

Scotland's Rural College

Moth responses to forest-to-bog restoration

Pravia, A; Andersen, R; Artz, R R E; Boyd, K; Cowie, N R; Littlewood, N A

Published in:
Mires and Peat

DOI:
[10.19189/MaP.2019.OMB.StA.1787](https://doi.org/10.19189/MaP.2019.OMB.StA.1787)

First published: 21/12/2020

Document Version
Publisher's PDF, also known as Version of record

[Link to publication](#)

Citation for published version (APA):

Pravia, A., Andersen, R., Artz, R. R. E., Boyd, K., Cowie, N. R., & Littlewood, N. A. (2020). Moth responses to forest-to-bog restoration. *Mires and Peat*, 26, Article 27. Advance online publication. <https://doi.org/10.19189/MaP.2019.OMB.StA.1787>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Moth responses to forest-to-bog restoration

A. Pravia^{1,2}, R. Andersen¹, R.R.E. Artz², K. Boyd¹, N.R. Cowie³, N.A. Littlewood^{2,4}

¹ Environmental Research Institute, University of the Highlands and Islands, Thurso, UK

² James Hutton Institute, Craigiebuckler, Aberdeen, UK

³ RSPB Scotland, Edinburgh, UK

⁴ Department of Rural Land Use, SRUC North Faculty, SRUC Aberdeen, Bucksburn, Aberdeen, UK

SUMMARY

The responses of peatland invertebrates to land use changes and associated effects of peatland degradation are not well known, particularly for diverse and species-rich taxa such as moths. We investigated broad patterns of distribution in moth communities during the restoration of formerly afforested blanket bog, as well as their degree of habitat affinity (tyrphophilia). Thus, we examined the response of moth communities to peatland management across a restoration chronosequence and used information about species traits to explain the species' responses to restoration (trait syndromes). A clear shift towards open habitat moth species and away from specialist forest species took place following tree felling, and the moth communities of restoration treatments resembled the bog community within a few years following onset of restoration. Interestingly, species traditionally considered tyrphobionts (bog specialists) were not restricted to core bog habitats. Trait syndromes were identified for each treatment, highlighting the importance of phylogenetic, phenological and ecological performance traits linked mainly to species microhabitat selection, resource use and dispersal capability. The restoration of afforested blanket bog opens up the habitat for the recolonisation of bog-inhabiting moth species, mediated by species functional traits. However, a better understanding of moth functional traits, especially linked to moth ecology (including habitat preferences), is needed to aid understanding of the relationship between restoration trajectory, species traits and blanket bog habitat.

KEY WORDS: afforestation, blanket bog, functional traits, Lepidoptera, peatland

INTRODUCTION

Peatland fauna can display varying degrees of affinity with bog habitats (Peus 1928, Spitzer & Danks 2006). Tyrphobionts are specialised species that are found only in core peatland habitat while tyrphophiles are found mainly in core peatland but also in adjacent habitats. Tyrphoneutrals, on the other hand, show varying degrees of affinity with peatland but are often also found in other types of habitats (Mikkola & Spitzer 1983, Spitzer *et al.* 1999). However, the same species can display geographical differences in bog affinity (Spitzer & Danks 2006), particularly when latitude and altitude are taken into account (Mikkola & Spitzer 1983). There is evidence that, in central and eastern Europe, anthropogenic influence may reduce the abundances of tyrphobionts in favour of tyrphophile and tyrphoneutral species, with tyrphobiont species utilising bog remnants as refugia (Spitzer *et al.* 1999, Spitzer & Danks 2006). To date, however, such studies are lacking in the UK

and the tyrphophilia of many peatland species is not well known.

Tyrphobiont insects can face constraints that may be associated with stable habitats, such as having poor dispersal ability (e.g. the carabid beetle *Agonum ericeti*; de Vries & den Boer 1990). Thus, land-use changes and associated effects of peatland degradation, such as drainage and habitat fragmentation, may lead to replacement of these species (Vepsäläinen *et al.* 2000). Despite the often species-poor nature of peat bog faunas (Desrochers & van Duinen 2006, Batzer & Boix 2016), insects tend to be the most abundant and well-adapted animal inhabitants of bog, with more tyrphobiont species observed in some flying insect groups (such as butterflies) than amongst predominantly non-flying insects (Spitzer & Danks 2006). Amongst flying insects, fewer macro moth species are associated with blanket bog habitats than with other British habitats (e.g. Waring & Townsend 2009). Moth assemblages specifically associated with bogs in Europe are

composed of a large proportion of tyrphobiont and tyrphophile species with a relatively high proportion being stenotopic, i.e. able to tolerate a only narrow range of environmental change (Bezďek *et al.* 2006). Such strong habitat affinity facilitates the use of moths as indicators of peatland quality (Spitzer & Jaroš 1993, Spitzer *et al.* 1999, Dapkus 2000) and habitat stability (Bezďek *et al.* 2006), and thus potentially as targets by which to assess progress towards a desired state following restoration intervention.

In the UK, where moth populations have been systematically monitored since 1968, alarming declines in overall abundances have been identified in the southern half of the country, even within common and widespread species (Fox 2013). However, in the north of the UK, almost as many species have shown an increase in abundance as have decreased between 1968 and 2002 (Conrad *et al.* 2006). More recent research on Scottish moth data has revealed signs of both abundance declines and range expansions (Dennis *et al.* 2019). Overall, though, severely declining trends in moth populations have been observed in recent decades, primarily driven by land-use changes resulting in habitat fragmentation, degradation and loss as well as by climate change (Fox 2013, Fox *et al.* 2014). Studies of moth abundance and diversity have been conducted primarily in grasslands, agricultural land and broadleaf woodlands, with few investigating the effects of widespread coniferous plantation which is one of the main degrading agents for Scottish blanket bogs (Warren 2000). For the UK, a single study outlines negative effects of extensive conifer planting on moth populations, acting through changes to the habitat and loss of food resources (Ramchunder *et al.* 2009). Elsewhere, there is evidence that timber extraction may disrupt moth communities in native forests in the United States (e.g. Summerville & Crist 2002, Summerville 2014). In commercially managed non-native conifer plantations, clear-felling practices, as opposed to continuous forest cover, have demonstrable negative effects on moth species richness, abundance and diversity (Kirkpatrick 2016). To the best of our knowledge, however, there is a lack of studies investigating moth responses to felling of non-native conifer plantations on peatlands and formerly afforested peat bogs and, especially, concomitant recovery of peatland-associated moth fauna.

In this study we investigated broad patterns among moth communities in response to the restoration of a formerly afforested blanket bog, and the degree of habitat affinity (tyrphophilia) displayed by moth species. Specifically, we aimed to:

- 1) quantify changes in moth communities across a restoration chronosequence; and
- 2) identify key trait-habitat associations (trait syndromes). We hypothesised that: 1) moth communities will exhibit a non-linear temporal restoration trajectory, with a reduction of closed-habitat species and an increase of open-habitat species, as trees are felled and vegetation succession progresses; 2) regardless of the trajectory observed, tyrphobiont species will occur only in undamaged blanket bog habitats; and 3) moth assemblages associated with different successional stages will consist of species exhibiting trait syndromes related to habitat preference (degree of habitat openness) and types of vegetation available, as moths are intimately linked to host foodplants.

METHODS

Study site

This research took place at RSPB (Royal Society for the Protection of Birds) Forsinard Flows, a 154 km² National Nature Reserve (NNR) in the heart of the Flow Country (latitude 58.357, longitude -3.897), northern Scotland, UK. Following extensive planting of Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) (both non-native conifers) in the 1980s, restoration efforts since 1997 have created a chronosequence of restoration areas amongst residual open unmodified blanket bog and remaining forestry plantations on peat (Wilkie & Mayhew 2003, Hancock *et al.* 2018). Briefly, the restoration management involved various combinations of mechanical tree felling and harvesting, coupled with drain blocking ('fell-to-waste' management).

Study design

A chronosequence of restoration stages was sampled, encompassing a total of 13 restoration age classes (years since tree-felling) across the study area in a space-for-time substitution, as well as the established forest (starting state) and open blanket bog (target state) (Table 1). During the study period, restoration progressed to include further management actions such as brash crushing and furrow blocking in some felled areas. Due to these ongoing reserve management works, the same sites could not all be re-sampled each year, reducing the pool of sites available over the course of this study. Thus, the overall number of trapping nights per restoration age class varied. When interpreting the results, the age classes were aggregated into two categories: younger restoration (R3–R9, the number indicating years since tree felling at time of sampling, 38 replicates); and older restoration (R10–R18, 38 replicates).

Table 1. Experimental design for moth trapping at Forsinard. Bog, forestry and restoration treatments were simultaneously sampled over four consecutive years between July and August 2013–2016. Age class represents time in years since restoration began. Age classes in bold indicate older restoration sites.

Year	Treatment	Age class	No. samples
2013	Bog	-	18
	Forestry	-	18
	Restoration	R3	3
		R7	8
		R8	4
		R9	8
		R10	8
R11	2		
R15	3		
2014	Bog	-	17
	Forestry	-	16
	Restoration	R4	2
		R8	7
		R9	4
		R10	8
		R11	6
R12	2		
R16	2		
2015	Bog	-	10
	Forestry	-	10
	Restoration	R5	2
		R9	5
		R10	2
R12	1		
2016	Bog	-	7
	Forestry	-	7
	Restoration	R11	3
		R12	1
		R13	2
R18	1		

Moth sampling

Moths were sampled using Skinner moth traps, each fitted with a 15W horizontally mounted actinic bulb and a solar switch that activated the light as darkness fell (Anglian Lepidopterist Supplies, Norfolk, UK). Traps were powered by sealed lead acid batteries. Moth traps sampled relative moth activity during July and August in 2013 (15 nights), 2014 (15 nights), 2015 (10 nights) and 2016 (7 nights). Moth relative activity, referred to here as ‘abundance’, represented the total number of individual macro moths trapped in a single trap per night. Traps operated simultaneously from dusk to dawn in restoration, forestry and open blanket bog plots, at least 50 m from habitat boundaries. In 2013 and 2014, four traps were set each night (one in bog, two in different restoration plots and one in forestry), whereas in 2015 and 2016 only one trap was set for each treatment. Traps were set 170 times in total, over 47 trapping nights. Some sites were sampled more than once over the years, but not on consecutive nights. Only macro moths were counted and identified, following Townsend *et al.* (2010), Waring & Townsend (2009) and Manley (2015). All macro moths were used in data analyses, with the exception of pugs (F. Geometridae, SbF. Larentiinae), which were not always reliably identified to species.

Selection of moth functional traits

Moth functional traits (FTs) thought likely to influence species distribution and habitat affinity (e.g. dispersal, phenology, resource use) were taken from Waring & Townsend (2009), Manley (2015) and Money (2017) (Table 2). Moth traits were selected *a priori* (e.g. Spake *et al.* 2016), and included traits relating to morphology, phenology, physiology and ecological performance, referred to as the M-P-P-E functional framework (Fountain-Jones *et al.* 2014). Where possible, trait values specific to Scottish moths were used, but information on host plants used by moths was guided by British sources (Robinson *et al.* 2010).

Data analysis

All statistical analyses were performed with R v3.4.1 (R Core Team 2017). Principal response curves (PRC), a form of redundancy analysis focusing on the interaction between time and treatment (van den Brink & ter Braak 1999), were used to evaluate the restoration trajectory of moth assemblages in restoration blocks of different age classes. Although PRCs were initially developed for time series, they have since been applied in other contexts including testing of treatment effects in space-for-time substitution (e.g. Gaffney *et al.* 2018), line-transect

Table 2. Functional traits of Scottish moths used in the calculation of community weighted means.

Code	Functional trait	Fitness links
Morphological		
WS	Wingspan	Dispersal capability
FW	Forewing length	Dispersal capability
Phylogenetic		
F	Family (Ereb = Erebidae; Geom = Geometridae; Hep = Hepialidae; Las = Lasiocampidae; Noc = Noctuidae)	Dispersal Capability
SbF	SubFamily (En = Ennominae; Had = Hadeninae; He = Hepialinae; Hy = Hypenodinae; Lar = Larentiinae; Noc = Noctuidae; Pin = Pinarinae; Plu = Plusiinae; Xyl = Xyleninae)	Dispersal Resource Use
Phenological		
O	Larval Overwintering (egg; larva; pupa; absent)	Microhabitat Use Resource Use
LF	Larval Feeding Period (SP = Spring; SU.SP = Summer–Spring; SU = Summer; SP.AU = Spring–Autumn; SP.SU = Spring–Summer; AU.SP = Autumn–Spring; AU.SU = Autumn–Summer)	Microhabitat Use Resource Use
AF	Adult Flying Period (SU = Summer; SU.AU = Summer–Autumn; SP.SU = Spring–Summer; SP.AU = Spring–Autumn)	Habitat Use Resource Use
HF	Host Plant Family (Bet.Eri = Betulaceae-Ericaceae; Camp = Campanulaceae; Cap.Urt = Caprifoliaceae-Urticaceae; Cruc = Cruciferae; Cyp.Gram = Cyperaceae-Gramineae; Cyp.Jun = Cyperaceae-Juncaceae; Den = Dennstaedtiaceae; Eri = Ericaceae; Eri.Ros = Ericaceae-Rosaceae; Fil.Den = Filicopsida-Dennstaedtiaceae; Gram = Gramineae; Gram.Jun = Gramineae-Juncaceae; Gut = Guttiferae; Lab = Labiatae; Pin = Pinaceae; Pin.Fag = Pinaceae-Fagaceae; Poly = Polyphagous; Ros = Rosaceae; Rub = Rubiaceae; Rub.Prim = Rubiaceae-Primulaceae; Sal.Bet = Salicaceae-Betulaceae; Sal.Eri = Salicaceae-Ericaceae; Scro = Schrophulariaceae)	Resource Use Habitat Use
Ecological performance		
D	Distribution (common; local; scarce)	Vulnerability
HP	Habitat Preference (bog; open habitat; open & closed habitat; conifer; woodland)	Microhabitat Use

datasets (Heegaard & Vandvik 2004), and testing the effect of treatment over spatial structures (Auber *et al.* 2017). Our data included both real time series (sites which were visited in successive years) and space-for-time substitution (sites which were visited only once but were of various ages) elements. In this case, the underlying assumption for the PRC is that spatial and temporal variation are equivalent and can be used to create the interaction between treatment and time (explanatory variable). Open blanket bog sites were classified as the target state (baseline), whilst forestry sites were classified as the first point of the restoration trajectory ($t=0$ years since restoration), and all restoration age classes (R3, R4, R5, R7, R8, R9, R10, R11, R12, R13, R15, R16 and R18, with the number indicating years since tree-felling - although follow-up management such as ditch blocking was sometimes carried out in subsequent years) were the response treatments over time. Sample sites were classified each year according to their age, e.g. an R3 site in 2013 was an R4 site in 2014. The significance of the PRC axes was assessed by a Monte Carlo test with 999 permutations (ter Braak & Šmilauer 2002), where permutations were blocked by age class (i.e. whole age class groups were permuted instead of individual traps) to account for the fact that some sites were visited more than once. The response variables were log transformed and the resulting species scores displayed on the PRC diagram, reflecting the influence of particular species on the overall moth community response described by the PRC trend line. The strength and sign of the species scores indicates the magnitude of the changes in abundance relative to the baseline, whereby species with high positive scores (>0.5) follow the same trend as the PRC line; whilst negative scores (<-0.5) follow the opposite trend. Species with near-zero values do not follow the same temporal patterns (ter Braak & Šmilauer 2002).

Redundancy analysis (RDA) was used to explore the relationship between moth communities, species FTs and aggregated restoration age classes using the *vegan* (Oksanen *et al.* 2017) package. Julian day and distance to remaining standing plantation forest were analysed as potential covariates. Separate ordinations of each covariate explained significant proportions of variation in the data (Julian day: $F=17.53$, $p=0.001$; distance to forestry: $F=8.06$, $p=0.001$). However, a partial ordination showed that more variation was explained by Julian day alone than by both variables combined, and thus only Julian day was used as a covariate in final analyses. Community weighted means (CWMs; Petchey & Gaston 2006), a metric of functional community composition that represents the diversity of traits present in a community,

weighted by species relative abundances, were also used in RDA. The CWMs were calculated with the *FD* package (Laliberté *et al.* 2014). Categorical FTs were fuzzy coded following Chevene *et al.* (1994).

RESULTS

The dataset contains a total of 4,387 recorded macro moths (2,311 in 2013, 859 in 2014, 518 in 2015 and 699 in 2016) belonging to five different families (Table A1). Of the 64 macro moth species recorded, the most abundant (by a great margin) was *Hylaea fasciaria* (1,383 individuals), followed by *Diarsia mendica* (438 individuals), *Lycophotia porphyrea* (424 individuals) and *Diarsia rubi* (227 individuals). *D. mendica*, *L. porphyrea*, *Apamea monoglypha*, *H. fasciaria*, *D. rubi* and *Xestia xanthographa* each occurred in more than 25 % of the trap samples. All other moths were recorded in numbers below 200 individuals, and 10 species were recorded only once. According to known species habitat preferences, there were twelve candidate tyrphobiont or tyrphophylic species amongst the species sampled (Table A2), many of which were recorded in low numbers. These species were: *L. porphyrea*, *Photedes minima*, *Xestia sexstrigata*, *Schrankia costaestrigalis*, *Eulithis populata*, *Apamea exulis*, *Xestia castanea*, *Oligia fasciuncula*, *Carsia sororiata*, *Plusia putnami*, *Amphipoea lucens* and *Celaena haworthii*.

Restoration trajectory

Moth community composition differed between the forestry plantation ($t=0$, forestry) and the bog baseline (Figure 1; RDA 1 = 24.1 %; $F=28.2$; $p=0.001$). The moth communities of younger restoration treatments (R3–R9) resembled the bog community within a few years following onset of restoration (R3), despite some oscillation suggesting that differences in species composition persisted between sites of different restoration ages and the bog references. Older restoration (R10–R18) moth communities were generally more similar (closer to the bog baseline) and less variable (fewer ‘fluctuations’) than those of younger treatments. When looking at species scores, *L. porphyrea* (tyrphophilia) is the only species that stands out as being consistently more prevalent in bog than in forested or restoration areas (i.e. PRC score <-0.5), but this species also increased in the latter, particularly in older sites. On the other hand, abundances of *H. fasciaria*, *C. pectinataria* and *Abraxas grossulariata* were highest in forested areas and decreased sharply following tree removal. While

other species have changed in abundance across the chronosequence, the results from the PRC suggest that they followed a different overall trend.

Relationship between CWMs and treatment

Some moth species showed specific habitat preferences (Figure 2a). Whilst *H. fasciaria* was clearly associated with forestry, other species were more loosely associated with this type of habitat (e.g. *C. pectinataria*, *Cerapteryx graminis*, *Entephria caesiata*). A small collection of species (*X. xanthographa*, *Xanthorhoe decoloraria*, *D. mendica*, *D. rubi* and *C. haworthii*) showed a higher affinity to both younger and older restoration treatments than to open blanket bog, and only one species, *L. porphyrea*, was most closely associated with open blanket bog.

The trait syndromes identified in bog mainly highlighted species preference for habitat openness, phylogeny and vegetation composition (Figure 2b). Blanket bog trait syndromes were characterised by host plants mainly belonging to the Ericaceae family (among which *Erica tetralix* and *Calluna vulgaris* were the most common in the study area), which are the only feeding resource for the larvae of species such as *L. porphyrea* and *Anarta myrtilli*. The moth communities observed in older restoration treatments

were predominantly dissimilar to those of open blanket bog but highly similar to those in younger restoration sites. Older restoration sites and open bog were characterised by larger species belonging to the family Noctuidae, subfamily Noctuinae (with more numerous species including *X. xanthographa*, *X. baja*, *L. porphyrea*). Younger and older restoration treatments displayed CWMs for species occurring in both open and closed habitats. These were primarily noctuid moths from the subfamily Xylenidae, such as *Photedes minima* and *A. exulis*, which feed on a wide range of graminoid plants; as well as moths such as *C. haworthii* which feed on Cyperaceae sedges (e.g. *Eriophorum vaginatum*, *Eriophorum angustifolium*, *Trichophorum cespitosum*) and rushes (Juncaceae, e.g. *Juncus* spp.). Lastly, the moths of forestry habitats included members of the family Geometridae, subfamily Ennominae (e.g. *H. fasciaria*, *C. pectinataria*, *A. grossulariata*) and subfamily Larentiinae (e.g. *G. pyraliata*, *Epirrhoe alternata*, *Dysstroma citrata*). These species exhibited trait syndromes based on phylogenetic relationships and host plant family. Some of them feed primarily on coniferous trees such as *Picea sitchensis* and *Pinus contorta*, while others use different foodplants which are apparently favoured by the forest environment.

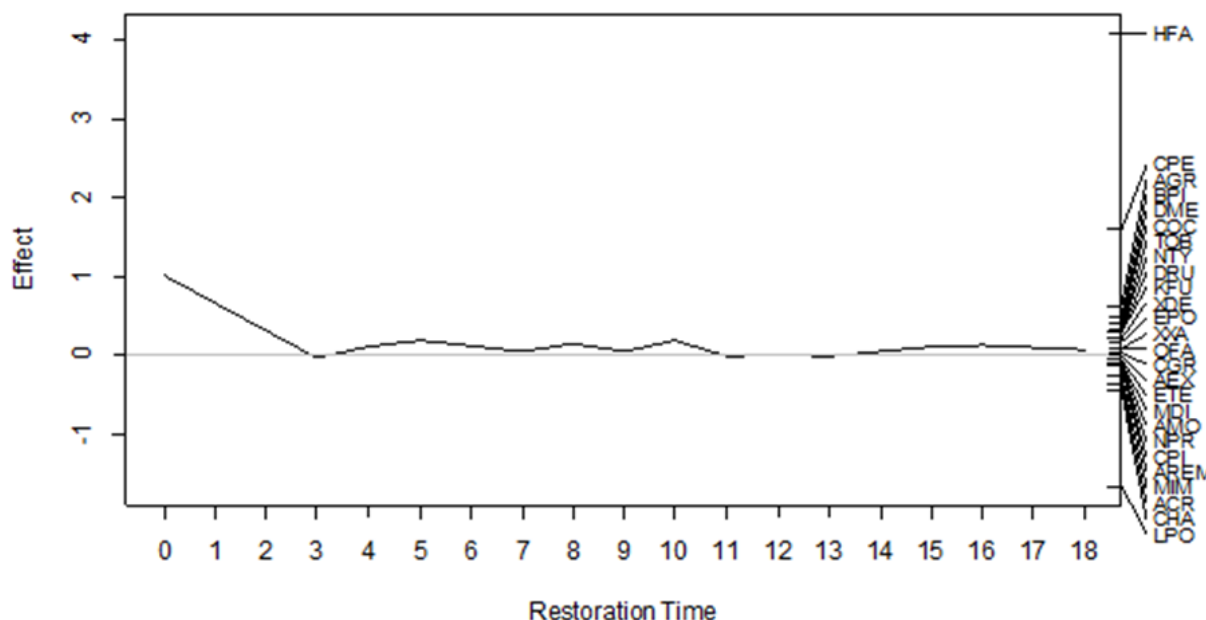


Figure 1. Principal Response Curve (PRC) for the restoration trajectory of moth assemblages. The Y axis represents the PRC scores at each restoration age class; the X axis represents the time (in years) since restoration began. Open blanket bog (baseline) is the grey line; restoration is the solid black line (hidden behind bog baseline when values overlap); forestry (unfelled conifer plantations) is the first point of restoration ($t=0$). With bog as the baseline, species above 0.5 on the Y axis display strong affinity with restoration treatments, whereas species below 0.5 display strong affinity with bog treatments. Only best fitting species are shown (species weight >0.5). Species names are provided in Table A1.

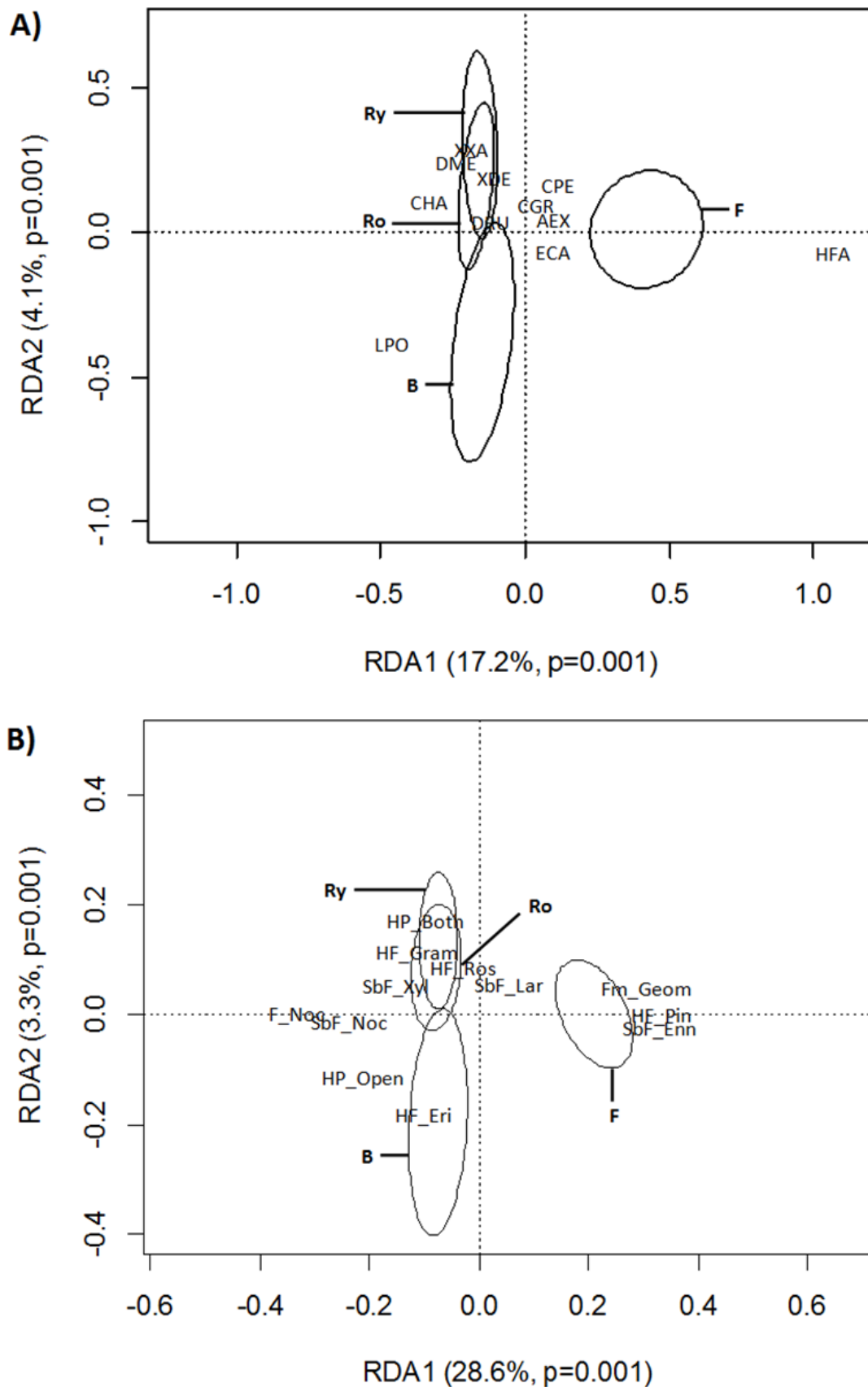


Figure 2. A) Redundancy Analysis (RDA) diagram for moth communities. B) RDA diagram for moth Community Weighted Means (CWMs). Treatments: F = forestry; B = bog; Ro = older restoration; Ry = younger restoration. Functional traits and species code names are shown in Tables A1 and A2.

DISCUSSION

Trajectory of moth communities following forest-to-bog restoration

The use of a space-for-time substitution method has a number of limitations that require consideration when interpreting results. In our case, as articulated above, the PRC datasets included both real time-series and space-for-time substitution elements, which assume that temporal and spatial changes are equal, but this assumption is not entirely valid. For instance, in this study the starting point for each of the sites was different. The first restoration attempts were conducted when trees were relatively small (canopy open, cut by chainsaw), while later restoration sites had closed canopy plantations and were felled with specialised low ground pressure machinery. Thus, it might be expected that sites restored earlier (old restoration sites) will come to resemble bog habitats in a shorter time after tree removal than will later (young) restoration sites and so this may, in effect, lengthen the time period represented by the chronosequence. Recent vegetation analyses have shown that plant communities in felled-to-waste sites shifted towards those of open bog following restoration, but some typical bog species - including *Sphagnum* spp. - did not return to similar cover classes or returned only in wetter micro-sites, effectively “stalling” restoration progress (Hancock *et al.* 2018). While acknowledging this, we can be confident that the effect of restoration (i.e. tree removal) is genuine, as the moth communities converge rapidly through replacement of tree-associated species with those of open habitats, despite younger sites being more disturbed than older sites.

The results support our first hypothesis, as a non-linear restoration trajectory was observed for moth communities. Following initial restoration management, we observed a rapid reduction (but not absence) of closed-habitat species such as *H. fasciaria* and a subsequent increase in open-habitat species associated with newly establishing vegetation. Indeed, our study showed a clear forest-to-bog restoration gradient, likely due to the strong association of moth communities with vegetation structure and composition (Kremen *et al.* 1993, New *et al.* 1995). Commercial forestry plantations have dense canopies that can negatively affect their biodiversity (Humphrey *et al.* 1999), and they tend to harbour a less developed understorey than do natural forests as a result of site preparation and silvicultural practices (Aubin *et al.* 2008). Thus, forestry plantations lack the food and host plants needed by many open habitat moth species. In our study, both

younger and older restoration treatments supported similar moth communities comprising species of conifer, open ground and generalist habitats. These include *X. xanthographa*, *D. mendica*, *Xanthorhoe designata* and *C. haworthii*. Whilst the latter is a specialist of peat bogs in Central and Eastern Europe (Spitzer & Danks 2006), in the UK it occupies a wider range of habitats including moors and marshes (e.g. Waring & Townsend 2009). The relative abundances of these species at our field sites suggest that they might behave as tyrphophile and/or tyrphoneutral species, not restricted to core bog habitats and often increasing in abundance after disturbance to the detriment of tyrphobiont species (c.f. Spitzer & Danks 2006). In conifer plantations on mineral soils, the presence of a large proportion of habitat generalist moths has been linked to felling practices, as these species can rapidly colonise newly opened niches (Kirkpatrick 2016). Therefore, the increase of habitat generalists in restoration plots in our study area might have been prompted by the initial tree felling. This offers further support for the idea that habitat specialists are more sensitive to disturbance than are habitat generalists, and that peatland restoration could therefore lead to positive changes for specialist species over time (Noreika *et al.* 2016).

Rapid recovery of moth assemblages has previously been observed in the restoration of forested boreal mires in Finland, where ditch infilling and partial tree removal led to a positive response by tyrphobiont moths to increased *Sphagnum* cover and reduced numbers of tall trees (Noreika *et al.* 2015). In comparison with these Finnish pine mires, where sparsely forested or open sites were drained in the 1960s and 1970s to increase forest cover and timber yield, Forsinard experienced more radical habitat change involving ploughing and large-scale planting of exotic conifers on completely open blanket bog.

It may be that some of the key restoration thresholds for moth communities are linked to habitat connectivity and plant diversity, since moth life cycles are strongly linked to their larval host plants and adult nectaring resources. However, the limited vegetation and environmental data available for this experiment prevent us from identifying these thresholds clearly and this should be addressed in future studies of moth communities in these changing landscapes. Nevertheless, the rapid shift in moth communities seen following tree removal suggests that the degree of habitat fragmentation and habitat quality (Fahrig 2003), perhaps acting in combination with functional traits of moths in the vicinity (Nichols *et al.* 2013), could be more important determining factors than time in the recovery of moth

communities typical of open blanket bog.

The landscape matrix of open bog -restoration-forestry found at Forsinard, and the internal patch configuration of near-natural blanket bog (macro- to microtopo level; Lindsay *et al.* 1988), are likely to influence the composition of moth assemblages. Indeed, peatland taxa are often distributed across marked ecological gradients, e.g. of moisture and vegetation (Desrochers & van Duinen 2006). These gradients are disrupted as afforestation fragments core peatland and mire margin habitats, as well as peatland macrotopes overall. In turn, this potentially affects the microhabitat diversity associated with microtopographical features (hummocks, hollows, lawns, pools, etc.), which frequently increases with the size of the peatland (e.g. Nilsson 1986, Calmé & Desrochers 2000). Such disruption to microhabitat diversity may reduce the resilience of populations of moth species that require persistence of precise suites of conditions within a certain proximity. Therefore, the recovery of microtopographical features and microhabitats may be necessary for these species to recover.

In blanket bogs, microtopographical features are formed by distinct vegetation assemblages composed primarily of *Sphagnum* species (Lindsay 1988). A recent study at Forsinard Flows NNR showed that, following a rapid shift in habitat conditions after forest removal, fell-to-waste restoration failed to recreate the diversity of microhabitats found in open blanket bog; largely because, even after 18 years, the peat remained too dry for typical bog species like *Sphagnum* to re-establish, especially on slopes and plough throws (Hancock *et al.* 2018). Similar forestry legacy effects have been reported for water quality (Gaffney *et al.* 2018), testate amoebae (Creevy *et al.* 2018) and even plant traits (Konings *et al.* 2019). Thus, our findings contribute to an ever-growing body of evidence. The rapid initial shift observed in the moth community comes in response to the initial removal of conifer trees, but the shortcomings in the recovery indicate that legacy effects are persistent, preventing the re-establishment of typical blanket bog moth communities within the timescale studied here. Some management practices addressing microtopographical issues are currently under trial across a range of sites in the UK (Hancock *et al.* 2018) and may help to overcome these legacy effects faster.

No tyrphobiont species were identified in our moth communities, leading us to reject our second hypothesis, although a strong association was found between *L. porphyrea* and blanket bog. In general, studies looking at terrestrial invertebrate -peatland habitat associations in Britain, particularly amongst

Lepidoptera, are lacking. A single study on Irish Lepidoptera compared degraded and protected areas of raised bog and found a number of moth species specifically associated with protected raised bogs (Flynn *et al.* 2016). Some of these species were also found in Forsinard but were rather stenotopic in comparison (i.e. *C. haworthii*, *Ceramica pisi*, *D. mendica*, *A. monoglypha*, *Mythimna impura* and *Noctua pronuba*, with the strongest affinity for blanket bog shown by *L. porphyrea*). It is not uncommon for a moth species to show trait variation across its geographical range of distribution. For instance, the noctuid moth *Coranarta cordigera* is a strict tyrphobiont in central and northern Europe (Yela 2002), but it is found on drier or even gravelly moors in the UK (e.g. Waring & Townsend 2009). However, we suspect that part of the variation in bog affinity shown among species in both our study and that of Flynn *et al.* (2016) could be due to the trait selection process. Whilst FTs were selected *a priori* in both studies, Flynn *et al.* (2016) based habitat preferences on food plants of moth species found amongst typical raised bog vegetation, whereas our habitat preferences were based on the most common habitat type that species are recorded in across Great Britain.

The lack of tyrphobionts in Forsinard's moth communities may not be particularly remarkable, since the number of tyrphobionts present in an assemblage seems generally to decrease in northern latitudes (Mikkola & Spitzer 1983). Our sampling was designed to detect broad patterns of macro moth distribution and included species that are nevertheless traditionally considered tyrphobionts in other European peatlands. Whilst many such bogs are characterised by open spaces, some continental European peatlands are naturally wooded, and thus tend to offer a considerable variety of ecological niches that are often associated with higher plant species richness (Rydin & Jeglum 2013). We did not sample vegetation at or around our moth trap sites, so cannot directly relate moth species occurrence to larval foodplant availability or assess how variation amongst the plant communities of restoration sites mediates moth communities. However, it is possible that some foodplants characteristic of near-natural bog may have been among the early colonisers of restoration sites (e.g. *Calluna vulgaris*, *Eriophorum vaginatum*; Hancock *et al.* 2018), and so have been able to support some of the moth species that also occurred in our bog samples. Thus, moths such as *Celaneia haworthii* and *Amphipoea lucens*, which are considered tyrphobionts in at least some central European and Irish raised bogs (Spitzer & Jaroš 1993, Dapkus 2001, Bezděk *et al.* 2006, Flynn *et al.*

2016) but are not generally confined to bogs in the UK (Waring & Townsend 2009), may be able to readily colonise restoration areas as foodplants become available.

Vulnerability to habitat disturbance, such as tree felling, has been observed in families of moth taxa in broadleaf forest in the UK (Slade *et al.* 2013). The fragmentation of habitat into forest, open blanket bog and areas under restoration makes it difficult to clearly differentiate habitat types, especially with the establishment of bog vegetation as restoration progresses (Hancock *et al.* 2018). If key bog species - including tyrphobionts - disappear, they may be unable then to recolonise new restoration areas, potentially leading to loss of peatland biodiversity and FTs, species homogenisation and further implications for ecosystem functioning (Sodhi *et al.* 2009). Whilst this may be a lesser issue at our study site, given the substantial areas of relatively unmodified bog in the wider landscape, further research targeting species-specific bog macrotope associations is desirable to shed more light on the ecological and functional role of moths in open blanket bog.

Trait syndromes in moth communities

Before interpreting the results further, it is important to reiterate that while the sampling range covered by our study at Forsinard was relatively local, it represented the nocturnal macro moth species normally inhabiting each treatment. Despite intrinsic differences in light attraction between moth species (Merckx & Slade 2014) and the sampling being undertaken during summer months, traps were set simultaneously in order to control for weather variability and, therefore, the data across treatments are comparable. Moth species may move beyond the immediate vicinity of their larval foodplants, either to find adult nectar resources or as dispersal activity. Thus, they may be caught in lower numbers in habitat types that would not be suitable for maintaining populations of such species. However, we preserved the original counts rather than using presence/absence data. Thus, differences in catches between treatments should indicate which are the preferred habitats for a species.

To the best of our knowledge, this is the first study using trait syndromes to assess the response of peatland moths to management. Here we adopt Garnier's definition of trait syndrome, as a suite of traits correlating within an ensemble of species, genotypes or individuals (Garnier *et al.* 2016). The results obtained clearly support our third hypothesis, as we were able to observe clear associations between FTs and treatments. The trait syndromes identified in

Forsinard's moths are primarily based on phenological, phylogenetic and ecological performance FTs that are potentially linked to microhabitat and resource use, and to dispersal capability.

In the context of restoration, species mobility is certainly key for the adequate progression of this complex process. In Lepidoptera, mobility has been linked to species traits (Betzholtz & Franzén 2011), and specific traits such as wingspan and adult/larval foodplant preferences have been identified as key for dispersal of Lepidoptera in fragmented forests (Slade *et al.* 2013). Yet, in our study, traits such as wingspan and forewing length do not seem to play a strong role in moth species distribution.

Phylogeny is likely also to play a role in moth responses to environmental change, as differential responses to habitat fragmentation have been observed between moth families that are most likely to also display different FTs (Summerville & Crist 2004). For example, two of the largest moth families sampled by New (2004), Noctuidae and Geometridae, display clearly opposite habitat choices (restoration and forestry respectively) in our data. These species can also display different seasonal behaviour in peat bogs. For example, eastern European tyrphobiontic geometrids seem more active on warm mid-summer nights whilst noctuids favour colder late-summer nights (Dapkus 2001). We observed habitat affinity differences, as Noctuidae (subfamily Noctuinae) moths tended to be more linked with restoration and bog, whereas Geometridae (subfamily Larentiinae, Ennominae) tended to be present in greater numbers in forestry. This difference is easily explained: these moths are active in the habitat where their larval food plants are found, additionally seeking shelter and prospective partners.

In our study, the traits supporting the syndromes identified show strong linkages with dispersal capability, resource use and microhabitat selection, and could be considered indicative predictors of peatland moth distribution. Going forward, differences emerging amongst moth species, potentially affecting species dispersal behaviour and thus distribution across the peatland, could be explored further. For instance, it would be worth investigating whether certain traits become more dominant or disappear within moth communities across restoration areas, and what the wider ecological implications of those changes are.

Future research

A clear limitation highlighted in this study is the selection of animal FTs. In many studies this

selection tends to be done *a priori*, often finding the values needed for the species sampled in available literature. This comes with obvious restrictions as, for some species, there is a large range of published studies with different traits and values for taxa. This may cause researchers to select traits for analysis in subjective ways. Thus, whilst there are reliable databases that allow a standardised approach to the study of plant traits (e.g. TRY, LEDA), this is not the case for many invertebrates, and certainly not for British moths. In addition, despite British Lepidoptera being relatively well known, there are still unknown aspects of their ecology. Effort has been put into standardising protocols for the use of functional traits (e.g. we used the M-P-P-E framework here), and similar effort to create a database of invertebrate FTs would facilitate the potential comparison and extrapolation of trait syndromes across habitat types or even geographical regions.

Another limitation of our study was the lack of data on vegetation and other environmental variables. Since the functional approach has proved useful in the study of peatland moth communities, the combination of vegetation, environmental and species FTs and abundance data into RLQ and fourth corner analyses has led to an integrated approach that accounts for the mathematical shortcomings identified in the use of CWMs alone (Peres-Neto *et al.* 2017). This approach has been successfully used to disentangle community responses to disturbance, developing trait-based metrics to provide advance warning of disturbance events (Mouillot *et al.* 2013). Similarly, it has been used to assess the effects of environmental change (Lindo *et al.* 2012) and environmental filtering on communities (Dufлот *et al.* 2014). However, before these methods can be applied to fully elucidate the effect that peatland restoration is having on arthropod communities, more information is required on microhabitat use and habitat preference in moth species. This may lead, for example, to identifying which features of restoration were most closely linked to colonisation of our restoration plots by a suite of peatland-associated species or, indeed, which species have been unable to exploit restoration plots as yet.

This study was limited by the coarse scale at which data on these mobile taxa were collected. Since this was, to our knowledge, the first study attempting to link moth responses to peatland restoration and moth FTs, our intention in this pilot study was to obtain preliminary results from which further research hypotheses could be derived. Our discussion highlights the lack of understanding of habitat preferences in moth species (although this is also the

case for other peatland arthropods). Filling those gaps would allow us to better understand how species are distributed across peatland macrotopes, and how management can improve the conservation of typical tyrphobiont species. Ideally, sampling of both adult and larval stages should be undertaken in order to understand how moths make use of peatland habitat during their life cycles. Sampling could also be conducted over a longer period through the spring to autumn months, even though catches may be small outside the period covered by our study. This might enable sampling of a wider range of species and investigation of potential linkages with weather patterns and habitat seasonality, both of which may potentially be linked to climate change.

Finally, with peatland restoration likely to continue at pace following pledges for future funding across the UK and in Scotland in particular, it is more important than ever to understand which interventions are successful in reinstating the complex biodiversity and ecohydrological feedbacks that maintain peatland functions over time. Therefore, further research should seek to integrate invertebrates as part of multi-trophic studies investigating the relationships between functional diversity and fluxes of C, nutrients and energy in the context of large-scale management and restoration activities.

ACKNOWLEDGEMENTS

We thank the RSPB, and particularly Daniela Klein and Mark Hancock, for allowing access to Forsinard Flows and providing logistical support; as well as Chris Ross and Fountain Forestry for coordinating access to deer stalking areas. We are grateful for the help with navigating the analysis of FTs provided by Robin Pakeman. This research was part-funded (Rebekka Artz) by the Rural & Environment Science and Analytical Division of the Scottish Government. We also thank Mark Harrison and two anonymous referees for their comments, which greatly improved the manuscript.

REFERENCES

- Agassiz, D.J.L., Beavan, S.D., Heckford, R.J. (2013) *Checklist of the Lepidoptera of the British Isles*. Royal Entomological Society, St Albans, UK. 206 pp.
- Auber, A., Travers-Trolet, M., Villanueva, M.C., Ernande, B. (2017) A new application of principal response curves for summarizing abrupt and

- cyclic shifts of communities over space. *Ecosphere*, 8, e02023, 13 pp.
- Aubin, I., Messier, C., Bouchard, A. (2008) Can plantations develop understory biological and physical attributes of naturally regenerated forests? *Biological Conservation*, 141, 2461–2476.
- Batzer, D.P., Boix, D. (eds.) (2016) *Invertebrates in Freshwater Wetlands: An International Perspective on their Ecology*. Springer International Publishing, Switzerland, 645 pp.
- Betzholtz, P.E., Franzén, M. (2011) Mobility is related to species traits in noctuid moths. *Ecological Entomology*, 36, 369–376.
- Bezděk, A., Jaroš, J., Spitzer, K. (2006) Spatial distribution of ground beetles (Coleoptera: Carabidae) and moths (Lepidoptera) in the Mrtvýlůh bog, Šumava Mts (Central Europe): A test of habitat island community. *Biodiversity and Conservation*, 1, 381–395.
- Calmé, S., Desrochers, A. (2000) Biogeographic aspects of the distribution of bird species breeding in Québec's peatlands. *Journal of Biogeography*, 27, 725–732.
- Chevone, F., Dolédec, S., Chessel, D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31, 295–309.
- Conrad, K.F., Warren, M., Fox, R., Parsons, M., Woiwod, I.P. (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132, 279–291.
- Creevy, A.L., Andersen, R., Rowson, J.G., Payne, R.J. (2018) Testate amoebae as functionally significant bioindicators in forest-to-bog restoration. *Ecological Indicators*, 84, 274–282.
- Dapkus, D. (2000) Comparison of Lepidoptera communities of Čepkeliai raised bog, Baloša and Palios peatlands. *Acta Zoologica Lituanica*, 10, 85–88.
- Dapkus, D. (2001) Macrolepidoptera of Lithuanian peatbogs. *Norwegian Journal of Entomology*, 48, 161–166.
- Dennis, E.B., Brereton, T.M., Morgan, B.J.T., Fox, R., Shortall, C.R., Prescott, T., Foster, S. (2019) Trends and indicators for quantifying moth abundance and occupancy in Scotland. *Journal of Insect Conservation*, 23, 369–380.
- Desrochers, A., van Duinen, G.J. (2006) Peatland fauna. *Boreal Peatland Ecosystems*, 188, 67–100.
- de Vries, H.H., den Boer, P.J. (1990) Survival of populations of *Agonum ericeti* Panz. (Col., Carabidae) in relation to fragmentation of habitats. *Netherlands Journal of Zoology*, 40, 484–498.
- Dufлот, R., Georges, R., Ernoult, A., Aviron, S., Burel, F. (2014) Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica*, 56, 19–26.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, 34, 487–515.
- Flynn, C., Griffin, C.T., Coll, J., Williams, C.D. (2016) The diversity and composition of moth assemblages of protected and degraded raised bogs in Ireland. *Insect Conservation and Diversity*, 9, 302–319.
- Fountain-Jones, N.M., Baker, S.C., Jordan, G.J. (2014) Moving beyond the guild concept: developing a consistent functional trait framework for terrestrial beetles. *Ecological Entomology*, 40, 1–13.
- Fox, R. (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity*, 6, 5–19.
- Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D., Roy, D.B. (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, 51, 949–957.
- Gaffney, P.P., Hancock, M.H., Taggart, M.A., Andersen, R. (2018) Measuring restoration progress using pore-and surface-water chemistry across a chronosequence of formerly afforested blanket bogs. *Journal of Environmental Management*, 219, 239–251.
- Garnier, E., Navas, M.L., Grigulis, K. (2016) *Plant functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*. Oxford University Press, Oxford, 231 pp.
- Hancock, M.H., Klein, D., Andersen, R., Cowie, N. R. (2018) Vegetation response to restoration management of a blanket bog damaged by drainage and afforestation. *Applied Vegetation Science*, 21, 167–178.
- Heegaard, E., Vandvik, V. (2004) Climate change affects the outcome of competitive interactions - an application of principal response curves. *Oecologia*, 139, 459–466.
- Humphrey, J.W., Hawes, C., Peace, A.J., Ferris-Kaan, R., Jukes, M.R. (1999) Relationships between insect diversity and habitat characteristics in plantation forests. *Forest Ecology and Management*, 113, 11–21.
- Kirkpatrick, L. (2016) *Bat Exploitation of Sitka Spruce Plantations: Impacts of Management on Bats and Nocturnal Invertebrates*. PhD thesis,

- University of Stirling, 219 pp. Online at: https://dspace.stir.ac.uk/bitstream/1893/25312/3/Thesis_LucindaKirkpatrick.pdf
- Konings, W., Boyd, K.G., Andersen, R. (2019) Comparison of plant traits of sedges, shrubs and *Sphagnum* mosses between sites undergoing forest-to-bog restoration and near-natural open blanket bog: a pilot study. *Mires and Peat*, 23, 07, 10 pp.
- Kremen, C., Colwell, R.K., Erwin, T.L., Murphy, D.D., Noss, R.A., Sanjayan, M.A. (1993) Terrestrial arthropod assemblages: Their use in conservation planning. *Conservation Biology*, 7, 796–808.
- Laliberté, E., Legendre, P., Shipley, B. (2014) Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12. Online at: <http://CRAN.R-project.org/package=FD>
- Lindo, Z., Whiteley, J., Gonzalez, A. (2012) Traits explain community disassembly and trophic contraction following experimental environmental change. *Global Change Biology*, 18, 2448–2457.
- Lindsay, R. (1988) Part I: Peatland ecology. The Flow Country: The peatlands of Caithness and Sutherland. In: Lindsay, R., Charman, D.J., Everingham, F., O'Reilly, R.M., Palmer, M.A., Rowell, T.A., Stroud, D.A. (eds.) *The Flow Country: The Peatlands of Caithness and Sutherland*. Joint Nature Conservation Committee (JNCC), Peterborough, 9–18.
- Lindsay, R.A., Charman, D.J., Everingham, F., O'Reilly, R.M., Palmer, M.A., Rowell, T.A., Stroud, D.A. (1988) *The Flow Country: The Peatlands of Caithness and Sutherland*. Joint Nature Conservation Committee, Peterborough, 174 pp.
- Manley, C. (ed.) (2015) *British Moths: A Photographic Guide to the Moths of Britain and Ireland*. Bloomsbury Natural History, London, 448 pp.
- Merckx, T., Slade, E.M. (2014) Macro-moth families differ in their attraction to light: implications for light-trap monitoring programmes. *Insect Conservation and Diversity*, 7, 453–461.
- Mikkola, K., Spitzer, K. (1983) Lepidoptera associated with peatlands in central and northern Europe: a synthesis. *Nota Lepidopterologica*, 6, 216–229.
- Money, N. (2017) *The Moths of Caithness*. Online at: <http://www.caithnessmoths.org.uk/>
- Mouillot, D., Graham, N.A., Villeger, S., Mason, N.W., Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28, 167–177.
- New, T.R. (ed.) (2004) *Insects, Fire and Conservation*. Springer International Publishing, Switzerland, 220 pp.
- New, T.R., Pyle, R.M., Thomas, J.A., Thomas, C.D., Hammond, P.C. (1995) Butterfly conservation management. *Annual Review of Entomology*, 40, 57–83.
- Nichols, E., Uriarte, M., Bunker, D.E., Favila, M.E., Slade, E.M., Vulinec, K., Larsen, T., Vaz-de-Mello, F.Z., Louzada, J., Naeem, S., Spector, S.H. (2013) Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. *Ecology*, 94, 180–189.
- Nilsson, S.G. (1986) Are bird communities in small biotope patches random samples from communities in large patches? *Biological Conservation*, 38, 179–204.
- Noreika, N., Kotiaho, J.S., Penttinen, J., Punttila, P., Vuori, A., Pajunen, T., Autio, O., Loukola, O.J., Kotze, D.J. (2015) Rapid recovery of invertebrate communities after ecological restoration of boreal mires. *Restoration Ecology*, 23, 566–579.
- Noreika, N., Kotze, D.J., Loukola, O.J., Sormunen, N., Vuori, A., Päivinen, J., Penttinen, J., Punttila, P., Kotiaho, J.S. (2016) Specialist butterflies benefit most from the ecological restoration of mires. *Biological Conservation*, 196, 103–114.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H. (2017) vegan: Community Ecology Package. R package version 2.4-3. Online at: <https://cran.rproject.org/package=vegan>
- Peres-Neto, P.R., Dray, S., ter Braak, C.J.F. (2017) Linking trait variation to the environment: critical issues with community-weighted mean correlation resolved by the fourth-corner approach. *Ecography*, 40, 806–816.
- Petchey, O.L., Gaston, K.J. (2006) Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9, 741–758.
- Peus F. (1928) Beiträge zur Kenntnis der tierwelt Nordwestdeutscher Hochmoore. Eine ökologische Studie. Insekten, spinnentiere (Teilw.), Wirbeltiere (A contribution to the knowledge of wildlife of Northwestern German peat bogs. An ecological study. Insects, arachnids (in part), and vertebrates). *Zeitschrift für Morphologie und Ökologie der Tiere*, 12, 533–683 (in German).
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for

- Statistical. Computing, Vienna, Austria. Online at: <http://www.R-project.org/>
- Ramchunder, S.J., Brown, L.E., Holden, J. (2009) Environmental effects of drainage drain-blocking and prescribed vegetation burning in UK upland peatlands. *Progress in Physical Geography*, 33, 49–79.
- Robinson, G.S., Ackery, P.R., Kitching, I.J., Beccaloni, G.W., Hernandez, L.M. (2010) *HOSTS - A Database of the World's Lepidopteran Hostplants*. Natural History Museum, London. Online at: <http://www.nhm.ac.uk/hosts>
- Rydin, H., Jeglum, J.K. (2013) *The Biology of Peatlands*. Oxford University Press, Oxford, 798 pp.
- Slade, E.M., Merckx, T., Riutta, T., Bebbler, D.P., Redhead, D., Riordan, P., Macdonald, D.W. (2013) Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. *Ecology*, 94, 1519–1530.
- Sodhi, N.S., Brook, B.W., Bradshaw, C.J.A. (2009) Chapter VI: Causes and consequences of species extinctions. In: Levin, S.A. (ed.) *The Princeton Guide to Ecology*, Princeton University Press., 514–520.
- Spake, R., Barsoum N., Newton, A.C., Doncaster, C.P. (2016) Drivers of the composition and diversity of carabid functional traits in UK coniferous plantations. *Forest Ecology and Management*, 359, 300–308.
- Spitzer, K., Danks, H.V. (2006) Insect biodiversity of boreal peat bogs. *Annual Review of Entomology*, 51, 137–161.
- Spitzer, K., Jaroš, J. (1993) Lepidoptera associated with the Cervene Blato bog (Central Europe): Conservation implications. *European Journal of Entomology*, 90, 323–336.
- Spitzer, K., Bezděk, A., Jaroš, J. (1999) Ecological succession of a relict Central European peat bog and variability of its insect biodiversity. *Journal of Insect Conservation*, 3, 97–106.
- Summerville, K.S. (2014) Do seasonal temperatures species traits and nearby timber harvest predict variation in moth species richness and abundance in unlogged deciduous forests? *Agricultural and Forest Entomology*, 16, 80–86.
- Summerville, K.S., Crist, T.O. (2002) Effects of timber harvest on forest Lepidoptera: community guild and species responses. *Ecological Applications*, 12, 820–835.
- Summerville, K.S., Crist, T.O. (2004) Contrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography*, 27, 3–12.
- ter Braak, C.J.F., Šmilauer, P. (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5)*. Online at: <https://library.wur.nl/WebQuery/wurpubs/reports/341885>
- Townsend, M., Clifton, J., Goodey, B. (2010) *British and Irish Moths: An Illustrated Guide to Selected Difficult Species (Covering the Use of Genitalia Characters and Other Features)*. Butterfly Conservation, Wareham, 91 pp.
- van den Brink, P.J., ter Braak, C.J. (1999) Principal response curves: Analysis of time-dependent multivariate responses of biological community to stress. *Environmental Toxicology and Chemistry*, 18, 138–148.
- Vepsäläinen, K., Savolainen, R., Tiainen, J., Vilén J. (2000) Successional changes of ant assemblages: from virgin and ditched bogs to forests. *Annales Zoologici Fennici*, 37, 135–149.
- Waring, P., Townsend, M. (2009) *Field Guide to the Moths of Great Britain and Ireland*. Bloomsbury Publishing, London, 444 pp.
- Warren, C. (2000) “Birds bogs and forestry” revisited: The significance of the Flow Country controversy. *Scottish Geographical Journal*, 116, 315–337.
- Wilkie, N.M., Mayhew, P.W. (2003) The management and restoration of damaged blanket bog in the north of Scotland. *Botanical Journal of Scotland*, 55, 125–133.
- Yela, J. (2002) The internal genitalia as a taxonomic tool: description of the relict endemic moth, *Coranarta restricta* sp. n., from the Iberian Peninsula (Lepidoptera: Noctuidae: Hadeninae). *Entomologica Fennica*, 13, 1–12.

Submitted 01 May 2019, revision 02 Sep 2020
 Editor: Mark Harrison

Author for correspondence:

Dr Ainoa Pravia, Forest Research, Northern Research Station, Roslin, Midlothian, EH25 9SY, UK.

E-mail: ainoa.pravia@ForestResearch.gov.uk

Appendix

Table A1. List of moth species trapped at Forsinard (nomenclature follows Agassiz *et al.* 2013). R3–9 and R10–18 refer to restoration plots three to nine years and ten to eighteen years, respectively, after the onset of restoration at time of sampling.

Family	Subfamily	Common Name	Latin Name	Code	Bog (47 traps)	R3–9 (38 traps)	R10–18 (38 traps)	Forest (46 traps)	TOT
Erebidae	Hypenodinae	Pinion-streaked Snout	<i>Schrankia costaestrigalis</i> Stephens, 1834	SCO	0	0	0	2	2
Geometridae	Ennominae	Barred Red	<i>Hylaea fasciaria</i> Linnaeus, 1758	HFA	9	1	7	1336	1383
Geometridae	Ennominae	Bordered White	<i>Bupalu spiniaria</i> Linnaeus, 1758	BPI	1	0	0	58	59
Geometridae	Ennominae	Brimstone Moth	<i>Opisthograptis luteolata</i> Linnaeus, 1758	OLU	1	0	0	1	2
Geometridae	Ennominae	Common White Wave	<i>Cabera pusaria</i> Linnaeus, 1758	CPU	0	1	0	0	1
Geometridae	Ennominae	Light Emerald	<i>Campaea margaritaria</i> Linnaeus, 1761	CMA	1	0	0	0	1
Geometridae	Ennominae	Magpie	<i>Abraxas grossulariata</i> Linnaeus, 1758	AGR	3	1	13	130	147
Geometridae	Ennominae	Mottled Beauty	<i>Alcis repandata</i> Linnaeus, 1758	ARE	0	0	0	1	1
Geometridae	Ennominae	Satin Beauty	<i>Deileptenia ribeata</i> Clerck, 1759	DRI	0	0	0	6	6
Geometridae	Ennominae	Scalloped Oak	<i>Crocallis elinguaris</i> Linnaeus, 1758	CEL	1	0	0	0	1
Geometridae	Ennominae	Tawny-barred Angle	<i>Macaria liturata</i> Clerck, 1759	MLI	0	0	0	2	2
Geometridae	Larentiinae	Barred Straw	<i>Gandaritis pyraliata</i> Denis & Schiffermüller, 1775	GPY	1	3	1	5	10
Geometridae	Larentiinae	Chevron	<i>Eulithis testata</i> Linnaeus, 1761	ETE	3	5	6	0	14
Geometridae	Larentiinae	Common Carpet	<i>Epirrhoe alternata</i> Müller, 1764	EAL	1	2	3	0	6
Geometridae	Larentiinae	Common Marbled Carpet	<i>Dysstroma truncata</i> Hufnagel, 1767	DTR	0	1	1	15	17
Geometridae	Larentiinae	Dark Marbled Carpet	<i>Dysstroma citrata</i> Linnaeus, 1761	DCI	0	1	0	7	8
Geometridae	Larentiinae	Flame Carpet	<i>Xanthorhoe designata</i> Hufnagel, 1767	XDES	0	0	0	1	1
Geometridae	Larentiinae	Green Carpet	<i>Colostygia pectinataria</i> Knoch, 1781	CPE	1	32	44	121	198

Family	Subfamily	Common Name	Latin Name	Code	Bog (47 traps)	R3-9 (38 traps)	R10-18 (38 traps)	Forest (46 traps)	TOT
Geometridae	Larentiinae	Grey Mountain Carpet	<i>Entephria caesiata</i> Denis & Schiffermüller, 1775	ECA	6	0	0	44	50
Geometridae	Larentiinae	Grey Pine Carpet	<i>Thera obeliscata</i> Hübner, 1787	TOB	1	3	3	16	23
Geometridae	Larentiinae	July Highflyer	<i>Hydriomenafurcata</i> Thunberg, 1784	HFU	0	3	0	8	11
Geometridae	Larentiinae	Manchester Treble-bar	<i>Carsia sororiata</i> Prout, 1937	CSO	4	3	0	0	7
Geometridae	Larentiinae	Northern Spinach	<i>Eulithis populata</i> Linnaeus, 1758	EPO	3	13	10	13	39
Geometridae	Larentiinae	Pine Carpet	<i>Pennitherafirmata</i> Hübner, 1822	PFI	0	1	2	10	13
Geometridae	Larentiinae	Pretty Pinion	<i>Perizoma blandiata</i> Denis & Schiffermüller, 1775	PBL	2	0	4	0	6
Geometridae	Larentiinae	Purple Bar	<i>Cosmorhoe ocellata</i> Linnaeus, 1758	COC	2	10	14	23	49
Geometridae	Larentiinae	Red Carpet	<i>Xanthorhoe decoloraria</i> Esper, 1806	XDE	9	50	39	9	107
Geometridae	Larentiinae	Silver-ground Carpet	<i>Xanthorhoe montanata</i> Denis & Schiffermüller, 1775	XMO	0	0	3	11	14
Geometridae	Larentiinae	Small Rivulet	<i>Perizoma alchemillata</i> Linnaeus, 1758	PAL	1	0	0	1	2
Geometridae	Larentiinae	Treble-bar	<i>Aplocera plagiata</i> Linnaeus, 1758	APL	0	0	1	0	1
Geometridae	Larentiinae	Twin-spot Carpet	<i>Mesotype didymata</i> Linnaeus, 1758	MDI	5	1	4	1	11
Geometridae	Larentiinae	Yellow Shell	<i>Camptogramma bilineata</i> Linnaeus, 1758	CBI	0	0	0	1	1
Hepialidae		Map-winged Swift	<i>Korscheltellus fusconebulosa</i> De Geer, 1778	KFU	0	0	8	21	29
Lasiocampidae	Pinarinae	Drinker	<i>Euthrixpotatoria</i> Linnaeus, 1758	EPOT	0	1	0	0	1
Noctuidae	Hadeninae	Antler Moth	<i>Cerapteryx graminis</i> Linnaeus, 1758	CGR	2	25	14	1	42
Noctuidae	Hadeninae	Beautiful Yellow Underwing	<i>Anarta myrtilli</i> Linnaeus, 1761	AMY	1	0	0	0	1
Noctuidae	Hadeninae	Broom Moth	<i>Ceramica pisi</i> Linnaeus, 1758	CPI	6	1	10	0	17
Noctuidae	Hadeninae	Smoky Wainscot	<i>Mythimna impura</i> Hübner, 1808	MIM	27	18	21	0	66
Noctuidae	Noctuinae	Archer's Dart	<i>Agrotis vestigialis</i> Hufnagel, 1766	AVE	1	0	1	0	2
Noctuidae	Noctuinae	Autumnal Rustic	<i>Eugnoris maglareosa</i> Esper, 1788	EGL	0	2	0	0	2
Noctuidae	Noctuinae	Dark Brocade	<i>Mniotype adusta</i> Esper, 1790	MAD	3	1	3	3	10

Family	Subfamily	Common Name	Latin Name	Code	Bog (47 traps)	R3-9 (38 traps)	R10-18 (38 traps)	Forest (46 traps)	TOT
Noctuidae	Noctuinae	Dotted Clay	<i>Xestia baja</i> Denis & Schiffermüller, 1775	XBA	1	0	0	0	1
Noctuidae	Noctuinae	Flame Shoulder	<i>Ochropleura plecta</i> Linnaeus, 1761	OPL	3	1	7	0	11
Noctuidae	Noctuinae	Gothic	<i>Naenia typica</i> Linnaeus, 1758	NTY	1	4	6	19	30
Noctuidae	Noctuinae	Ingrailed Clay	<i>Diarsia mendica</i> Fabricius, 1775	DME	40	150	189	59	438
Noctuidae	Noctuinae	Large Yellow Underwing	<i>Noctua pronuba</i> Linnaeus, 1758	NPR	12	47	5	5	69
Noctuidae	Noctuinae	Lesser Yellow Underwing	<i>Noctua comes</i> Hübner, 1813	NCO	1	0	2	2	5
Noctuidae	Noctuinae	Neglected Rustic	<i>Xestia castanea</i> Esper, 1798	XCA	1	0	0	2	3
Noctuidae	Noctuinae	Six-striped Rustic	<i>Xestia sexstrigata</i> Haworth, 1809	XSE	0	2	0	1	3
Noctuidae	Noctuinae	Small Square-spot	<i>Diarsia rubi</i> Vieweg, 1790	DRU	25	44	102	56	227
Noctuidae	Noctuinae	Square-spot Rustic	<i>Xestia xanthographa</i> Denis & Schiffermüller, 1775	XXA	14	76	60	13	163
Noctuidae	Noctuinae	True Lover's Knot	<i>Lycophotia porphyrea</i> Denis & Schiffermüller, 1775	LPO	224	54	138	8	424
Noctuidae	Plusiinae	Beautiful Golden Y	<i>Autographa pulchrina</i> Haworth, 1809	APU	0	4	2	0	6
Noctuidae	Plusiinae	Gold Spot	<i>Plusia festucae</i> Linnaeus, 1758	PFE	0	2	0	0	2
Noctuidae	Plusiinae	Lempke's Gold Spot	<i>Plusia putnami</i> Lempke, 1966	PPU	3	4	5	0	12
Noctuidae	Plusiinae	Silver Y	<i>Autographa gamma</i> Linnaeus, 1758	AGA	0	2	0	0	2
Noctuidae	Xyleninae	Clouded-bordered Brindle	<i>Apamea crenata</i> Hufnagel, 1766	ACR	19	15	11	0	45
Noctuidae	Xyleninae	Dark Arches	<i>Apamea monoglypha</i> Hufnagel, 1766	AMO	67	51	23	32	173
Noctuidae	Xyleninae	Dusky Brocade	<i>Apamea remissa</i> Hübner, 1809	AREM	8	10	14	1	33
Noctuidae	Xyleninae	Haworth's Minor	<i>Celaena haworthii</i> Curtis, 1829	CHA	40	99	58	1	198
Noctuidae	Xyleninae	Large Ear	<i>Amphipoea lucens</i> Freyer, 1845	ALU	0	2	2	1	5
Noctuidae	Xyleninae	Middle-barred Minor	<i>Oligia fasciuncula</i> Haworth, 1809	OFA	1	9	116	2	128
Noctuidae	Hadeninae	Beautiful Yellow Underwing	<i>Anarta myrtilli</i> Linnaeus, 1761	AMY	1	0	0	0	1
Noctuidae	Xyleninae	Small Dotted Buff	<i>Photodes minima</i> Haworth, 1809	PMI	1	7	1	9	18

Table A2. Moth species functional traits. Taken from Waring & Townsend (2009), Manley (2015) and Money (2017). Species codes are given in Table A1 and trait codes are defined in Table 2. Fm= family; SbF= subfamily; FW= forewing length; WS= wingspan; VOL= voltinism; O= larval overwintering; LF= larval feeding season; AF= adult flying period; D= distribution; HP= habitat preference; HF= host plant family.

Species	Functional traits										
	Fm	SbF	FW	WS	VOL	O	LF	AF	D	HP	HF
NTY	Noc	Noc	19.5	44	1	larva	SU.SP	SU	local	both	poly
CBI	Geom	Lar	14.5	27	1	larva	SU.SP	SU	com	both	poly
MDI	Geom	Lar	13	26	1	egg	SP	SU	com	both	poly
LPO	Noc	Noc	13.5	30	1	larva	SU.SP	SU	com	open	Eri
APL	Geom	Lar	20.5	40	1	larva	SU.SP	SU	com	both	Gut
MLI	Geom	Enn	15.5	33	1	pupa	SU	SU	com	con	Pin
XXA	Noc	Noc	15.5	36	1	larva	SU.SP	SU	com	both	Gram
MIM	Noc	Had	16	34	1	larva	SU.SP	SU	com	open	Gram.Jun
DRU	Noc	Noc	14	32	1	larva	SU.SP	SU	com	both	poly
PAL	Geom	Lar	10	26	1	pupa	SU	SU	com	both	Lab
PMI	Noc	Xyl	12.5	28	1	larva	SU.SP	SU	com	both	Gram
XSE	Noc	Noc	16	36	1	larva	SU.SP	SU	com	both	poly
XMO	Geom	Lar	15.5	34	1	larva	SU.SP	SU	com	both	Rub.Prim
AGA	Noc	Plus	17	40	3	absent	SP.AU	SP.AU	com	both	poly
CEL	Geom	Enn	20	38	1	egg	SP	SU	com	wood	poly
DRI	Geom	Enn	22	42	1	larva	SU.SP	SU	com	con	Pin.Fag
XDE	Geom	Lar	13.5	32	1	larva	SU.SP	SU	com	open	Ros
COC	Geom	Lar	14	25	1	larva	SU	SU	com	open	Rub
PBL	Geom	Lar	10	20	1	pupa	SU	SU	local	open	Scro
SCO	Ereb	Hyp	10	20	1	larva	AU.SP	SU	local	open	Camp
PFI	Geom	Lar	14.5	30	1	egg	AU.SU	SP.AU	com	con	Pin
EPO	Geom	Lar	15.5	32	1	egg	SP	SU	com	open	Eri
AEX	Noc	Xyl	18	40	1	larva	AU.SU	SU.AU	scarce	open	Gram
XCA	Noc	Noc	17	39	1	larva	AU.SP	SU.AU	local	open	Eri
ARE	Geom	Enn	22.5	45	1	larva	SU.SP	SU	com	both	poly
OFA	Noc	Xyl	11	22	1	larva	SU.SP	SU	com	both	Gram
KFU	Hep	Hep	20	40	1	larva	SU.SP	SU	local	both	Den
CSO	Geom	Lar	13	24	1	egg	SP	SU	local	bog	Eri
AGR	Geom	Enn	21.5	40	1	larva	SU.SP	SU	com	open	poly
CMA	Geom	Enn	22	40	1	larva	SU.SP	SU	com	wood	poly

Species	Functional traits										
	Fm	SbF	FW	WS	VOL	O	LF	AF	D	HP	HF
NCO	Noc	Noc	18.5	40	1	larva	SU.SP	SU	com	both	poly
PPU	Noc	Plus	14.5	35	1	larva	SU.SP	SU	local	bog	Gram
NPR	Noc	Noc	23.5	55	1	larva	SU.SP	SU.AU	com	open	poly
ALU	Noc	Xyl	15.5	36	1	egg	SP.SU	SU.AU	local	open	Gram
HFU	Geom	Lar	16	32	1	egg	SP	SU.AU	com	both	Sal.Eri
DME	Noc	Noc	15	35	1	larva	SU.SP	SU	com	both	Eri.Ros
CHA	Noc	Xyl	12	25	1	egg	SP	SU.AU	local	open	Cyp.Jun
TOB	Geom	Lar	15	30	2	larva	AU.SU	SP.AU	com	con	Pin
ECA	Geom	Lar	17.5	36	1	larva	SU.SP	SU.AU	com	open	Eri
CPE	Geom	Lar	13.5	25	1	larva	SU.SP	SU	com	open	Rub
PFE	Noc	Plus	16.5	38	1	larva	SU.SP	SU	com	open	poly
OPL	Noc	Noc	13.5	30	1	pupa	SU	SP.SU	com	both	poly
XDES	Geom	Lar	12.5	25	1	pupa	SU	SP.SU	com	both	Cruc
AREM	Noc	Xyl	18	40	1	larva	SU.SP	SU	com	open	Gram
EPOT	Las	Pin	23	55	1	larva	SU.SP	SU	com	open	Cyp.Gram
XBA	Noc	Noc	19	40	1	larva	SU.SP	SU	com	both	poly
DCI	Geom	Lar	16.5	32	1	egg	SP	SU	com	open	Bet.Eri
MAD	Noc	Noc	19.5	40	1	larva	SP	SP.SU	com	open	poly
AMO	Noc	Xyl	22.5	50	1	larva	SU.SP	SU.AU	com	open	Gram
CPU	Geom	Enn	16	30	2	pupa	SP.AU	SP.SU	com	wood	poly
DTR	Geom	Lar	16.5	32	1	larva	SU.SP	SU	com	both	poly
EAL	Geom	Lar	13.5	25	2	pupa	SU	SP.SU	com	open	Rub
ACR	Noc	Xyl	20	42	1	larva	SU.SP	SP.SU	com	open	Gram
ETE	Geom	Lar	16	36	1	egg	SP.SU	SU	com	open	Sal.Bet
CPI	Noc	Had	18	40	1	larva	SP.AU	SP.SU	com	open	Fil.Den
OLU	Geom	Enn	17.5	35	1	pupa	AU.SP	SP.SU	com	open	Ros
BPI	Geom	Enn	18	36	1	pupa	SP.AU	SU	com	con	Pin
AMY	Noc	Had	11	24	1	larva	SU	SU	com	open	Eri
APU	Noc	Plus	18.5	37.5	1	larva	SU	SU	com	both	Cap.Urt
GPY	Geom	Lar	16.5	30.5	1	egg	SP	SU	scarce	open	Rub
HFA	Geom	Enn	19	38	1	larva	SU.SP	SU	com	con	Pin
EGL	Noc	Noc	15.5	35	1	larva	AU.SP	SU	com	open	Gram
AVE	Noc	Noc	16	35	1	larva	AU.SU	SU	local	open	Gram
CGR	Noc	Had	14.5	28	1	egg	SP	SU	com	open	Gram