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Spatial and temporal patterns of insect-order activity in the fynbos, South Africa

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Abstract
The fynbos of South Africa is renowned for its high richness of plant species, many of which are insect-pollinated. We conducted a visual survey of arthropod activity to examine how environmental factors influence activity patterns across the biome. We estimated the activity of moving medium- to large-sized Hymenoptera, Diptera, Lepidoptera and Coleoptera using an abundance-weighted presence score. Broken stick regression analysis shows that insect activity increased with ambient air temperatures to between 22 and 30 °C and then stabilized in the case of Hymenoptera, or decreased for Diptera, Lepidoptera and Coleoptera. There was also a clear negative impact of wind speed on arthropod activity. Insect activity across the biome was poorly explained by landscape temperature and rainfall variables, and was instead best explained by flower availability. A summer-autumn survey observed greater insect activity with no within-month variation, while the transition from winter to spring for the winter-spring survey saw more insect activity associated with the later months. More detailed studies of activity in the fynbos are needed at the species level, as predicted climate change impacts on temperature suggest likely consequences for plant-pollinator interactions, agricultural pest species, and arthropod-predator interactions.

Keywords: Coleoptera, Diptera, Hemiptera, Lepidoptera, Cape Floristic Region.

Introduction

Insect activity is important because the movement of insects is associated with various ecological services ranging from pollination [1], pest control [2] to seed dispersal [3], but also spread of disease [4] and predation of economically important crops [5, 6]. Ecological processes are of particular interest in the fynbos biome, where plants are heavily reliant on insects for seed dispersal and pollination [7, 8] and the risk of plant extinction among the Cape flora from failed pollinator or dispersal mutualisms is high [9].

The Cape Floristic Region, dominated by mountain fynbos, is famous as a biodiversity hotspot and centre of plant endemism [10]. Invertebrate communities here have been the focus of several studies on arthropod diversity and abundance [e.g. 11, 12-14]. Compared to plant species richness of the fynbos arthropod species richness is not notably higher compared to other southern African biomes as the vegetation is a poor food source for herbivores and is morphologically simple [15, 16]. However, some insect families are notably species rich and dominated by species of conservation concern [17].

While many arthropod species depend on plants for food, and are influenced by vegetation structure [18], their activity is also influenced by different abiotic factors like rainfall, altitude, temperature or wind [19-21]. This can result in seasonal peaks in abundance and species richness, for example spider species richness was highest in autumn on the fynbos shrub *Protea nitida* [22] and arthropod abundance and richness in protea inflorescences was higher in autumn and winter [23]. The abiotic environment often varies along altitudinal gradients, with consequences for composition and activity of arthropod assemblages.

Insects often show specific annual activity patterns frequently linked to phenology [24]. In north-temperate regions, these patterns are often triggered by photoperiod in combination with temperature and humidity [25] causing high insect activity usually during spring and summer, but similar phenological patterns have not been well documented in the southern-temperate regions [26]. In this paper we identify temperature thresholds for the activity of four major arthropod orders: Diptera, Hymenoptera, Coleoptera and Lepidoptera. We further model activity in relation to broad spatial and temporal parameters for a biome-wide survey in the fynbos. We predict that activity patterns to be limited by those linked to temperature and moisture gradients, the main predictors of insect activity.

Methods

Study area

The fynbos occurs on nutrient-poor soils in and around the Cape fold mountains of South Africa [10]. It is dominated by small and leathery-leafed shrubs (notably Ericaceae, Proteaceae, Rutaceae and Geraniaceae) and evergreen, grass-like perennials (Restionaceae) [10]. While lowland areas are heavily transformed by agriculture [27], very little anthropogenic land transformation is found in montane range heartlands [28]. Fynbos is a fire dependent vegetation type, with an intermediate fire return interval of 7 – 40 years [29, 30]. Fire is an important natural disturbance essential to the life-history strategies of many fynbos plant species and insects [14, 31]. Temperatures of the fynbos are generally mild (5 – 30 ºC), typical of a Mediterranean climate, with rainfall highest in the southwest mountains with over 1 000 mm but ranging from 250 to 650 mm per year [32]. Rainfall occurs predominantly during the austral winter months in the western regions of the fynbos, but falls throughout the year further east.

Estimation of arthropod activity

Arthropod activity was monitored using a point-based visual survey method. Visual observations were conducted for ten minutes of both birds and arthropods. The numbers of insects observed for each order were scored into three categories (1: 1-10 individuals, 2: 11-100, 3: >101). This is thus an index of activity weighted by abundance, which we refer to simply as activity. As counts were conducted from around daybreak, this survey is biased for above ground, diurnal, non-cryptic and mobile insects of medium to large size (> 0.5 cm).

We consider Hymenoptera as the group of mostly flying insects excluding Formicidae as ants are usually ground dwelling and in high abundances, especially near their nest, so this group may have a deviating influence on a group more associated with their pollination abilities. For each order except Lepidoptera, activity was scored for a radius of five meters around the researcher. For Lepidoptera, a radius of 25 meters was chosen due to good visibility of flying specimens, so relative activity is not comparable between groups. Overall visible arthropod activity in the fynbos was low: no arthropod activity was recorded for 47.5% of summer and 50.9% of winter surveys. Diptera were observed during 288 surveys of the 887 summer survey points (32%), Hymenoptera (15%), Lepidoptera (12.6%) and Coleoptera (4.5%). These represent the four groups most dominant in Protea inflorescences [6].

Spatial and temporal patterns of arthropod activity

During 2012 a biome-wide survey was conducted at 899 points across the fynbos biome, consisting of two monitoring periods: one over the late summer-autumn period (January – June; summer); and a second repeat survey during the winter-spring period (July – October; winter). At each survey point the following abiotic information was recorded: longitude, latitude and altitude (using a Garmin Etrex GPS), date and time. Temperature and wind speed were measured using a Kestrel 3000 handheld weather station (Nielsen Kellerman, USA). Cloud cover was estimated by a horizon to horizon visual scan to the closest 10% (0 = no clouds, 100 = overcast).

Vegetation height from a radius of 25 m was calculated as the average height from a subset of over 200 plant species or functional groups, with height recorded as <0.25 m, 0.5 m, and for 0.5 m increments from thereon, weighted by basal cover (to closest 10% of each species or functional group, a Braun-Blanquet method modified from Siegfried and Crowe [33]). Flowering capacity was scored for non-wind pollinated species (from 0 with no flowers to 100% with all branches with flowers in a state receptive to pollination). A combined flower score was calculated for each point based on the sum of: (flower score * basal cover * height) for each group, divided by sum of basal cover for all groups. The time since fire was estimated in the field from growth nodes of *Protea* species where possible, and cross-checked against local knowledge or fire incidence maps held by Cape Nature, a provincial conservation body. The following fire age categories were considered: 0-5 years since fire, > 5 years since fire, and mixed/ indeterminate. We extracted the mean annual temperature (mat) and mean annual rainfall (rainfall) for each point from the Hijmans, Cameron [34] Worldclim dataset. Monitoring was not conducted under poor weather conditions including very high winds or rain. Sites with more than 50% of alien vegetation were not monitored (we assume these areas will have lower activity as per Magoba and Samways [35].

Data analysis

The influence of weather on arthropod activity

Davies‘ tests using the segmented package in R [36] were used to detect changes in the slopes of relationships between activity scores and air temperature. Where the Davies‘ test identified a significant change in a slope, broken stick regression analyses, using the segmented package (Muggeo 2003), was used to define the inflection points in temperature above which activity changed for each group. We examined correlations between wind (km/h), temperature (ºC) and percentage cloud cover on arthropod activity using Spearman’s ranked correlation coefficients.

Spatial and temporal modelling of arthropod activity

To explore spatial and temporal patterns of arthropod activity we used zero-inflated negative binomial regression for modelling arthropod activity using R package pscl [37], as the influence of temperature and wind likely resulted in excessive zeros. The excess zeros are likely generated by a separate process from the count values and can be modelled independently using this package. We choose logistic regression over Poisson models after initial modelling showed this to be more suitable for these over-dispersed counts. We model activity for each of the four orders as a function of: month, vegetation height, logged flower score, altitude, rainfall, mean annual temperature, latitude, longitude and numbers of groups of birds recorded during each count. We modelled zero-inflation as a function of time (hour), temperature, and wind speed and vegetation height. We present model averaged results for the top models (delta AIC <2) using the R package MuMIn [38]. Each survey was modelled separately, and after accounting for missing values summer n = 808 and winter n = 688.

Results

Influence of temperature, cloud and wind

There was a clear impact of the weather variables on observed insect activity, with temperature and wind having the greatest influence (Table 1, Figures 2 & 3). Inflection points for peak arthropod activity were detected for the four most common groups, all of which fell between 20 and 30 ºC for this survey where temperatures ranged from -1 °C to 38.4 °C (25-75% quantiles for summer: 16.6 – 24 °C, winter: 10.4 - 17 °C).

Table 1: Temperature inflection points for arthropod activity for four insect orders in the fynbos

Order:	Davies' Test for change in slope (p)	Temperature of activity inflection	Std. error
Diptera	< 0.001	22.8	1
Lepidoptera	< 0.001	30.06	1.9
Hymenoptera	< 0.001	23.02	1.5
Coleoptera	< 0.001	24.4	2.1

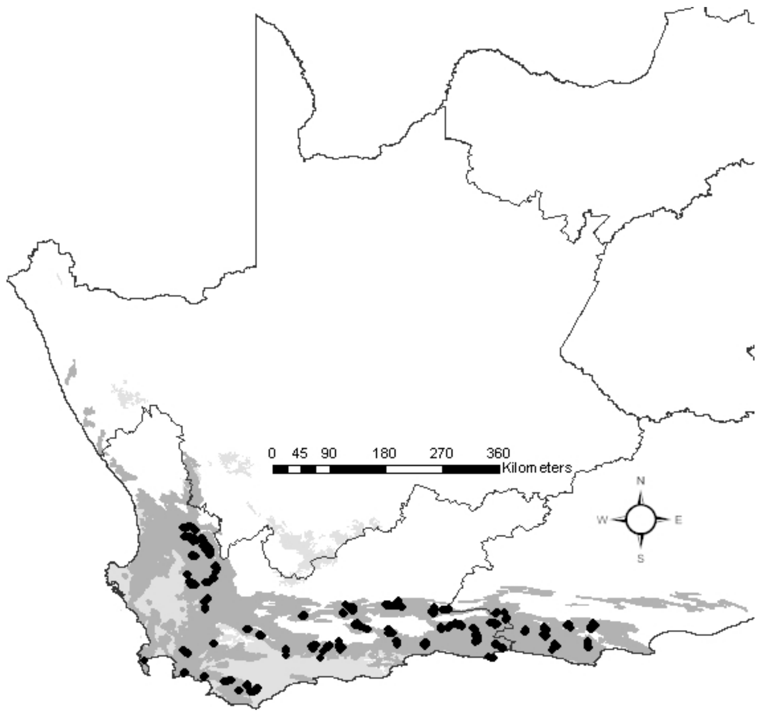

Fig 1: Study area and study sites. The fynbos bioregion where the survey has been conducted is shaded dark grey. Light grey areas are bioregions excluded from the survey which belong additionally to the Cape Floristic Region according to Mucina and Rutherford [51]. The location of survey points are indicated as black dots.

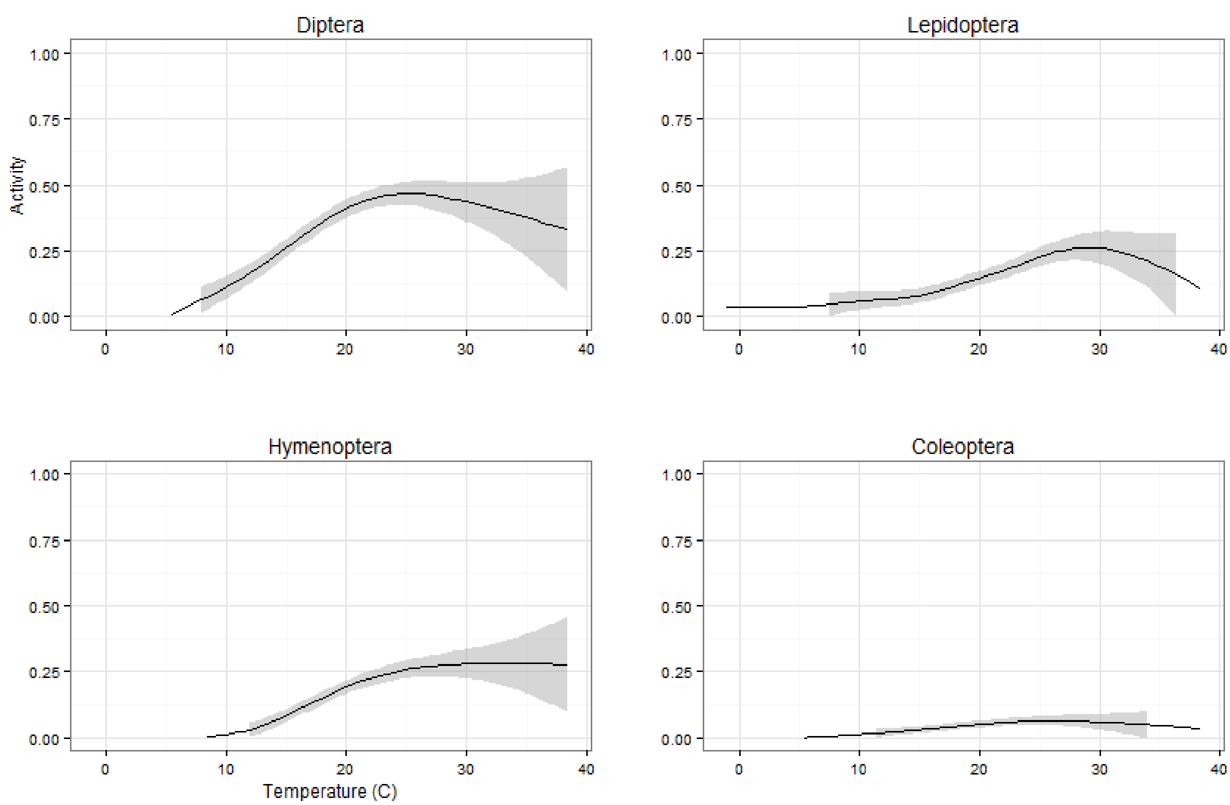

Fig 2: Arthropod activity in relation to air temperature in °C for four orders of insects across the fynbos. The line is a loess smoother of mean insect activity across all points for each order, with shading indicating standard error.

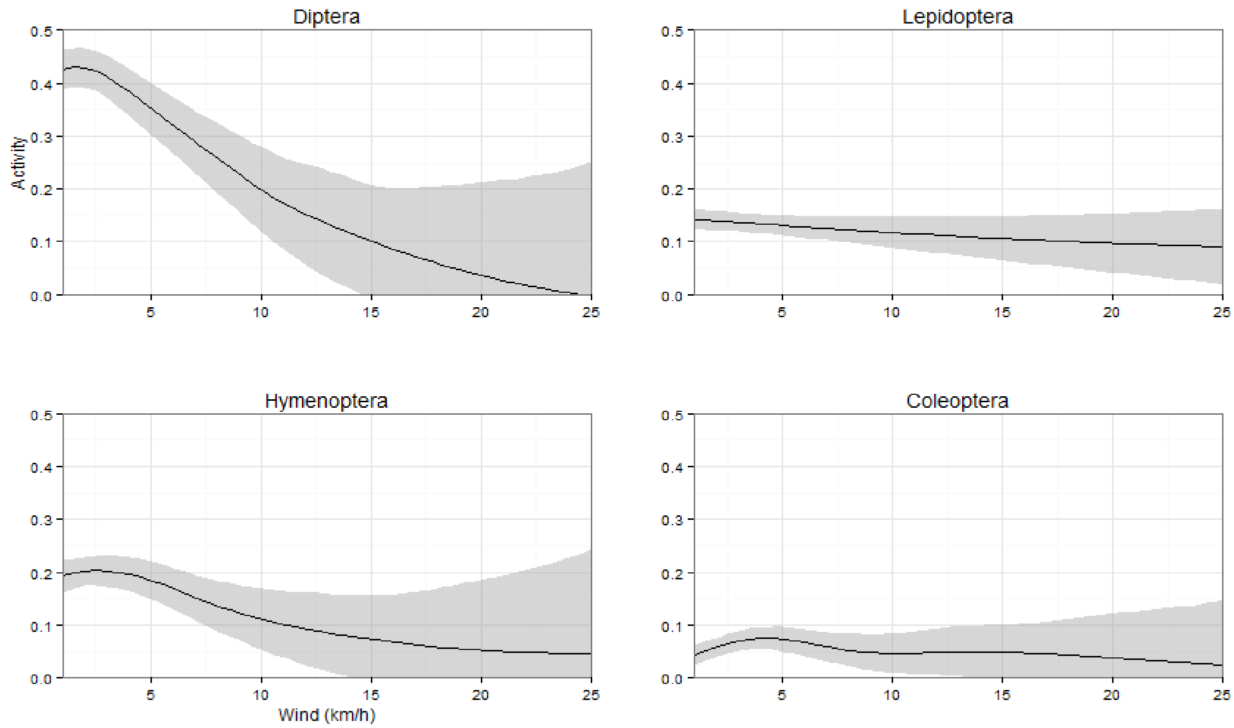

Fig 3: The influence of wind on insect activity. Mean activity across all points is plotted against wind speed via a loess smoother with shading indicating standard error.

Arthropod activity was negatively correlated with wind speed as well as cloud cover (wind: rs = -0.11, $p < 0.01$, n = 1513, cloud: rs = -0.14, $p < 0.01$, n = 1579). Cloud cover was negatively correlated with temperature (rs = -0.18, $p < 0.01$, n = 1579) and for temperatures of >19 ^{o}C, no cloud effect on arthropod activity was observed (rs = -0.2, p = 0.69, n = 770). The influence of wind on arthropod activity was not evident for wind speeds <6km/h (rs = -0.1, p = 0.8, n = 604).

As expected, in the spatial and temporal models temperature accounted for most of the zero-inflation observed in the activity scores across all insect orders (Table 2). Wind and vegetation height were less important, while time of survey was least important, possibly as this variable co-varies with temperature.

Table 2: Model averaged covariate values explaining zero-inflation in observed insect activity for models within delta 2 AIC of the top model for four insect orders across two survey periods (summer-autumn/winter-spring) across the fynbos biome. Significant predictors are indicated in bold ($p < 0.05$). Missing values indicate covariates not in the averaged model. Veght = vegetation height; hour = time survey was conducted to within the hour; temp = temperature (^{o}C); wind = wind speed in km/h. Importance is the importance of the covariate in the list of top models (1= high).

Model covariates	**Summer**					**Winter**				
	Estimate	Std. Error	z value	Pr(>|z|)	importance	Estimate	Std. Error	z value	Pr(>|z|)	importance
Coleoptera										
Intercept	13.794	6.404	2.154	0.031	0.000	6.937	1.803	3.847	0.000	0.000
Hour	-1.529	0.921	1.660	0.097	0.852					
Temp	-0.057	0.144	0.396	0.692	0.217	-0.461	0.128	3.614	**0.000**	1.000
Veght	0.011	0.088	0.124	0.901	0.068	0.106	0.302	0.350	0.726	0.173
Wind	0.021	0.116	0.182	0.856	0.077	0.002	0.020	0.103	0.918	0.028
Diptera										
Intercept	16.388	4.948	3.312	0.001	0.000	26.221	37.149	0.706	0.480	0.000
Hour	-0.100	0.219	0.457	0.648	0.298	-1.731	2.931	0.590	0.555	1.000
Temp	-1.163	0.332	3.507	**0.001**	1.000	-1.639	2.177	0.753	0.452	1.000
Veght	0.309	0.338	0.915	0.360	0.593	0.032	0.228	0.142	0.887	0.116
Wind	0.247	0.189	1.307	0.191	0.875	1.230	1.915	0.642	0.521	1.000
Hymenoptera										
Intercept	553.329	734.630	0.753	0.451	0.000	8.958	1.984	4.516	0.000	0.000
Hour	7.420	12.916	0.575	0.566	1.000	0.251	0.152	1.652	0.099	0.933
Temp	-37.685	51.272	0.735	0.462	1.000	-0.779	0.162	4.815	**0.000**	1.000
Veght	11.957	16.782	0.713	0.476	1.000	0.003	0.031	0.106	0.916	0.035
Wind	-20.548	29.017	0.708	0.479	1.000	0.119	0.103	1.149	0.251	0.784
Lepidoptera										
Intercept	4.415	2.324	1.900	0.057	0.000	-263.83	665.918	0.396	0.692	0.000
Hour	0.354	0.506	0.700	0.484	0.819	14.732	36.465	0.404	0.686	0.940
Temp	-0.548	0.478	1.147	0.252	1.000	-0.287	0.253	1.133	0.257	0.663
Veght	0.122	0.238	0.512	0.608	0.347	11.239	29.263	0.384	0.701	0.805
Wind	0.053	0.100	0.530	0.596	0.358	2.597	6.365	0.408	0.683	0.700

Spatial and temporal modelling of arthropod activity

Overall, support for the hypothesis suggesting that insect activity should be higher in regions of higher temperature and rainfall was low. Only for Diptera was there the expected increase in activity with increasing mean annual temperature. Mean annual rainfall was not identified as an important variable in any models (Table 3). For Diptera and Lepidoptera there was an observed decrease in activity with longitude i.e. a general gradient of decreasing rainfall and decreasing rainfall seasonality eastwards. Rainfall increases with altitude in the fynbos, and altitude was an important covariate explaining Hymenoptera activity in summer but not winter. Instead, the most important variable influencing spatial distribution of insect activity was flower availability, which increased for three of the four orders: Hymenoptera, Diptera and Coleoptera. The fire categories considered here were not important predictors in any of the models.

Table 3: Covariate contribution to spatial modelling and temporal modelling of insect activity. Model averaged covariate values explaining insect activity for models within delta 2 AIC of the top model for four insect orders across two survey seasons (summer/winter) across the fynbos biome. Significant predictors are indicated in bold ($p < 0.05$). Missing values indicate covariates not in the averaged model. Altitude = altitude in meters; birds = number of bird groups observed; lnflower = log of flower availability; mat = mean annual temperature; rainfall = mean annual rainfall;

	Model covariates	**Summer**					**Winter**				
Order		**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**importance**	**Estimate**	**Std. Error**	**z value**	**Pr(>|z|)**	**importance**
Coleoptera	(Intercept)	-5.894	7.222	0.816	0.414	0.000	2.566	5.592	0.459	0.646	0.000
	Altitude						0.000	0.000	0.180	0.857	0.132
	Birds	0.164	0.057	2.888	**0.004**	1.000	-0.021	0.043	0.475	0.635	0.297
	Longitude	-0.026	0.087	0.302	0.762	0.150	-0.053	0.089	0.596	0.551	0.388
	Lnflower	0.702	0.232	3.023	**0.003**	1.000	0.426	0.163	2.614	**0.009**	1.000
	Mat						-0.112	0.142	0.786	0.432	0.541
	Month	0.050	0.164	0.304	0.761	0.152	-0.022	0.097	0.230	0.818	0.096
	Latitude	-0.051	0.212	0.241	0.810	0.134	0.037	0.151	0.242	0.809	0.099
	Rainfall	0.000	0.001	0.326	0.745	0.151	-0.002	0.001	1.140	0.254	0.715
	fire >5	-0.832	0.482	1.728	0.084	0.000					
	mixed fire	-17.552	1841.336	0.010	0.992	0.000					
	Veght	0.015	0.066	0.233	0.816	0.095	-0.211	0.251	0.843	0.399	0.596
Diptera	(Intercept)	-4.037	3.582	1.127	0.260	0.000	-6.091	5.382	1.132	0.258	0.000
	Altitude	0.000	0.000	0.186	0.852	0.087	0.000	0.000	0.266	0.791	0.133
	Birds	0.000	0.002	0.025	0.981	0.010	-0.056	0.022	2.612	0.009	1.000
	Longitude	-0.011	0.027	0.422	0.673	0.243	-0.106	0.039	2.696	**0.007**	1.000
	Lnflower	0.112	0.054	2.082	**0.037**	0.989	0.026	0.052	0.496	0.620	0.330
	Mat	0.122	0.057	2.156	**0.031**	0.924	-0.007	0.027	0.241	0.810	0.182
	Month	0.016	0.042	0.391	0.696	0.220	0.385	0.110	3.514	**0.000**	1.000
	Latitude	-0.050	0.104	0.486	0.627	0.307	-0.138	0.154	0.895	0.371	0.636
	Rainfall	0.000	0.000	0.777	0.437	0.519	0.000	0.000	0.103	0.918	0.059
	Veght	-0.056	0.061	0.933	0.351	0.641					
Hymenoptera	(Intercept)	-2.401	0.720	3.336	0.001	0.000	-3.230	5.167	0.625	0.532	0.000
	altitude	0.001	0.000	3.599	**0.000**	1.000	0.000	0.000	0.183	0.855	0.069
	longitude	0.009	0.031	0.293	0.770	0.264	0.067	0.070	0.956	0.339	0.637
	lnflower	0.271	0.076	3.566	**0.000**	1.000	0.249	0.119	2.090	0.037	1.000
	Mat						-0.006	0.036	0.169	0.866	0.065
	month	-0.002	0.041	0.056	0.956	0.221	-0.195	0.154	1.265	0.206	0.789
	latitude						-0.040	0.142	0.284	0.776	0.116
	rainfall	-0.001	0.001	1.304	0.192	1.000	0.000	0.000	0.142	0.887	0.039
	fire >5						0.638	0.480	1.327	0.185	0.000
	mixed fire						0.514	0.493	1.042	0.297	0.000
	Veght						0.010	0.036	0.292	0.770	0.173
Lepidoptera	(Intercept)	-37.281	16.187	2.303	0.021	0.000	-10.166	1.574	6.458	0.000	0.000
	altitude	0.003	0.001	1.843	0.065	1.000	0.001	0.001	1.097	0.273	0.663
	Birds	-0.001	0.009	0.065	0.948	0.069	0.002	0.010	0.149	0.882	0.057
	longitude	-0.274	0.084	3.277	**0.001**	1.000					
	lnflower						0.050	0.093	0.543	0.587	0.396
	Mat	0.367	0.344	1.068	0.285	1.000	-0.003	0.025	0.133	0.895	0.065
	month	-0.006	0.021	0.279	0.781	0.072	0.923	0.178	5.172	**0.000**	1.000
	latitude	-1.015	0.354	2.868	**0.004**	1.000					
	rainfall	0.000	0.000	0.275	0.783	0.071					
	Veght	0.008	0.042	0.201	0.840	0.138	0.004	0.030	0.137	0.891	0.127

For the four orders, there were several notable differences between covariates identified as important for the summer and winter surveys, most notably for Diptera where no variable was identified as a common covariate between surveys. The explicit temporal variable – month – was only identified as important for Diptera and Lepidoptera, and here only during the winter survey, possibly associated with the change in flower availability from winter to spring, especially in the aseasonal rainfall regions.

Significant intercept values for Hymenoptera and Lepidoptera indicates covariates other than those considered here should be considered as explanatory variables for their activity. To explore the possible confounding effect of counting bird and insects at the same time, birds was also included as a covariate in the models. The number of groups of birds seen displayed contrasting effects Coleopteran and Diptera, suggesting no systematic bias in observations to the method used here. Contrasting effects are more likely to explain the number of groups of birds as a function of the other variables examined.

Discussion

Weather effects on insect activity

Both wind and temperature significantly impacted medium to large insect activity in the fynbos, not surprisingly given that temperature has been identified as the dominant abiotic factor directly affecting herbivorous insects directly affects development, survival, range and abundance [39]. However, we are unaware of any field study that has demonstrated an upper temperature threshold to insect activity and we identify these four orders of insects in the fynbos beyond which activity levels stabilize or decrease. Insect surveys that rely on a degree of insect mobility, e.g. pit-traps and sticky traps, should consider standardizing their sampling windows for periods of temperature between 20 and 30 degrees for the four orders examined here in the fynbos: Hymenoptera, Diptera, Lepidoptera and Coleoptera.

Wind had a notable impact on arthropod activity for all orders, with very low activity under very windy conditions. The influence of wind speed has been demonstrated for different arthropod groups e.g. the number of flying adult stoneflies (Plecoptera) captured in malaise traps was negatively related to wind speed [20]; and the light trap efficiency for moths is modified by wind [40].

Climate change in the fynbos is already manifesting in terms of extreme temperature events [41] and so how ecological processes mediated by arthropods respond to increasing mean temperatures or extreme temperature events is an area in sore need of further study. As an example, while lower temperature thresholds to bee activity may mediate increased pollination efficiency by extending the pollinator activity window, extreme weather events may result in increased hive mortality. Bee fauna of the fynbos has been identified as the most vulnerable to climate change of all those occurring in South African in species distribution modeling exercises [42].

Spatial patterns of insect activity across the fynbos

Warmer areas showed only a limited association with higher activity overall across the fynbos, an area where higher altitudes are associated with cooler temperatures. On Table Mountain Pryke and Samways [13] found vegetation structure and elevation were the most important environmental variables determining surface-active invertebrate diversity. Temperature decreases with increasing altitude, and influences arthropod activity directly or indirectly as it might mediate access to food resources, such that more time can be spent foraging for resources at low than at high elevation [43]. Studies at the species level, for instance in ants across the Cederberg, showed changes in species composition due to different elevations [44]. In the Cape Floristic Region gall-insects were not significantly influenced by elevation and aspect [45], but this may be due to the temperatures buffering effects of their life-history strategy. Rainfall however increases with increasing altitude, and hence moisture and temperature with their contrasting influence on abundance act against each other, perhaps explaining the low importance of temperature, altitude and rainfall in these models of insect activity.

Flower availability was the best explanatory variable of overall insect activity across the fynbos. This spatial pattern of activity is correlated with the pattern of plant species richness documented for across the biome [46]. We by no means imply a causal relationship although Procheş and Cowling [47] found a remarkably strong positive relationship between plant and insect species richness in a local study from the fynbos. However, it would appear fynbos vegetation does not represent a significant exception from the broad positive relationship between plant diversity and insect diversity [48]. Procheş and Cowling (2006) found more species of Coleoptera, Hymenoptera, Hemiptera as well as Diptera in the Baviaanskloof area (non-seasonal rainfall area) compared to the winter rainfall region of fynbos.

There are certainly more abiotic factors influencing arthropod activity which haven't been considered in this survey. For instance, Holyoak *et al.* (1997) showed a positive correlation in some moth species to rainfall but in other species no correlation occurred, while we did not consider local rainfall events and these are known to be very important in determining insect activity [49]. Fast changing weather conditions may influence general activity patterns more than broad climatic variables. For instance, daily variation in weather altered the flight activity in moths whereas changes in abundance were low [40].

Temporal patterns of insect activity in eastern fynbos

Our survey indicated significantly higher arthropod activity in warmer compared to winter months, closely tied to changes in monthly temperature. Reasons for this would include not only detectability due to activity, but would also be a function of changes in abundance due to life-history strategies and below-ground dormancy. Procheş and Cowling (2006) found the maximum biological activity in October (spring) in the Baviaanskloof, Eastern Cape Province.

Flowering in fynbos is concentrated in spring between September and October when pollinating insects should be most evident (Johnson 1992). Indeed, we found flower availability to be the best explanatory variable of insect activity. The flora of the winter rainfall region shows a peak in September- October (spring), while the flora of the non-seasonal rainfall region shows a peak in October-November (late spring/early summer) [50].

Conclusion

This analysis focused on medium to large-bodied moving arthropods, including crawling or flying specimens of four arthropod orders. These orders represent only a small component of all free living arthropods inhabiting the surveyed fynbos habitats. Since this survey dealt with the activity of medium to large-sized main insect orders, rather than of species, our results highlight general activity patterns of quite different ecological guilds with different ecological requirements and responses. However, we believe this information will inform work analyzing the vulnerability of fynbos biodiversity to broad-scale variation in climate, whether along latitudinal or elevational gradients, and it sheds light on the limits to activity of arthropod communities.

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Author contributions

A.T.K.L. (University of Cape Town, SANBI) was responsible for field observations, data collection, analysis and writing. P.B. provided funding and made conceptual contributions.

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