

Research

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Author for correspondence:

Elske K Tielens

e-mail: elske.tielens@gmail.comElectronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.7159009>.Temperature, not net primary
productivity, drives continental-scale
variation in insect flight activity

Elske K Tielens and Jeff Kelly

School of Biological Sciences, University of Oklahoma, Norman, OK 73019-0390, USA

EKT, 0000-0001-7940-5657; JK, 0000-0002-8255-7990

The amount of energy available in a system constrains large-scale patterns of abundance. Here, we test the role of temperature and net primary productivity as drivers of flying insect abundance using a novel continental-scale data source: weather surveillance radar. We use the United States NEXRAD weather radar network to generate a near-daily dataset of insect flight activity across a gradient of temperature and productivity. Insect flight activity was positively correlated with mean annual temperature, explaining 38% of variation across sites. By contrast, net primary productivity did not explain additional variation. Grassland, forest and arid-xeric shrubland biomes differed in their insect flight activity, with the greatest abundance in subtropical and temperate grasslands. The relationship between insect flight abundance and temperature varied across biome types. In arid-xeric shrublands and in forest biomes the temperature–abundance relationship was indirectly (through net primary productivity) or directly (in the form of precipitation) mediated by water availability. These results suggest that temperature constraints on metabolism, development, or flight activity shape macroecological patterns in ectotherm abundance. Assessing the drivers of continental-scale patterns in insect abundance and their variation across biomes is particularly important to predict insect community response to warming conditions.

This article is part of the theme issue 'Towards a toolkit for global insect biodiversity monitoring'.

1. Introduction

A key objective in ecology is to understand how properties such as abundance, diversity and biomass vary across gradients in time and space [1]. At macro-scales, the amount of energy available in a system sets the upper limit to the abundance of individuals. Energy can be quantified in several ways; in 'solar energy metrics' or temperature that drives biological processes including metabolism, or in 'productive energy metrics', in resources available for consumers [2,3]. Understanding the role of temperature and productivity as drivers of abundance across broad scales will improve our understanding of how insect communities respond to changing climatic conditions.

Species–energy theory posits that the number of individuals in a system is primarily restricted by energy in the form of net primary productivity [4]. Net primary productivity (NPP) quantifies the amount of resources available to consumers, with more productive sites able to support more individuals. NPP may also be a more accurate proxy for available energy than solar energy, because it accounts for the amount of energy as well as the water availability necessary to convert that energy into biomass [2,5]. While a positive relationship between net primary productivity and abundance is widely assumed, the evidence for the abundance–productivity relationship is mixed. For example, continental-scale abundance of African ungulates was correlated with primary productivity, while for bird abundance some studies have found a positive relationship and others have found no correlation with productivity [6–8].

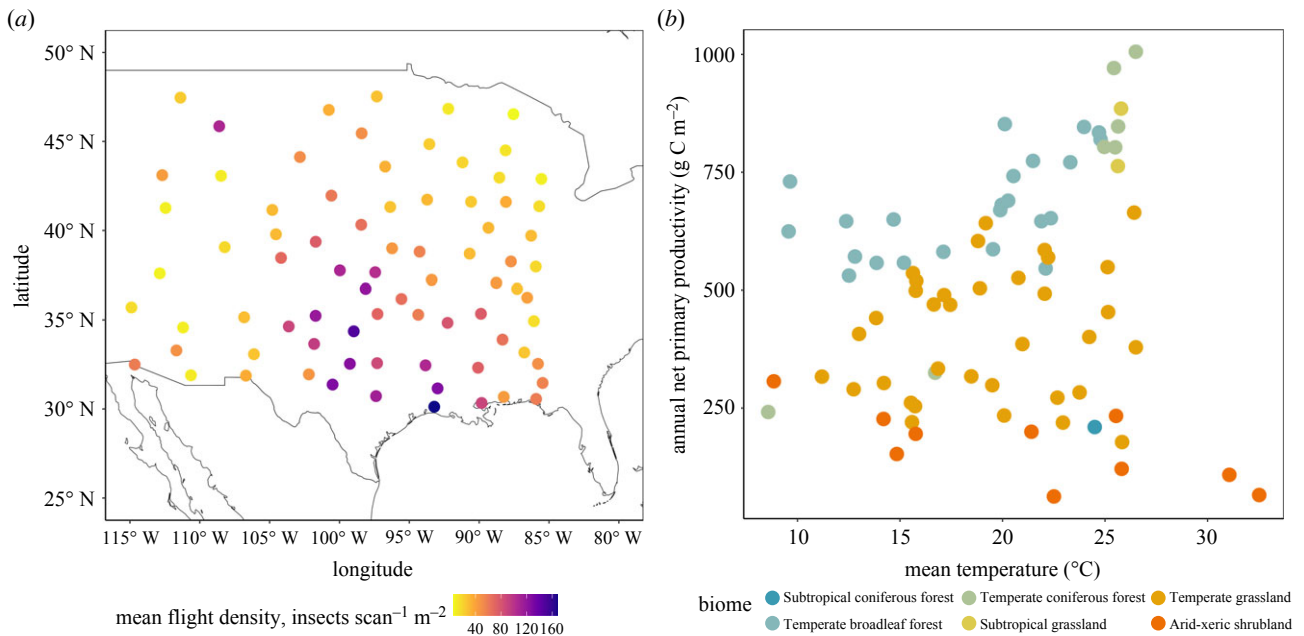


Figure 1. Sites along a gradient of temperature and productivity. (a) Geographic location of sites, colour indicates observed insect flight density per radar snapshot; i.e. mean site insect flight density $\text{scan}^{-1} \text{m}^{-2}$. (b) Site mean annual temperature, annual net primary productivity, and biome.

Geographical patterns in abundance and distribution may differ between endotherms and ectotherms due to their differences in energy use and performance constraints. While energy availability is a primary constraint on endotherm abundance and distribution, ectotherms have much lower energetic maintenance costs [9] and are restricted by rates of energy assimilation rather than resource availability [10]. As a result, endotherm abundance is hypothesized to be more strongly associated with primary productivity, whereas ectotherm abundance is better predicted by temperature [11].

Temperature drives key functions in ectotherms such as insects, and influences rates of development, reproduction and movement. Basal metabolic rates are a positive nonlinear function of temperature between thermal minima and maxima [12]. Metabolic rate constrains development, with development rate a function of energy input in the form of heat. Thermal development curves are commonly used in agriculture to develop degree day models and predict pest emergence or outbreak as a function of temperature [13]. Macroecological patterns in insect abundance may result from variation in temperature and growing seasons, which are associated with increased development rates, higher fecundity, shorter generation times and higher voltinism, leading to larger population sizes and higher abundances in warmer regions. Movement itself, including insect flight, is metabolically constrained and therefore also predicted to vary unimodally with temperature between thermal limits. Ant activity at baits for example increases predictably with temperature throughout the day and season [14]. Various mechanisms may be responsible for greater abundances in regions with warmer temperatures.

Quantifying the role of temperature and productivity as drivers of abundances across regional or continental scales can be challenging due to the number of species and populations, particularly in species-rich groups such as insects. One study of ant abundance in communities spanning from desert to rainforest biomes found that NPP explained more than half of the geographical variation in colony abundance, with another 13% explained by temperature through foraging time and metabolic rate [15]. Similarly, continental-scale variation in ‘discovery rates’—a proxy for ant predation—was explained by NPP, with annual NPP accounting for 40% of variation and temperature failing to account for more [16]. However, moth abundance was not explained by NPP across a continent-wide gradient of productivity in South African savannahs [17]. Analysis of continental patterns in Lepidoptera abundance across the contiguous US showed that temperature did not drive butterfly abundance in annual NABA counts [18]. The role of productivity and temperature as drivers of insect abundance has not been clarified, perhaps due to the challenge of monitoring insects at large spatial scale in a standardized way.

Here, we test the temperature and productivity hypotheses using a novel continental-scale data source on insects in the air: weather surveillance radar. Weather surveillance radar networks are widely distributed across large spatial scales, providing automated and standardized data collection at low cost. Radars have a long history of use in monitoring animals in the air [19,20], have been extensively validated [21,22], and weather radar has become a standard tool to quantify bird migration [23,24]. Novel methods are rapidly being developed to adapt weather radar for quantitative entomological applications [25,26], with recent studies using weather radar to quantify mayfly emergence [27], monitor pest exodus flights [28], and differentiate classes of insects [29]. Weather radar only observes insects in flight in the free airspace (i.e. at least 20 m above ground level, depending on topography and beam blockage of the radar) which excludes local flights such as foraging. While not all insects engage in high-altitude flights, these represent a broad range of taxa from most insect orders with diverse life histories, including aphids (Hemiptera), small flies and wasps (Diptera and Hymenoptera), ladybugs (Coleoptera), and butterflies and moths (Lepidoptera). Aerial habitats are key environments for winged organisms that have remained challenging to study, but radar can provide unique insights.

We explore large-scale drivers of aerial insect abundance along a gradient of productivity and temperature using ten-year means of day-flying insect abundance quantified with the United States weather surveillance radar network. The analysis focuses on radars in the central United States (figure 1a), providing coverage across the parameter space for both variables (figure 1b).

We test two alternate hypotheses: (1) insect flight density is principally limited by net primary productivity; or (2) insect flight density is primarily limited by temperature. We also analyze the role of secondary climatic and landscape covariates, including precipitation, biome and forested land cover, in explaining variation in insect flight activity.

2. Methods

(a) Site selection

To focus on the role of temperature and productivity as drivers of insect density in the air, we selected the central United States region (figure 1a). We omitted coastal regions because these areas may experience greater effects of urbanization and anthropogenic activity (EK Tielens 2012–2021, unpublished data). We included radar stations between 30° and 48° latitude and between –85° and –115° in longitude, resulting in 78 radar sites. These sites covered 18° in latitude, more than 20°C in mean annual temperature, and a factor of ten variation in annual net primary productivity (figure 1b).

(b) Radar monitoring

We generated a dataset of day-flying insect density using the NEXRAD weather surveillance system, a network of high-resolution Doppler weather radars (WSR-88D) operated by the NOAA National Weather Service (NWS), the Federal Aviation Administration and the US Air Force. Use of the NEXRAD radar system for ecological applications has been widely discussed elsewhere [30–32]. NEXRAD radar stations operate at S-band, with a frequency of 2.7–3.0 GHz and an approximate 10.7 cm wavelength. The NWS provides technical details on the NEXRAD system,¹ and radar data is archived and publicly available from Amazon Web Services.²

(c) Data generation

Insect density in the air was quantified from radar products following workflows laid out in previous work [33]. We produced a near daily dataset of insect density aloft across 78 radar stations in the contiguous United States and for the period for which dual-polarized radar data has been archived (2012–2021). To minimize interference from other aerial animals and to avoid double-counting insects we used a daily noon radar scan to provide a snapshot of insect density. We generated the initial radar product dataset using Python 3.7.4, and processed as described in previous work [27]. Broadly, we read radar scans from the NEXRAD archive into Python using the Py-Art package [34]. We subset each volumetric scan to non-redundant sweeps, converted radar reflectivity factor (dBZ) to total scattering area (cm²) and scattering area density (cm² km^{–3}) in each resolution volume [21]. We used a binary clutter mask to filter pixels with persistent or permanent features (i.e. ground clutter) following van Doren & Horton [24], using an 85th percentile cutoff and removing pixels with permanent features from the scan. We restricted our sampling to 150 km radius from the radar. We limited non-arthropod signals by focusing our analysis on diurnal insects and sampling at noon. We removed non-arthropod signals on the radar scans based on depolarization ratio (CDR), which is calculated from differential reflectivity and correlation coefficient. Differential reflectivity is the ratio of horizontal to vertical polarized equivalent reflectivity factor, providing information on the aspect ratio. Correlation coefficient is given by the cross correlation between the time of arrival of horizontal and vertical polarized waves. Together, these variables allow reliable distinction between round water drops in the air and biological signals of varying shapes [35]. We filtered for weather and avian signals on a pixel by pixel basis, excluding weather signals by removing pixels with circular depolarization ratio of less than –12.5 and reflectivity greater than 40 dBZ, and potential avian signals by excluding pixels with differential reflectivity less than 5 dB. This resulted in a scatter density of insects for each pixel in the volume scan.

We generated an altitudinal profile of scattering density by integrating over the mean density in 50 m bins up to 3 km above ground level, producing column-summed scattering density (cm² km^{–2}). We converted scattering density (cm² km^{–2}) to insect density (insects km^{–2}) by assuming the most common day-flying insect scatterers are micro-insects [36] with a radar cross section (RCS) of 1×10^{-6} cm² [36,37]. This RCS corresponds to common day-flying micro-insects, including Aphididae (Hemiptera), braconid wasps (e.g. *Aphidius nigripes*, Hymenoptera), thrips (e.g. *Frankliniella* sp., Thysanoptera) and fungus gnats (e.g. *Sciara* sp., Diptera) [38,39]. Our filtering was efficient in removing the main expected sources of non-insect signal (precipitation), and we conducted quality control by calculating weekly mean biomass and removing all data points greater than two standard deviations from the weekly mean. We then visually inspected a subset of scans and removed observations with potential contamination from the dataset.

(d) Analyses

We calculated mean insect flight abundance by taking the site mean of 10 years of near-daily observations in the dataset (median = 2937 observation scans per site), resulting in a mean flight abundance per m² at a given snapshot in time. We extracted monthly data on local climatic conditions from WorldClim for each radar station for the period 2012–2021 [40] and calculated 10-year mean annual temperatures. We identified biomes for each site based on the WWF Terrestrial Ecoregions of the World [41], and analysed insect flight abundance per biome as well as in three general biome types: forests (consisting of subtropical coniferous forests, temperate broadleaf forests, and temperate coniferous forests), grasslands (consisting of temperate grasslands and subtropical grasslands), and arid-xeric shrublands. We extracted annual net primary productivity from the NASA MODIS satellite at 500 m pixel resolution, which is derived from the sum of all 8-day GPP Net Photosynthesis products for a given year [42], calculating mean site annual NPP within an 80 km radius from the radar.

All statistical analyses were conducted using R [43]. We evaluated the role of mean annual temperature and mean annual net primary productivity in explaining site-to-site variation in insect flight abundance. We log₁₀-transformed insect flight density as it varied by a factor 100 and the relationship between insect flight density and drivers such as temperature or productivity best fit a log-linear response. We confirmed this choice by comparing between models with linear and log-linear relationships using the Akaike information criterion (AIC).

We then used model selection and averaging to estimate the effects of mean annual temperature, annual net primary productivity, and other potential variables including latitude, longitude, mean precipitation and biome on log insect flight abundance with linear models

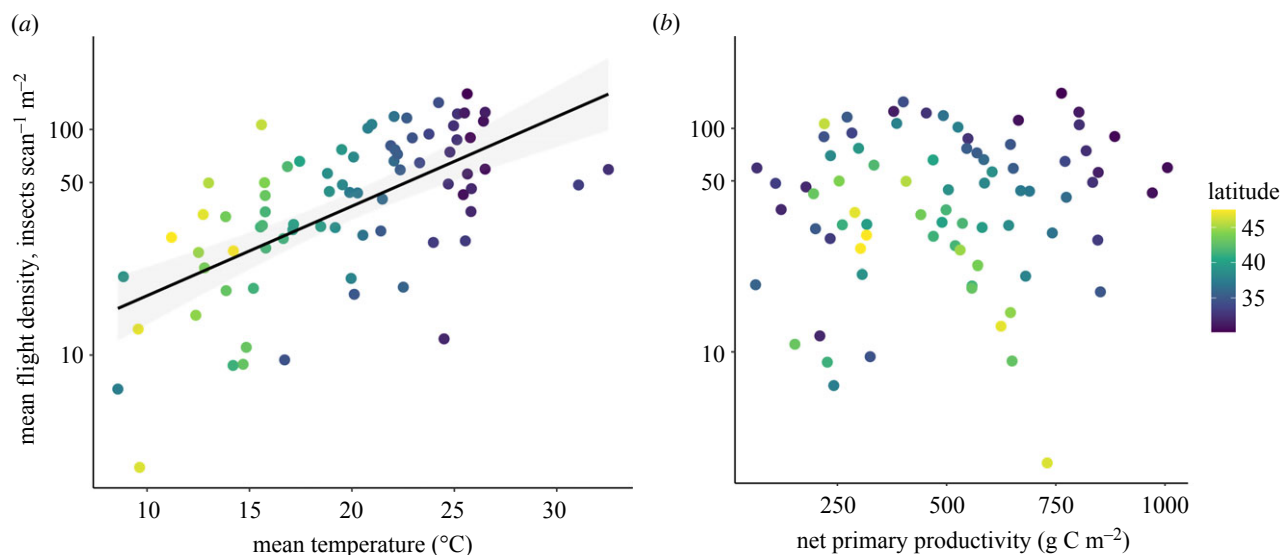


Figure 2. Mean insect flight density ($\log_{10}$, $\text{scan}^{-1} \text{m}^{-2}$) as a function of mean summer temperature (a) and net primary productivity (b). Fitted line and 95% confidence interval are derived from OLS regression.

[44]. Correlations between explanatory variables are provided in the electronic supplementary material, figure S3. These variables were all included in a global model, with no interaction effects, and we then used the function dredge to identify component models within the global model [45]. We conducted model averaging of all component models for which ΔAIC was less than 4, and reported conditional averaged coefficients. Fitted line and 95% confidence interval in figures were derived from ordinary least squares (OLS) regression.

We analysed insect flight abundance and its drivers per biome and per biome type. We tested for differences in mean flight abundance using ANOVA. We analysed the relationship between insect flight abundance and temperature and between insect flight abundance and productivity for each biome and biome type using separate linear models for each biome. To reflect figure slopes, we reported the estimates and p -values are reported for the relationship between a single potential driver and insect flight abundance within a biome. We then tested whether the relationship with temperature and the relationship with productivity differ significantly between biomes by adding an interaction effect to the global model above.

After identifying mean annual temperature as main explanatory variable, we evaluated residual variation across biome types. We evaluated all explanatory variables from the global model and used model selection to identify for each biome type which variables best explained residual variation after accounting for temperature. We then reported coefficients for the best model per biome type.

3. Results

Temperature was the strongest driver of insect flight abundance, with surface air temperature explaining 38% of variation in abundance across sites (figure 2a, LM, coefficient $\pm$ 95% CI = 0.045 ± 0.014 , $p < 0.0001$). By contrast, net primary productivity did not explain significant variation in flight abundance (figure 2b, LM, $p = 0.32$). Insect flight abundance decreased with increasing latitude, which explained 22% of variation (LM, coefficient $\pm$ 95% CI = -0.0085 ± 0.025 , $p < 0.001$). While flight abundance showed a strong latitudinal pattern, temperature explained additional variation beyond that of latitude ($\Delta\text{AIC} = 6.2$; electronic supplementary material, table S1). The full model with all variables explained 67% of variation (full model included temperature, precipitation, net primary productivity, biome, latitude and longitude; $F_{10,67} = 16.9$ $p < 0.00001$). Model averaging estimates of all candidate models within ΔAIC less than 4 of the full model are shown in table 1, with mean annual temperature and biome as significant predictors retained in all candidate models over which averaging took place.

Insect flight abundance varied across biome (ANOVA, $F_{5,72} = 5.9$ $p < 0.0005$; electronic supplementary material, figure S5). We combined subtropical grasslands with temperate grasslands, and subtropical coniferous forests with temperate broadleaf forests and temperate coniferous forests to create three biome types. Insect flight abundance also varied across biome type, and was greatest in grasslands, intermediate in forests, and lowest in arid-xeric systems (electronic supplementary material, figure S4; ANOVA, $F_{2,74} = 11.4$ $p < 0.0001$).

The relationship between insect flight abundance and temperature and net primary productivity varied across biome types (figure 3). Insect flight abundance increased with temperature in all three biome types but differed in magnitude, showing the weakest increase in arid-xeric systems (est. = 1.9 $p < 0.05$), stronger increases in forested systems (est. = 5.8 $p < 0.0001$), and the greatest increase in grasslands (est. = 9.4 $p < 0.0001$). These slopes differed significantly across biome types (temperature $\times$ biome type interaction with arid-xeric as intercept, $p < 0.05$). For net primary productivity within biome types, insect flight abundance increased with NPP only for forested systems (est. = 0.007 $p < 0.05$), while flight abundances did not vary with NPP in grasslands or arid-xeric systems.

For all biome types temperature was the main driver of insect flight abundance. Key variables explaining patterns in residual variation in insect abundance differed across biome types. We used model selection to identify variables that best explain residual variation within each biome type (see electronic supplementary material, table S3 for model selection output). In forests, residual variation was best explained by mean precipitation ($\Delta\text{AIC} = 3.4$, d.f. = 3), where temperature overpredicted insect abundance in drier areas (figure 4a, est. = 0.085 , Adj. $R^2 = 0.15$, $p < 0.05$). In grasslands, residual variation was best explained by longitude ($\Delta\text{AIC} = 2.0$, d.f. = 3),

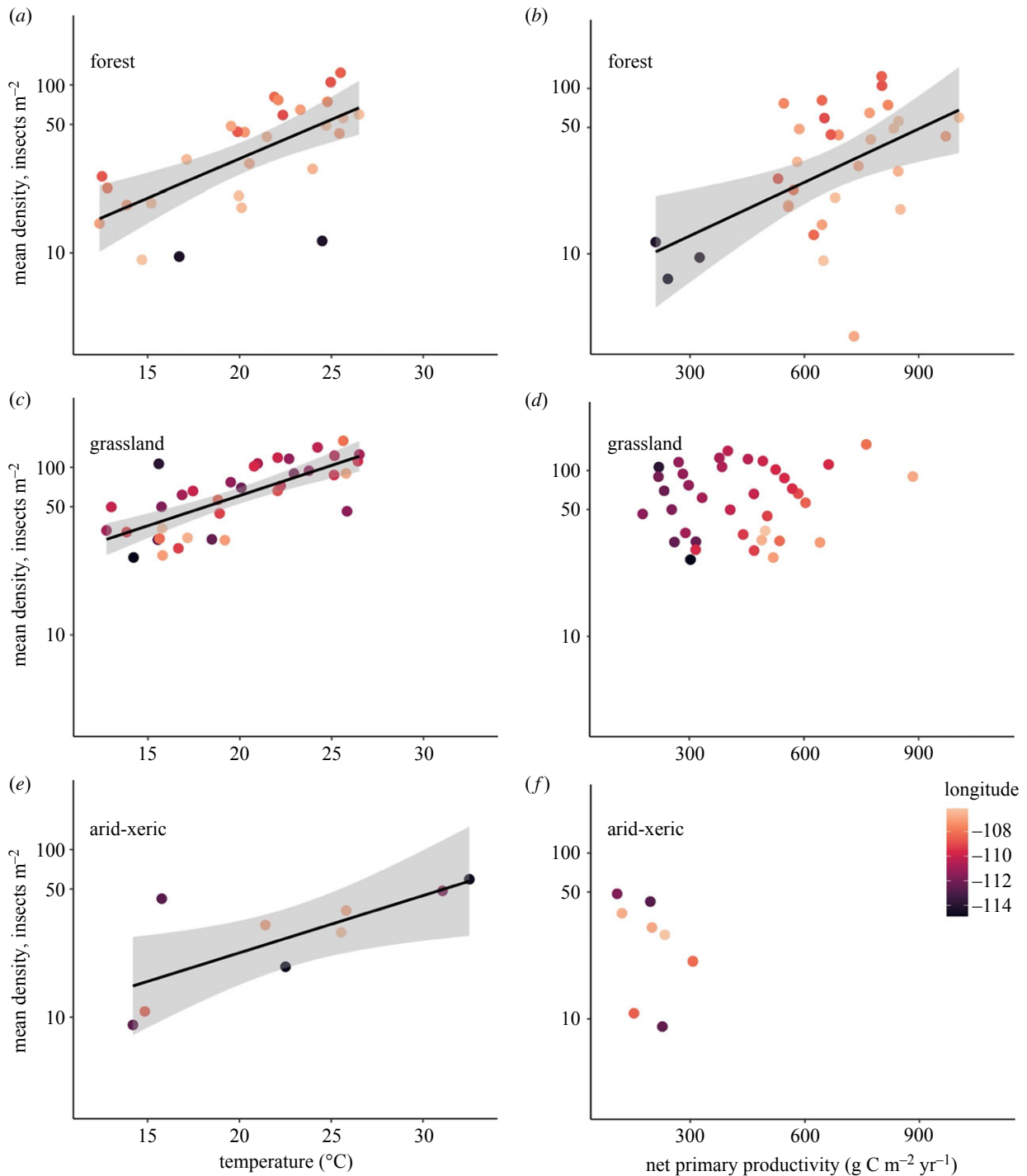


Figure 3. Biome type patterns in the relationship between mean insect flight density ($\log_{10}$, scan⁻¹ m⁻¹) and temperature (left) and net primary productivity (right). Insect flight density in forest biomes (a,b), grassland biomes (c,d), and arid-xeric biomes (e,f). Fitted line and 95% confidence interval are derived from OLS regression.

where insect flight abundance was underpredicted by temperature further west (i.e. at lower longitudes, figure 4b, est. = -0.016, Adj. R^2 = 0.20, p < 0.005). In arid-xeric shrublands, residual variation was best explained by net primary productivity (Δ AIC = 3.4, d.f. = 3), where insect flight abundance was lower than predicted based on temperature at sites with lower net primary productivity (figure 4c, est. = 0.00025, Adj. R^2 = 0.42, p < 0.05).

4. Discussion

Understanding drivers of insect abundance across large geographical scales is challenging due to the lack of standardized data spanning habitats and taxa. Here, we use a unique data source, 10 years of weather surveillance radar observations across the central United States, to test drivers of macroecological patterns in insect high-altitude flight. We find that temperature forms the primary driver of insect flight activity in the air at this scale, explaining nearly half of site-to-site variation. These results correspond with previous work on activity density of invertebrates moving across the soil surface, which found that air temperature explained between one third and three quarters of variation in pitfall trap abundances across the US NEON network [46]. Our

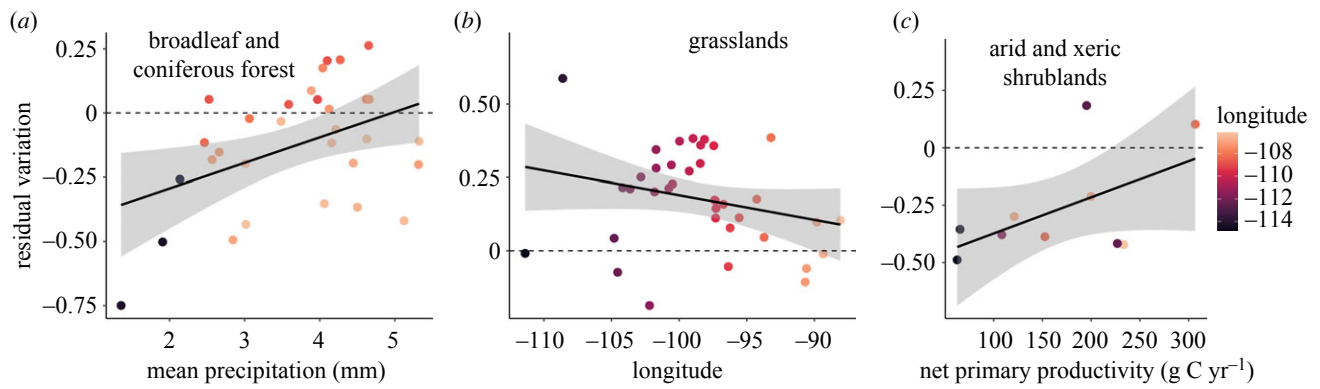


Figure 4. Key predictors of residual variation per biome type. Residual variation after accounting for temperature effects on insect flight abundance, for forest biomes (a), grassland biomes (b), and arid & xeric shrublands (c). Points are coloured by longitude. Predictors for each biome type were selected using AIC. Fitted line and 95% confidence interval provided for significant predictors, derived from OLS regression.

Table 1. Model averaging output for conditional average estimates. Model averaging conducted on all candidate models within ΔAIC less than 4 of the global model. Model selection resulted in 10 candidate models for model averaging. Model selection table provided in electronic supplementary material, table S2.

variable	estimate	standard error	z-value	p-value
intercept	−0.57	0.93	0.62	0.54
latitude	0.0085	0.013	0.65	0.52
longitude	−0.0090	0.0071	1.2	0.21
mean annual temperature	0.045	0.0073	6.0	$<2 \times 10^{-16}$
annual net primary productivity	−0.000072	0.00036	0.197	0.84
mean precipitation	0.063	0.055	1.1	0.26
biome: temperate broadleaf & mixed forests	0.69	0.22	3.0	0.0024
biome: temperate conifer forests	0.66	0.22	2.9	0.0038
biome: tropical & subtropical grasslands	0.98	0.26	3.7	0.00019
biome: temperate grasslands	0.96	0.21	4.5	6.2×10^{-6}
biome: arid-xeric shrublands	0.50	0.21	2.3	0.019

results suggest that large-scale abundance may be more limited by direct effects of energy on insects than indirectly through resource availability.

By contrast, net primary productivity was not an important driver of regional patterns in insect flight abundance. Productivity only explained a significant portion of flight abundance in forested biomes, and this effect was strongly driven by the inclusion of coniferous forest sites in the western US. Contrary to species–energy theory, an increase in productivity did not result in a proportionate increase in insect flight abundance. Within the contiguous United States, productivity varies only by one order of magnitude, and strong productivity effects on secondary production and biomass may only be apparent when a wider range of ecosystems are considered (i.e. when comparing along gradients from tundra to tropical systems; [16]). A study in South Africa along a productivity gradient comparable to that in our study similarly found that moth abundance did not vary in response to productivity [17].

We show clear support for temperature as the strongest driver of radar-observed insect flight activity. However, extrapolating from this study to insect abundance patterns generally is challenging, as insect activity observed in the air may not be representative of overall insect abundance in a system. Only a subset of insect species fly at altitudes high enough to be visible on radar, although those that do are diverse in size, life history, feeding strategy and order [39]. High-altitude flight may be more common in some biomes than others, for example because open habitats produce more convective lift to bring insects aloft [47]. However, our main result identifying temperature rather than annual net primary productivity as a strong driver of insect activity density was consistent both within and across biomes. Moreover, this corresponds with patterns of invertebrate biomass moving across the soil surface [46], suggesting that this pattern may be general beyond flying insects.

Systematic bias may also arise when an individual's propensity to engage in flight behaviour varies across habitats or latitude. Flight is an energetically expensive activity, which is temperature limited and does not occur below a lower temperature threshold [48]. At higher latitudes, where temperatures are typically cooler, insects may be present in similar abundances as at lower latitudes but less likely to engage in flight behaviour. A temperature–activity pattern can result from differences in the inclination to move as well as differences in population size. This potential bias is present in all activity-based entomological methods, such as pitfall traps or nationwide butterfly counts (i.e. the UK 'Big Butterfly Count'), and is specifically challenging for large-scale analyses spanning a wide gradient in habitats or temperature [16]. A deeper understanding of spatial variation in insect movement behaviour is integral to the use of activity density-based methods in large-scale insect monitoring. With these considerations, weather surveillance radar can

prove a valuable tool for addressing macroecological questions, given the standardized nature of data collection and the spatial extent of nationwide weather radar networks, which frequently span climatic gradients and multiple biomes.

While flight abundance increased with temperature across all biome types in the study, the magnitude of the response was mediated by biome type. The strongest effect of temperature on insect flight abundance occurred in temperate and subtropical grasslands, with less strong increases in flight abundance with temperature in coniferous and broadleaf subtropical and temperate forests, and the smallest effect of temperature on flight abundance in arid-xeric shrublands. In forested biomes, the effects of temperature may be less strong due to differences in microclimate; insects likely experience buffered temperatures under the forest canopy. In arid and xeric shrublands, temperature effects on abundance are likely mediated directly or indirectly by water limitation. In this biome, residual variation after accounting for temperature varied across a productivity gradient, indicating that low productivity sites observed lower flight abundances than expected based on temperature. Similarly, temperature residuals varied with precipitation in forest biomes, with lower abundances at drier sites. These results indicate that other gradients, and particularly direct and indirect water limitation, affect the way temperature drives insect flight activity.

Our results suggest that in spite of higher productivity, insect flight abundances were lower in temperate forests than in grasslands or other biomes. This pattern of high altitude insect flight corresponds with observations of day-flying butterfly abundance in the US, which found highest abundance in the Great Plains region [18], and flying insect abundance in Germany (at ground level), where insect biomass was lowest in forests [49]. Forests may provide fewer floral resources for flying insects [50]. Grassland productivity may also be more readily available for conversion to insect biomass, as more of it is stored in leaf or underground material. By contrast, biomass in forests is heavily defended by secondary metabolites and plant structural elements such as lignin, which reduce incidence of herbivory, reducing herbivore population sizes and reproductive success [51]. The difference between forest and grassland insect flight abundances may also result indirectly from temperature. Forest microclimates experience lower air temperatures, as solar radiation is intercepted by the canopy. This difference between interpolated temperature data at 1-km resolution and effective local temperature may result in the residual differences in observed insect flight abundance in our study. Lastly, radar-based estimates of insect abundance measure flight activity, and observed activity density is a function of both the number of individuals present in a system and their velocity [16]. In forested habitats, increased structural complexity of the habitat likely reduces velocity, and may then result in lower observed activity density. A recent study on activity density of insects moving across the soil surface suggested that differences in velocity across habitats in the US was an important driver of variation in pitfall trap observations at NEON sites spanning from Alaska to Puerto Rico [46]. This insight complicates entomological sampling that depends on activity (i.e. pitfall traps, flight intercept traps, radar observations), introducing bias if the relationship between observations of activity density and population size differs between systems. Understanding the relationship between abundances on the ground and in the air, and direct measurements of velocity and activity in different habitats, would provide insight into these hypotheses.

Temperature constrains metabolic activity and development time [52], and high latitudes may not accumulate the thermal units necessary for reproductive success in some taxa. Insect species may have fewer generations in parts of their range with lower temperatures and shorter growing seasons, and taxa may also increase population sizes in response to temperature. For example, during warmer years, 190 out of 263 lepidopteran species in central Europe had increased abundance in the second or following generations relative to the first generation [53]. However, such responses have rarely been studied at levels above the population, and results on large-scale abundance across taxa are mixed. Continental patterns in US butterflies did not show a positive relationship with temperature or latitude [18], while NEON pitfall traps found higher abundances in warmer regions [46].

Differences in the importance of temperature and productivity as drivers of insect abundance may vary across taxa, particularly between herbivores and higher trophic levels. The rate at which energy is converted into resources, and the relationship between resource availability and temperature or precipitation, likely varies between types of resources. We lack life-history information in this study, as radar-based estimates of insect flight abundance are agnostic to species identity, although diurnal insect flight at higher altitudes is commonly made up of a combination of aphids, hoverflies and butterflies [39,54]. However, taxonomic composition will vary across sites, and the assemblage of flying insects likely shifts throughout the growing season as different species cycle in and out of seasonal abundance. While this complicates interpretation of the observed spatial patterns in flight abundance, shifts in composition across a sampling gradient is common regardless of sampling method.

Our findings that insect flight abundance does not correlate with productivity at regional scales has implications for species richness–energy theory, which aims to explain macroecological patterns in species richness as a function of productivity. One mechanism for this pattern hypothesizes that more productive areas support larger numbers of individuals, which leads to higher population sizes, lower extinction risk, and thus higher diversity (i.e. the More Individuals Hypothesis; [4]). However, experimental tests of this hypothesis in tree hole invertebrate communities found increased richness but not higher abundances in more productive tree holes [55]. Similarly, productivity was positively correlated with moth diversity, but not with abundance, in South African savannahs [17]. These results suggest that the role of abundance in driving species richness is complex [56], or that greater richness in productive areas is more likely to result from other mechanisms, such as greater niche breadth, reduced physiological limitation, or higher diversification rates [2].

Increased warming patterns under global change are likely to affect insect abundances. In particular, in temperate areas higher temperatures may result in higher abundances, while in other areas increased warming may generate high enough temperatures to cause overheating or heat avoidance behaviours [57,58]. While the magnitude of climate warming may vary across latitude, the consequences of such warming may also vary in predictable ways, with biome-specific patterns. Understanding large-scale drivers of insect abundance is key to predicting how insect populations will respond to ongoing global change.

Data accessibility. All data used in the study is publicly available. NEXRAD radar data is archived and publicly available from Amazon Web Services: <https://noaa-nexrad-level2.s3.amazonaws.com> [59].

Extra figures and tables are provided in electronic supplementary material [60].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.K.T.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; J.K.: conceptualization, funding acquisition, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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Endnotes

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