence of the rest of the Irish syrphid fauna.

The land mass of Great Britain intervenes, geographically, between continental Europe and Ireland, and is closer to Ireland than are other parts of the Atlantic Region. Also, the Irish syrphid fauna shares more species with Great Britain than any other part of Europe. For these reasons the question of whether there are species missing from the Irish fauna would seem most appropriately approached by examining whether there are British syrphid species which would be expected to occur in Ireland on the basis of habitat association, but which are not known from Ireland

Table 3 shows that the part of the Atlantic Region syrphid fauna that would be expected to occur in the habitats represented in Ireland does contain a substantial number of species that have not been found on the island. The Table also shows that 63 of the syrphid species occurring in Britain, but not in Ireland, would be expected to occur in Ireland on the basis of the habitats present, only 19 of the British species being apparently associated with habitats not represented in Ireland. Further, it shows that only one Irish species is unrecorded from Britain.

Essentially then, overall, in Ireland the same habitats support 26% less species than in Great Britain and 39% less species than in adjacent parts of the Atlantic Region in general. Is there reason to suppose that these habitats may be represented in Ireland only in a simplified, or truncated condition, such that they may be able to support only a reduced fauna? Given the long history of man's influence in the Irish landscape, and recognition that this influence has been on a scale sufficient to cause eradication of some habitats and introduction of others, it seems inconceivable that habitats remaining in Ireland today have not been modified by man. Whether the impact of such modifications upon the syrphid fauna can be identified is another question. One approach to this issue is to consider microhabitat occupancy by the species, to establish whether the expected fauna of particular microhabitats is under-represented in comparison with others, and thence whether human influence would be expected to impact upon those microhabitats more than on other microhabitats. Such an exercise has been conducted in Pt 3 of this text.

Tab. 3: the number of syrphid species known from Ireland, Britain and the Atlantic Region in general, together with the number of species from these parts of Europe predicted to occur in present-day Ireland, on the basis of their habitat associations, and the number of predicted species observed in Ireland. – GB = the island of Great Britain; IRL = the island of Ireland.

	IRL spp	GB spp	Atlantic Reg spp
Observed in and predicted for IRL	179	178	178
Predicted for IRL	179	242	293
Total observed	179	261	377

Part 3: differences in microhabitat occupancy levels, between the present day British and Irish syrphid faunas

Introduction

Based on habitat-association data it has been demonstrated in Part 2 of this text that the overall representation of syrphid species in habitats occurring in both Britain and Ireland is noticeably less in Ireland than in Britain. The habitat categories used in that comparison are those employed in the Macrohabitats file of the StN database, themselves based on the CORINE system of habitat classification. As such, each habitat category is a broad concept, usually defined primarily on vegetational characteristics, rather than ecosystem structure. Each habitat can be broken down into a series of structural components, or microhabitats, that identify more exactly the locations occupied by syrphid species, and in particular by their larvae. It is upon these individual structural components, rather than upon the habitat as a whole, that management actions tend to impact (Speight 2000b), with different management practices affecting different components with varying degrees of severity. So an examination of microhabitat occupancy levels, in which the expected fauna of a habitat is compared with its observed fauna, can highlight "underperforming" microhabitats, i.e. microhabitats for which the fauna is under-represented in comparison with other microhabitats in the same habitat. This approach was used by Goeldlin et al. (2003), for example, in identifying ecologically preferable management options in forests in the Swiss Jura. By considering all Irish syrphid species together it is possible to establish whether there are particular microhabitats for which the associated syrphids are generally under-represented, in comparison with others. That has been done here, to identify which Irish microhabitats have the most incomplete species complement and whether there are potential explanations for why these microhabitats might be under-performing.

Methods

Taking the list of Atlantic Region syrphid species predicted to occur in the habitats present in Ireland today (compiled during preparation of Part 1 of this text), plus the observed species lists for Ireland and Great Britain and the StN Microhabitats file (Speight et al. 2003b), lists were prepared of the Atlantic Region, British and Irish species predicted or observed to occur in Britain or Ireland today, in association with each microhabitat. From these lists the proportion of the predicted species observed was calculated, for each microhabitat. These proportions were calculated as percentages, so that, for each microhabitat, the percentage of the predicted Atlantic Region species present in Ireland was established, similarly the percentage of the predicted Atlantic Region species observed in Britain and the percentage of the predicted British species observed in Ireland. The results are presented in tabular form.

Results

Table 4 shows that, for the array of habitats represented in Ireland, an average of 61% of the associated Atlantic Region species occurs in Ireland, but that the percentage of predicted species observed in association with individual microhabitats varies considerably. Similarly, while the average representation of British species in Ireland is 74%, there is again much variation in the representation of species associated with individual microhabitats. The figures for microhabitats for which representation in Ireland of either Atlantic Region species or British species is less than the average, by 9% or more, are shown in bold in the table. Those microhabitats nearly all fall into three groups, and may be listed as follows:

(1) Overmature tree features: rot-holes, insect workings, sap runs, fallen timber, tree-nesting social insects, water-sodden woody debris.

(2) Ground-layer features: grass-root zone, nests of social insects on the ground or in fallen timber, root aphids.

(3) Tissues of herb-layer plants: leaves, stems, stem-bases and bulbs/corms

Discussion and conclusions

Considering first the species associated with overmature tree microhabitats, this same group of species shows (Table 4) under-representation in both Ireland and Great Britain, in comparison to the Atlantic Region fauna, but with a greater proportion of the species lacking in Ireland than in Britain. This suggests that species availability from Great Britain may be limiting the Irish fauna of overmature-tree syrphids, but that factors operating in Ireland have also restricted it further. Under-representation of old-forest insects in Ireland is not limited to the Syrphidae. It has also been noted for buprestid, cerambycid and elaterid beetles (Speight 1988a, 1989) and asilid flies (Speight, 1987).

The very small hectarage to which indigenous forest cover had apparently shrunk in Ireland by the beginning of the 20th century, and the associated virtual eradication of overmature trees within the remaining patches of forest, have already been alluded to, as has been the reality that man was the agent responsible for producing these effects.

So man's activities could offer a plausible explanation for the fact that the group of species associated with overmature tree micro-habitats is one of the most poorly represented components of the present-day Irish syrphid fauna. If so, this would imply not only that the lack of appropriate habitat in Ireland today is limiting the overmature-tree fauna but also that, prior to forest destruction, that fauna would have been better developed, since the syrphid fauna of Irish forest habitats should have been in

Tab. 4: Number of species associated with different microhabitats in Ireland, Britain and the Atlantic Region in general, in the array of habitats occurring in present-day Ireland, and the proportion of the Atlantic Region and British species known in Ireland, for these microhabitats. – Atlant Reg = Atlantic Region; GB = the island of Great Britain; IRL = the island of Ireland.

MICROHABITATS		Predicted species: Atlant Reg	Predicted species: GB	IRL species	% representation of predicted species: GB spp in IRL	% representation of predicted species: Atlant Reg.spp in IRL	% representation of predicted species: Atlant spp in GB
All microhabitats		293	242	179	74	61	83
Trees		110	94	69	73	63	86
Foliage		66	62	49	79	74	94
Overmature/senescent trees		36	24	17	70	**47**	**67**
Mature trees		63	58	43	74	68	92
Understorey trees		54	50	39	78	72	93
Shrubs/bushes/saplings		69	65	52	80	75	94
Upward climbing lianas		8	8	8	100	100	100
Herb layer		113	96	71	74	63	85
On herb layer plants		64	58	46	79	72	91
In herb-layer plants		52	41	28	68	54	79
	in leaves/stems	17	12	8	67	**47**	**71**
	Stem bases	32	28	19	68	59	88
	Bulbs/tubers	16	10	8	80	**50**	**66**
Timber		15	12	10	83	67	80
Standing		7	6	6	100	86	86
Fallen		8	6	4	67	**50**	75
Stumps		15	11	9	82	60	**73**
Ground surface debris		20	20	19	95	95	100
Dung		11	11	11	100	100	100
Litter		9	9	7	78	78	100
Stones		2	2	2	100	100	100
Nests of social insects		10	10	6	**60**	60	100
in trees		2	2	0	**0**	**0**	100
in fallen timber		2	2	1	**50**	**50**	100
ground level		9	9	5	**56**	57	100
Root zone		89	74	53	72	60	83
Rotting tree roots		16	14	13	93	81	88
Grass-root zone		28	25	16	**64**	57	89
With root aphids		20	17	11	**65**	55	85
On/in water plants		25	24	20	84	80	96
Submerged sediment		56	42	35	83	63	75
Fine sediment		34	25	20	80	59	74
Coarse sediment		51	38	32	84	63	75
Water-saturated ground		54	39	33	85	61	**72**
Wet mud/ooze		24	17	15	88	63	**71**
Peat		16	14	13	93	81	88
Sodden plant debris		49	37	31	84	63	76
	timber	7	5	3	**60**	**43**	**71**
	twigs	15	11	7	**64**	**47**	**73**
	non-woody	37	28	25	89	68	76
Soil drainage							
Poorly drained/gleyed		79	68	55	81	70	86
Freely draining		78	65	42	65	54	83
Food type (larvae)							
micro-organisms		116	83	63	76	54	72
	saproxylic	38	27	18	67	**47**	**71**
living plants		51	39	28	72	55	77
living animals		136	123	89	72	65	90

place by 7,000BP and would have been continuously present since then, but for human intervention. The alternative interpretation, that nearly all overmature-tree syrphids never arrived in Ireland during the postglacial, would seem untenable, since species of other forest habitats clearly did arrive. There is certainly some evidence (unfortunately mostly unpublished) that old-forest insects now absent from the Irish fauna were present in Ireland earlier during the postglacial, including the beetle *Prostomis mandibularis* (Caseldine et al. 2001), which is no longer found in either Ireland or Britain. Hammond (1974) lists 11 old-forest beetle species known to have been present in Bronze age Britain but believed to have been eradicated subsequently by man's forest clearance and forest management activity, and points out that this extinction process has to be regarded as still continuing. The direct evidence offered by the remains of this handful of species provides a basis for extrapolation to a more general impact of man's activities on the forest fauna – it can be presumed that many more species have been exterminated than have been found as remains, including old forest syrphids. The scarcity of overmature trees in Britain has led to their maintenance becoming a matter for concern in relation to conservation of invertebrates, as detailed by Read (2000). One might wonder what general basis there is for that author's statement "Britain is of European importance for the large number of old broadleaved trees still surviving here", given the extent to which overmature tree fauna is lacking in Britain. But it could prove true that establishment of a significant resource of overmature trees within deciduous forest in Britain would be of significance to the Irish syrphid fauna, since Great Britain is geographically the closest available source from which old forest species could colonise Ireland. Adjacent parts of continental Europe do not, for the most part, exhibit an under-representation of overmature-tree syrphids associated with the forest types occurring in Ireland (Table 5), so is possible that with appropriate forest management, both in Britain and Ireland, some of those species might eventually re-establish themselves first in Great Britain and then in Ireland. Reemer (pers.comm) has been able to show that there has been a general increase in overmature-tree-associated syrphids in the Netherlands during the last 25 years, and identifies changes in forest management as the reason for this increase.

Tab. 5: number of syrphid species associated with microhabitats of overmature/senescent trees in different parts of the Atlantic Region and the proportion of the Atlantic Region fauna for these microhabitats that is represented in each of these parts of the Atlantic Region. – At.R.= Atlantic Region; B = Belgium; DK = Denmark; F NW= north-western France; NL = The Netherlands; S-H = Schleswig-Holstein.

	Species associated with habitats occurring in Ireland										
	Number of species						As % of Atlantic Region species				
HABITAT COMPONENT/ MICROHABITAT	B	DK	F NW	NL	S-H	At. R.	B	DK	F NW	NL	S-H
All species	252	234	215	252	194	288	88	81	75	88	67
Overmature/senescent tree features	34	25	34	33	21	36	94	**69**	94	92	**58**
trunk cavities	18	14	18	17	11	19	95	**74**	95	89	**58**
rot-holes	19	13	19	19	10	20	95	**65**	95	95	**50**
insect workings	9	6	9	9	5	9	100	**67**	100	100	**56**
sap runs/lesions	20	14	20	20	13	21	95	**67**	95	95	62
Rotting tree roots	16	14	17	15	11	17	94	82	100	88	65

Under-representation of grass-root zone syrphids in Ireland relates almost exclusively to species whose larvae live either with social insects (as scavengers or predators in the nests of wasps, bumble bees or ants) or in a quasi-commensal association with ants (depending to a significant extent upon the "farming" activities of ants, in maintaining root-aphid populations on which the syrphid larvae feed). All of the British grass-root zone syrphids missing from Ireland require well-drained soils and there is a general under-representation in Ireland of syrphids associated with well-drained ground (see Table 4). Except during the last 500 years, when man's land drainage operations have increasingly had an effect, well-drained soils have been scarce in Ireland, other than in coastal dune systems. This is well evidenced from the predominance of gleys, podsolic and peaty soils in soil maps of Ireland (see, for instance, Royal Irish Academy 1979). Introduction of land-surface drainage has not been carried out as an end in itself, but as an aid to human activity, and the areas of well-drained soils now in existence in Ireland are, almost by definition, areas in use for intensive farming. Unimproved grassland on farms on well-drained soils in Ireland is today almost non-existent, with, once again, the exception of dune systems. So, the micro-habitat requirements, of the grass-root zone syrphids missing from Ireland, were probably not provided in Ireland until the latter part of the historic period. The land involved has by now been converted to more intensive use for farming than these syrphids (or the social insects with which they are associated) can survive. None of them would be predicted to survive in intensive grassland. This interpretation thus implies that these species have potentially had much less time in which to establish themselves in Ireland than the bulk of the predicted syrphid fauna of Ireland has had and that conditions are once again generally inappropriate in Ireland for these species to establish there now, albeit for different reasons than earlier in the postglacial. Syrphids are not the only group demonstrating under-representation in Ireland of species associated with well-drained ground. Asilidae (Speight 1987), show a distinct lack of species associated with well-drained grassland (except coastal grassland) in Ireland, when the British and Irish faunas are compared. But whether such species failed to establish themselves in Ireland or established themselves and have subsequently been lost is an open question.

Turning to the question of under-representation in Ireland of British syrphids associated with ground flora, the first point to note is that the syrphid species involved are plant-feeding as larvae. Representation of these species in Ireland contrasts strongly with that of syrphids with predatory larvae living *on* ground flora, which is above average (see Table 4). The British ground flora-associated hoverflies with phytophagous larvae that are absent from Ireland show little evidence that absence is due to lack of host plants, since the plants involved are reasonably frequent in Ireland (see Preston et al. 2002). These latter species, and their known plant hosts, may be listed as follows:

Cheilosia barbata: unknown
Cheilosia fraterna: *Cirsium palustre*
Cheilosia lasiopa: *Plantago lanceolata*
Cheilosia mutabilis: *Hieracium pilosella*

Cheilosia proxima: *Cirsium* spec.
Cheilosia ranunculi: (*Ranunculus bulbosus*)
Cheilosia sahlbergi: unknown
Cheilosia urbana: Hieracium pilosella
Eumerus ornatus: unknown
Eumerus sabulonum: *Jasione montana*
Pelecocera tricincta: unknown

Seven of these species (i.e. most of them) are associated with well-drained, unimproved grassland, and so form part of the group of absentee British species discussed above, in considering the general under-representation in Ireland of syrphids associated with well-drained ground. But the absence from Ireland of the other three species, particularly *Cheilosia fraterna* and *Eumerus ornatus*, does not seem open to explanation through what is currently known about them.

So, it can be argued that forest clearance by man and his domesticated livestock, during the last 5,000 years, has been responsible for under-representation of old-forest syrphid species of deciduous forest habitats in Ireland. Secondly, the late appearance of grassland (other than coastal grassland) in Ireland, and its total dependence upon the grazing activities of farm animals for both its establishment and continued existence (see part 1 of the present text), together with the intensity of its usage over the last 200 years, would seem to have conspired to limit the establishment of grassland-associated syrphid species.

The previous paragraphs suggest that the scarcity of overmature trees and unimproved, well-drained ground in Ireland require to be taken into account in the faunal prediction procedure. Based on this conclusion the habitat-association prediction procedure can be re-run, building in an assumption that there is effectively an absence of both well-drained ground (apart from in limestone pavement and dune systems) and overmature forest in Ireland.

Part 4: re-assessment of the syrphid fauna predicted to occur in Ireland, accommodating habitat modification imposed by human activities

Introduction

In previous parts of this text it was demonstrated that there is good reason to suppose that man's impact on the Irish landscape has not only caused loss of some habitats but also modification to the habitats in existence in Ireland today. It has also been argued that, although the Irish fauna is derived from the syrphid fauna of the Atlantic Region in general, the Atlantic Region syrphid fauna has been "filtered" en route to Ireland, by the land mass of Great Britain, so that the absence from Ireland of Atlantic Region species predicted to occur in Ireland but missing from the British fauna can be expected. It follows that these understandings require to be accommodated in compilation of the list of syrphid species predicted to occur in Ireland at present, in as much as this is possible. In this part of the text the list of species predicted to occur in Ireland is re-compiled, based on the assumptions that overmature forest habitats and unimproved, well-drained grassland habitats are absent due to man's activities and that the British syrphid list provides the species pool from which the Irish syrphid fauna is derived.

Methods

Using the Macrohabitats file (Speight et al. 2003a) in the StN database, a list of the Atlantic Region syrphid species predicted to occur in present-day Ireland was compiled, based on the habitats known to occur in the island. An overview of Irish habitats is provided by Fossitt (2000). This list was then reduced by removal of species occurring only in overmature forest habitats (as opposed to mature or saploing-stage forests) or only in well-drained, unimproved grassland.and then further reduced to British species predicted to occur in Ireland, using the British list incorporated into the StN Range and Status file (Speight and Castella 2003). Restricted in this way, the list of predicted species was then compared with the list of species known to occur in Ireland.

Results

The results of re-running the prediction procedure, with overmature forest species and well-drained grassland species excluded from the prediction, are summarised in Table 6.

Surprisingly few (4) of the syrphid species present in Ireland would not be predicted to occur there, when the faunal prediction is carried out on the basis of availability of this more restricted range of habitats. Those unpredicted species are: *Brachyopa insensilis*, *Brachypalpus laphriformis*, *Cheilosia vicina* and *Doros profuges*. At the same time the observed proportion of the British fauna predicted to occur increases to 83% (from 72%) and the observed proportion of the Atlantic Region fauna predicted to occur increases to 71% (from 62%). The predicted British species whose absence remains unexplained may be listed as follows:

Anasimyia interpuncta, Chalcosyrphus eunotus, Cheilosia fraterna, Cheilosia sahlbergi, Dasysyrphus friuliensis, Didea intermedia*, Epistrophe diaphana, Epistrophe melanostoma, Epistrophella euchroma, Eristalis rupium, Eristalis similis, Eumerus*

Tab. 6: the number of syrphid species known from Ireland, Britain and the Atlantic Region in general, together with the number of species from these parts of Europe predicted to occur in present-day Ireland, on the basis of their habitat associations, and the number of predicted species observed in Ireland, showing the result of re-running the prediction procedure with species of overmature forest and well-drained grassland excluded from the prediction. – GB = the island of Great Britain; IRL = the island of Ireland.

	IRL spp	GB spp	Atlantic Reg spp
Observed in and predicted for IRL	175	174	175
Predicted for IRL	175	212	247

*ornatus, Eupeodes lapponicus**, *Eupeodes lundbecki, Eupeodes nielseni**, *Hammerschmidtia ferruginea, Heringia brevidens, Heringia latitarsis, Heringia pubescens**, *Lejops vittata, Melangyna barbifrons, Melanostoma dubium, Meligramma triangulifera, Neoascia interrupta, Orthonevra brevicornis, Paragus albifrons, Parhelophilus frutetorum, Platycheirus europaeus, Platycheirus melanopsis, Scaeva albomaculata, Sphaerophoria potentillae, Sphaerophoria taeniata, Sphaerophoria virgata, Sphegina sibirica**, *Sphegina verecunda, Triglyphus primus, Xanthogramma pedissequum.*

The 6 species asterisked in the above list can occur in association with conifer plantations, which are present in the Irish landscape today. The conifer-associated syrphids that are known in Ireland can be listed as follows:

Dasysyrphus hilaris, Dasysyrphus pinastri, Didea alneti, Eriozona erratica, Eriozona syrphoides, Parasyrphus annulatus, Parasyrphus lineola, Parasyrphus malinellus, Xylota jakutorum.

With the exception of *Didea alneti*, these species would also be expected to occur in conifer plantations. But no appropriate habitat would have been available to them in Ireland 200 years ago, since the indigenous conifer forest had already disappeared from the island some hundreds of years previously and introduction of conifer plantations had not then commenced.

Discussion and conclusions

The previous paragraphs show that removing species associated with well-drained grassland and overmature forest from the list of predicted Irish syrphid species does achieve a closer approximation to the existing Irish syrphid fauna. The results also draw attention to potential difficulties in predicting the conifer-associated syrphid fauna of Ireland, caused by man's actions in first eradicating indigenous conifer forest and then, very recently, establishing commercial conifer plantations.

Using the recompiled version of the list of predicted species as the basis for comparison the group of conifer forest syrphids present in Ireland amounts to 60% of the British conifer forest species predicted to occur in Ireland, although the overall representation in Ireland of British syrphid species predicted to occur is 83% (Table 4). So representation of conifer species is clearly less than might be expected. Given that the rest of the Irish syrphid fauna appears to have had at least 5,000 years within which to establish in Ireland, while the conifer-associated species have had but 200 years (at most), can the prediction for occurrence of British conifer-associated syrphids in Ireland hold the same force as the prediction for occurrence of the rest of the syrphid fauna? Probably not, especially since some of the British species involved, like *Eriozona syrphoides* and *Sphegina sibirica*, seem to have been present in Britain for less than 100 years (Ball et al. 2000), having arrived there as part of a recent range expansion of certain conifer-plantation hoverflies into western Europe.

It is pointed out above that, without taking man's potential impact on habitats into account, some 60 of the British species predicted to occur in Ireland are absent from

Ireland, but with identifiable manifestations of man's potential influence considered approximately half that number of the expected British species are absent. The reality that the absence of certain species can be identified as probably due to human influence implies that, with better data available on the interaction between individual species and man's landscape management practices, reasons for the absence of further species might become apparent. But, at present, it remains true that the absence from Ireland of approximately half of British species predicted to occur there does not seem open to explanation through effects of human activity.

Considering individually the unexplained absentee British species provides a basis for arguing that predicting the occurrence of 3 of them (*Hammerschmidtia ferruginea, Heringia brevidens* and *Scaeva albomaculata*) in Ireland is inappropriate, i.e. that using habitat-association data alone as a basis for prediction does not adequately take into account the range of information that is available about the species. Thus *Scaeva albomaculata* is included on the British list only as an occasional migrant to SE England, so there is little wisdom in predicting its occurrence in Ireland. Similarly, the known larval host of *Hammerschmidtia* is *Populus tremula*, a tree now excessively rare in Ireland. And *Heringia brevidens* would seem to be particularly associated with *Populus* species, none of which are indigenous to Ireland, except *P. tremula*. But even if a few individual species can be removed from the prediction in this way there remain some 35 British species whose presence would be predicted in Ireland and whose absence remains unaccounted for.

In terms of the existing Irish syrphid list, 35 species would represent an increment of approximately 20% to the fauna, so it has to be said that appropximately 20% of the potential syrphid fauna of Ireland is apparently absent from the island, for reasons that remain unapparent. But is it reasonable to assume that all of the syrphid species present in Ireland have been recorded? If there are grounds for assuming that further inventory work might add species to the Irish syrphid list it follows that British species predicted to occur in Ireland, but as yet unknown there, might be discovered in Ireland as a consequence of further inventory activity.

Part 5: species predicted to occur in present-day Ireland but missing from the Irish list and the role of inventory work

Introduction

In Part 4 of this text it was established that, while impact of man's activities provide plausible explanations for the absence from Ireland of a proportion of the British syrphids predicted to occur in Ireland on the basis of habitat availability, the absence of the majority of these species does not seem open to such explanation.

Syrphid species are currently being added to the British list at a rate of 1 per year (Speight 1988b, 2000c), serving to illustrate the reality that, even in parts of Europe where the syrphid fauna is well-known, increments to local faunas are still occurring and can be expected to continue. Comparison between the syrphid list for Ireland given in Speight et al. (1975) with that for today (this text) shows that syrphids have also been added to the Irish list at a rate of more than 1 per year during the past 25 years. In Part 5 of this text the potential relevance of levels of inventory activity to the issue of species inexplicably absent from Ireland is considered.

Methods

Species added to the Irish syrphid list in the period 1975-2004 have been examined to see if there is reason why they might not have been recorded previously. This resulted in loose groupings of species, based on the probable reasons for their addition to the list being only recent. The first of these groupings comprises species that were either not described prior to 1975 or not adequately recognised as distinct taxa until more recently. The second grouping is of species exhibiting range expansion – essentially species associated with conifer plantations (see Speight 1998, 2000a). The third grouping is of species exhibiting considerable localisation within Ireland (see Speight 2000d). Some of the species in the first group probably belong also in the third group, but their separation from other taxa is so recent as to obscure their range status. Finally, there is a fourth group for which there is no obvious explanation of their late addition to the Irish list.

Results

The syrphid species added to the Irish list in the period 1975-2004 are shown in Table 7. It can be seen that the great majority of the 37 species involved would be judged to fall into one of two categories: either they were not described or adequately defined prior to 1975 or they exhibit a noticeable degree of localisation of occurrence in Ireland. Plotting the distribution in Ireland of all the species regarded as threatened there (see Speight & Castella 2003) produces the result shown in Figure 1, demonstrating that these species are widely scattered round the island, even if also showing some regional concentration of records. The maximum number of threatened syrphid species recorded from any 50km UTM square in Ireland is 12.

Discussion and conclusions

Among the British syrphids predicted to occur in Ireland but not recorded there are some that were not described or adequately defined prior to 1975. But inventory work

Table 7: species added to the list of Syrphidae known from Ireland during the period 1975-2004, categorised to show probable reasons for lack of earlier records. – recent taxon = species either undescribed or inadequately defined, prior to 1975; localisation = species exhibiting localised distribution in Ireland; expansion = species recognised as undergoing range expansion in western Europe; other = species not falling into the other categories.

SYRPHIDAE ADDED TO IRISH LIST 1975-2004	Reason for absence of prior records			
	recent taxon	localisation	expansion	other
Anasimyia contracta	1			
Brachyopa insensilis		1		
Cheilosia ahenea				1
Cheilosia psilophthalma	1	1		
Cheilosia uviformis		1		
Cheilosia vicina		1		
Chrysotoxum cautum		1		
Criorhina ranunculi		1		
Dasysyrphus hilaris	1			
Epistrophe nitidicollis		1		
Eriozona erratica			1	
Eriozona syrphoides			1	
Eumerus funeralis			1	
Helophilus trivittatus		1	1	
Heringia heringi		1		
Meligramma guttata		1		
Microdon analis		1		
Microdon myrmicae	1			
Neoascia obliqua		1		
Paragus constrictus	1			
Parasyrphus lineolus			1	
Parasyrphus nigritarsis		1		
Parasyrphus vittiger				1
Platycheirus amplus	1			
Platycheirus aurolateralis	1			
Platycheirus nielseni	1			
Platycheirus occultus	1			
Platycheirus ramsarensis	1			
Platycheirus splendidus	1			
Portevinia maculata				1
Sphaerophoria batava	1	1		
Sphaerophoria loewi		1		
Sphaerophoria rueppelli		1		
Syrphus rectus	1			
Xylota abiens		1		
Xylota jakutorum	1			
Xylota tarda		1		
	14	18	5	3

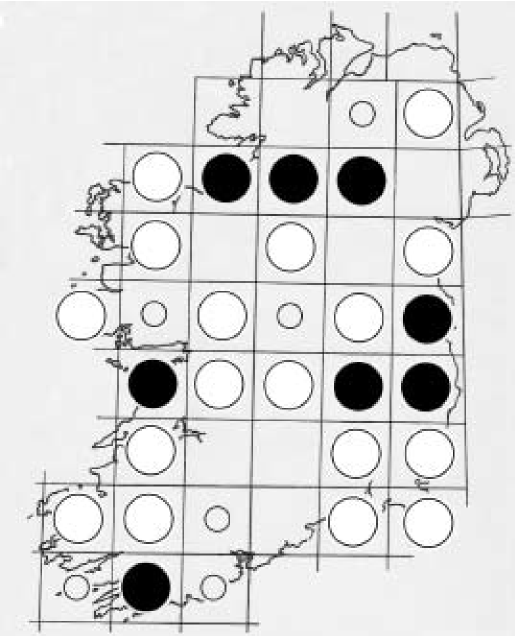

Fig. 1: Distribution of threatened syrphid species in Ireland, shown as a percentage of the species recorded from each 50km UTM square.
– solid black circles: 5% or more of recorded species categorised as threatened in IRL
– large, open circles: 2-4% threatened
– small, open circles: 1% threatened
– blank: no threatened species recorded

on syrphids in Ireland since 1975 has taken such taxa into account and it can be argued that collection effort in Ireland has been adequate to ensure that all of the taxonomically known, common and widely distributed species have been detected (Speight 2000d). But the 33 species that would be categorised as threatened in Ireland (see Speight & Castella 2003) are scattered over 31 of the 48 50km UTM squares that cover the island. Given that syrphids of very local occurrence are still being discovered in Great Britain, that Irish species falling into this category apparently occur in almost any Irish 50km UTM square and that collecting effort in Ireland has been substantially less than in Great Britain, with distinctly less inventory work in some 50km UTM squares than in others (see Speight, 2000d) it seems reasonable to conclude that there are locally occurring species present in Ireland that have not, as yet, been recorded.

Taking into consideration habitat availability, many of the British species predicted to occur in Ireland, but not known there, would be expected to be very localised in Ireland, were they to occur. These species can be listed, as follows:

Anasimyia interpuncta, Chalcosyrphus eunotus, Cheilosia sahlbergi, Epistrophe diaphana, Epistrophella euchroma, Eristalis similis, Eumerus ornatus, Hammerschmidtia ferruginea, Heringia brevidens, Lejops vittata, Melangyna barbifrons, Orthonevra brevicornis, Paragus albifrons, Parhelophilus frutetorum, Sphaerophoria potentillae, Sphaerophoria virgata, Sphegina verecunda, Triglyphus primus .

Taking into account the general landscape character of the least recorded parts of the island (see Speight 2000d) and availability of habitats within them, the following

British species can be highlighted as likely to be found in those parts of Ireland, and likely to be localised in their occurrence:

Anasimyia interpuncta, Neoascia interrupta, Sphaerophoria potentillae, Sphaerophoria taeniata. Sphaerophoria virgata.

Some of the other British syrphids predicted to occur in Ireland, but as yet unrecorded, would fall into the category of species undergoing range expansion in Europe (see Speight 2003). Among them are certain species that appear to have reached Britain only within the last fifty years. They thus form a small group of species that, while now predicted to occur in Ireland, would not have been predicted to do so 50 years ago, because they would only be expected to arrive in Ireland after they had spread through Britain. Indeed, whilst it might be realistic to forecast the arrival of these species in Ireland as imminent, it is perhaps less sound to expect them to be present in Ireland already. The following species are in this group:

Dasysyrphus friuliensis, Eristalis similis, Eupeodes lundbecki. Sphegina sibirica.

The arguments presented above suggest it is most very unlikely that all of the syrphid species currently occurring in Ireland have yet been recorded. It follows that some of the species predicted to occur in present-day Ireland, but not known from the island, may none-the-less be present, but unrecorded. Others, only recently established in Britain, might be expected in Ireland soon. With further collecting effort, especially in under-recorded parts of the island, it would seem that addition of 20 or so of the British species that are as yet unknown in Ireland would be likely during the next 25 years. If all of those species are among the British species currently *predicted* to occur in Ireland, this would account for more than half of the British syrphids whose apparent absence from Ireland cannot at present be explained. This would reduce the number of British species inexplicably absent from Ireland to between 10 and 15. Prominent among the group of species whose absence from Ireland would still remain incomprehensible are *Cheilosia fraterna, Eristalis rupium* and *Melanostoma dubium*.

It can be concluded that the present constitution of the Irish syrphid fauna is largely the product of the interaction between available habitats and the adjacent British species pool over the last 5,000 years, modified by the impact of man's activities throughout that period and by the amount of inventory work that has now been carried out on the Irish fauna. If so, other taxonomic groups should reflect the same influences and it would be interesting if similar investigations could be carried out on other invertebrates, for instance the molluscs, for which databased habitat-association data are also available (see Falkner et al. 2001). In particular, the enigmatic character of the fauna of Irish grasslands demands further examination.

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Appendix: Habitat change in Ireland during the postglacial

The review by Mitchell (1986) shows that the final ice retreat began some 11,000 years ago, leaving behind a tundra landscape.

11,000-7,000 BP: ice retreat to climatic optimum

Forests: As temperatures began to rise, first *Betula/Salix/Populus tremula* and then *Pinus sylvestris* established themselves in Ireland, to produce a sort of taiga accompanied by humid grasslands. These forests were in place 9,500-8,500BP, until continued climatic warming caused their progressive replacement by deciduous forest of *Quercus/Ulmus /Fraxinus*, starting at about 8,500BP (Mitchell 1986). During the period between 9,000 and 7,000BP alluvial forest would also have developed along the major rivers, and swamp forest in areas of impeded drainage.

Open ground habitats: The humid grasslands present in the early post-glacial were apparently progressively obliterated by forest growth as climate warmed. This would have reduced grassland to remaining areas of alpine vegetation on mountains, initially, and climatic climax grasslands would otherwise have been absent from the island. The only other natural grasslands present would be coastal grasslands, maintained by physiographic activity of erosion and deposition of dune systems. Whether the floodplains of major rivers incorporated grasslands at this time is difficult to say. Certainly, the absence of large herbivores other than the reindeer (*Rangifer tarandus*) from the island early in the postglacial (Woodman et al. 1997) ensured that grassland maintained by grazing activity did not occur, so that open areas within forest would have been of short duration. Even smaller herbivores were few in Ireland, during the postglacial, being limited initially to the arctic hare (*Lepus timidus*), which was probably present from 8,000BP onwards (Hayden & Harrington 2000). The wild pig (*Sus scrofa*) is also believed to have arrived around 8,000BP (Woodman et al. 1997). It can be deduced that, in the period 9,000-7,000BP grassland would have been more-or-less lost from the Irish landscape, except in coastal dune systems. Alpine grassland would have disappeared during this period, since the mountains in Ireland are not high enough to sustain this habitat and would progressively have become forested.

Wetlands: The abundance of shallow lakes and pools, left scattered over the Midland plain of Ireland after the ice retreat, quickly developed marginal fens and from at least 9,000BP (Mitchell 1986) many began to in-fill with vegetation. As the accumulation of fen peat rose above the level of influence of the ground water, so these erstwhile lakes became classical raised bogs. While the process of infilling has occurred at different rates, dependent upon size and depth of lake, and can still be seen today, raised bogs were already developed in Ireland by 7,000 years ago (Mitchell 1986) and have continued to develop since.

From the viewpoint of syrphid habitat, bogs and fens are rather large-scale landscape features and the much smaller wetlands provided by springs and flushes can be equally important. With a heavy rainfall and extensive areas of largely impermeable glacial till, springs and flushes were until recently frequent in the Irish landscape and must have been so since early in the post-glacial.

7,000-5,000 BP: the post-glacial climatic optimum

Forests: Once established, the deciduous forests seem to have changed little until approximately 7,000B.P., when areas of *Alnus glutinosa* forest developed, due, it is believed, to an increase in oceanicity of the climate. Around 5,000BP saw the end of the post-glacial climatic optimum, and with it the history of the post-glacial development of Irish forests becomes progressively one of their modification and destruction by human activity. In the case of the karst limestone region of the Burren, in western Ireland, until then covered by *Pinus/Corylus* forest with an admixture of other deciduous trees (Crabtree 1982), forest clearance toward the end of the climatic optimum resulted in rapid soil erosion (Drew 1982, 1983), exposing extensive areas of limestone pavement. The area has remained a predominantly open landscape colonised by thickets of *Corylus* and *Prunus spinosa* scrub to the present day (Jelicic & O'Connell 1992). Huang (2002) demonstrates that, in Connemara, there is chronological association between local forest burning and first evidence of cattle grazing at around 5,050BP, subsequent similar episodes leading progressively to de-forestation by 4,000BP and development of blanket bog, which has covered the region ever since.

Open ground habitats: The Irish landscape during most of the post-glacial climatic optimum is one in which grasslands were virtually absent, there being so few factors to either cause their development or maintain them, at that time. But domesticated cattle are now known to have been present by 5,500BP (Woodman et al. 1999), even though other elements of the neolithic phase of human development may not have been of general occurrence in Ireland until somewhat later. It has to be assumed that the cattle would have maintained open areas of grassland locally, and as much is indicated by pollen diagrams from the period, though these have been variously interpreted (Huang 2002, Mitchell 1986, Molloy 1997, Monk 1993). Prins (1998) points out that a lack of grazing animals prevented grassland development over much of northwestern Europe during the postglacial, until the advent of man's forest clearance activities and the associated cattle – animals like deer evidently do not maintain grassland, since they are primarily browsers.

Wetlands: Development of fen and raised bog seems to have continued unimpeded during this period. In the west of Ireland, the first evidence for localised occurrence of blanket bog dates from 7,000BP, though it is apparently only at the end of the post-glacial climatic optimum (Doyle 1982) that blanket bog became extensive.

5,000 BP to present-day: the neolithic onwards

Forests: The neolithic seems to have developed piecemeal in Ireland, but to have become generally established by 5,000BP (Woodman et al. 1999). From then on Ireland's forest cover – the climax vegetation type for all parts of the island except on the coast and where wetlands intervened – has been progressively eradicated by human activity, entire regions becoming deforested and certain types of forest being entirely lost.

The general occurrence of progressive forest clearance led, at about 1,000BP, to the disappearance of *Pinus sylvestris* forest from Ireland. It is uncertain to what extent other factors were also involved and it is a matter of controversy whether individual pines from the indigenous stock survived here and there in the Irish landscape until recently. But, as a habitat, humid pine forest certainly disappeared from Ireland at some point during the historic period and probably more than 500 years ago, a reality reflected in the Irish fauna (Speight 1985). More recently, lowland *Quercus/Ulmus* forest finally disappeared, again as a consequence of clearance. Remnants of this habitat type persisted until within the last 500 years, though whether any one example would have been sufficiently extensive to maintain much of its characteristic fauna is open to doubt. There is virtually no reference made in literature to the occurrence of alluvial hardwood forest in Ireland and, although there is no reason to suppose this forest type would not have been present along the edges of the flood plains of major rivers, the date of its demise has to remain conjectural. All that can be said is that lack of reference to it suggests it disappeared early, rather than late. Here, it is assumed it disappeared at some point within the last 2,000 years. Alluvial softwood forest associated with large rivers persisted longer, but forest clearance, coupled with land drainage and flood control works, have reduced its occurrence today to one or two sites, where the few hectares remaining provide little other than the evidence that this habitat did once occur on the island. It has to be said that, even when present, softwood alluvial forest must have been of a somewhat truncated nature, since characteristic elements of its composition, such as *Salix alba* and *Populus nigra*, do not seem to have been indigenous to Ireland in the post-glacial. Brook floodplain forest, on the other hand, with small *Salix* species, still occurs.

One difficulty in understanding the recent history of Irish deciduous forest is that authors have focused only on *Quercus*, or at most on *Quercus*, *Fraxinus* and *Ulmus* as forest trees. In particular, *Betula* has been ignored and the extent to which there may have been extensive areas of secondary *Betula* forest within the historic period remains unconsidered. All that can be said is that, by the beginning of the 20th century, the area covered by "oak forest" was reduced to less than 0.5% of the land surface (McCracken 1971).

A consequence of forest clearance has been the development of extensive areas of Atlantic scrub, that have ebbed and flowed across the Irish landscape, with cycles of clearance and abandonment of land locally. But even areas of scrub may have been virtually eradicated during the famine years of the first half of the 19th century – at that time the *Corylus* scrub which is today such a feature of the limestone karst region of the Burren, in western Ireland, was apparently entirely stripped away (Jelicic & O'Connell 1992). While individual thickets have to be regarded as highly transitory in nature, in most parts of Ireland Atlantic scrub is now a more-or-less permanent feature of the countryside, always present somewhere in the vicinity. Prior to the beginning of the 20th century furze (*Ulex*) was a crop grown extensively on farms in Ireland during the historic period, to provide fodder for horses. With the introduction of mechanised transport, fields used for growing furze were either abandoned or converted to other use, as horse numbers dwindled.

The management – or lack of it – to which Irish forests have been subject also has a potentially significant role to play in determining the constitution of their fauna. In the early part of the 19th century the appalling combination of over-population and famine gripped Ireland, with devastating consequences to both the human population and the environment. Today, there is hardly a tree more than 200 years old to be found on the island and certainly no extensive tract of overmature trees of the predominant forest-forming species anywhere. That the recent history of Irish forests may have had a very significant impact upon their fauna is apparent (Speight 1987, 1988a, 1989). Even if forest stands today where it did prior to the famine years, during that time the trees seem to have been stripped from the land surface almost everywhere. Further, whatever coherent management there may have been of deciduous woodland in Ireland prior to the 20th century, during the last hundred years that management has largely been discontinued and it is now difficult to establish even for what purpose the woodlands were once used. Another event of the 19th century with a bearing on the presence of trees in the Irish landscape, was the introduction of the Enclosure Acts, which led to extensive hedge planting for delimitation of properties and individual fields.

During the last 200 years establishment of conifer plantations has been increasingly extensive, using various North American and European tree species. This process accelerated with establishment of the State forest service in the 20th century, which both felled nearly all remaining areas of deciduous woodland at its disposal, converting them to conifer plantation, and initiated programmes of planting conifers into previously unforested ground. These conifer plantations had increased the "forest" cover present in Ireland to in excess of 3%, by the end of the 20th century and it is clear that they are accumulating a syrphid fauna – albeit truncated (Speight 1998, 2000a). The only significant replanting of deciduous woodland occurred in the 19th century. Beech (*Fagus sylvatica*), which is not indigenous to Ireland, became a feature of the Irish countryside during that time. Another recently introduced deciduous tree is the sycamore (*Acer pseudoplatanus*), which has latterly established itself with vigour wherever it had an opportunity to do so.

Open ground habitats: Domesticated sheep (*Ovis aries*) are believed to have appeared in the postglacial Irish landscape some 500 years later than cattle (Woodman et al. 1997), and it seems hardly surprising that the first evidence of forest clearance on a significant scale dates from this same period, 5,500-5,000BP. Red deer (*Cervus elephas*) are believed to have arrived in the island almost a thousand years later, around 4,000BP. So, from at least 5,000BP onwards, there were factors in place to provide circumstances in which both grasslands and heathlands could develop in the Irish landscape and other factors to maintain them once they came into being. The reality that these open expanses were largely man-made is reflected in a resurgence of secondary woodland which occurred a little more than 2,000 years ago, at a time when there is also other evidence for abandonment of farmed land, during a time of social unheaval in Ireland, characterising the transition from the bronze age to the iron age.

The reality that, since their development started some 5,000 years ago, Irish grasslands (except in dune systems) have been dependent upon the grazing activities of domestic stock for their maintenance, aided during the last 1000 years (Hayden & Harrington 2000) by the introduced rabbit (*Oryctolagus cuniculus*), has significance to the associated fauna. Since the grasslands were maintained by grazing, only grazing-tolerant elements of grassland fauna were likely to survive.

In the aftermath of the famine years, subsistence farming gave way to larger production units, the small farms being consolidated into large estate farms, extensive drainage operations and planting of hedges being conducted as part of the process. As elsewhere in western Europe, the 20th century saw one change in farming practice follow another in Ireland and, in the case of grasslands, this meant virtual disappearance of the permanent ley and ever increasing intensities of use. By the end of the 20th century unimproved grassland had virtually disappeared from farms, hay production had largely given way to silage production and removal of more than one grass crop per annum had become the norm, rather than the exception.

Open ground habitats which have remained in place in Ireland throughout the post-glacial, and persist today, are rock, cliff and scree. Active scree has progressively diminished and scree is today mostly vegetation-covered, but from the neolithic period onwards production of stone-built walls has both increased the availability of the bare rock habitat and introduced it into parts of the landscape from which it was previously missing. More recently, quarrying has done likewise.

Wetlands: The last major phase of wetland formation in Ireland was precipitated by the ice retreat, the geomorphological processes of that time leaving behind land forms ideal for colonisation by wetland organisms. But the resultant fens and raised bogs are vulnerable to land drainage carried out by man and, since the processes that gave rise to them no longer operate, they today become progressively rarer as drainage and exploitation continues. The only natural agency actively creating wetlands in the Irish landscape during most of the post-glacial period have been the rivers, which have constantly renewed wetlands on their floodplains, through intermittent changes in their channels and seasonal flooding. Flood control works have now largely brought this process to an end.

Blanket bogs appear to be the most recent type of wetland to develop in Ireland, their formation dating generally from the period of climatic deterioration that followed the post-glacial climatic optimum, though there is evidence for their more local occurrence earlier (Doyle 1982). In areas of western Ireland with poor soils, there are instances of neolithic farming activity occurring where blanket bog is found today (Mitchell 1986). This farming activity is believed to have given rise to leaching of soil minerals and podsolisation, and the farms were abandoned as the climate deteriorated, the combination of impermeable soils and high rainfall then causing them to became overwhelmed by bog growth. Huang (2002) presents comprehensive evidence for blanket bog developmnent in Connemara by 4000BP, mediated by forest burning (by man) and livestock grazing over the preceding 1,000 years. Indeed, as better information becomes available, this model of man-mediated generation of blanket bog would seem to explain its origin in general, in Ireland.

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