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Morphological Variation Tracks Environmental Gradients in an Agricultural Pest, *Phaulacridium vittatum* (Orthoptera: Acrididae)

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Abstract

Invertebrate pests often show high morphological variation and wide environmental tolerances. Knowledge of how phenotypic variation is associated with environmental heterogeneity can elucidate the processes underpinning these patterns. Here we examine morphological variation and relative abundance along environmental gradients in a widespread agricultural pest, native to Australia, the wingless grasshopper *Phaulacridium vittatum* (Sjöstedt). We test for correlations between body size, wing presence, and stripe polymorphism with environmental variables. Using multiple regression and mixed-effects modeling, body size and stripe polymorphism were positively associated with solar radiation, and wing presence was positively associated with foliage projective cover (FPC). There were no associations between body size or morphological traits with relative abundance. However, relative abundance was positively associated with latitude, soil moisture, and wind speed, but was negatively associated with FPC. Therefore, sites with low relative abundance and high forest cover were more likely to contain winged individuals. Overall, our results suggest that environmental and climatic conditions strongly influence the relative abundance and the distribution of morphotypes in *P. vittatum*, which is likely to affect dispersal and fitness in different landscapes. This knowledge is useful for informing how environmental change might influence the future spread and impact of this agricultural pest.

Key words: wingless grasshopper, *Phaulacridium vittatum*, agricultural pest, relative abundance, morphological variation

The distribution, abundance, and phenology of several insect pests have altered in response to changing climatic conditions (Olfert and Weiss 2006, Parmesan 2007, Trnka et al. 2007, Da Silva et al. 2011). Shifts in environmental variables, such as temperature, play a key role in the severity of phytophagous insect pest infestations (e.g., Baker et al. 2015). Major outbreaks of phytophagous insects are exacerbated by ongoing warming conditions and extreme climatic events such as drought and floods (Jepsen et al. 2008, Zhang et al. 2009). Furthermore, the negative impacts of phytophagous insect pests on crop production (Oerke 2006) and forest harvest (Aukema et al. 2011) are often economically significant (Bradshaw et al. 2016). Therefore, it is important to understand the environmental determinants and interactions that facilitate the occurrence and spread of insect pests under currently shifting climatic regimes.

Some insects show variation in genetic, physiological, and morphological traits across broad climatic gradients (Lancaster et al. 2015, 2016, reviewed in Hoffmann et al. 2017, Dudaniec et al. 2018). For insect pests, variations in morphological traits may confer benefits that enable wide environmental tolerances, survival, and colonization across large geographic areas (Gomez and Van Dyck 2012, Parsons and Joern 2014, Bai et al. 2016), or increased chances of spread through efficient use of local resources (e.g., as shown in pest aphids; Simon and Peccoud 2018). The relationship between environmental variables and the distribution of morphological variation can therefore be indicative of the capacity of insect pests to persist under shifting environmental conditions and may also provide evidence for local selection processes.

Polymorphism in insects can be maintained by various mechanisms such as balancing selection (Lindtke et al. 2017), a combination of multiple selection pressures (Takahashi et al. 2011), or adaptive or nonadaptive phenotypic plasticity (Ghalambor et al. 2007, Kelly et al. 2012, Sgrò et al. 2016). Morphological traits may also be regulated via frequency or density dependence. In this case, the fitness of different morphs shifts in response to their prevailing frequencies or in response to competitive interactions among conspecifics (Le Rouzic et al. 2015, Lancaster et al. 2017, Nosil et al. 2018). In addition, a clear role of climatic and ecological factors in shaping morphological variations in insects is reported in several

studies (Dearn 1990, Zera and Denno 1997, Chown and Gaston 2010). For example, different color morphs can be selected for according to local environmental variables (Tanaka 2004, Tanaka et al. 2012). Dispersal traits such as wing dimorphism may show variation under temporally and spatially diverse climatic gradients (Harrison 1980, Roff 1986) and in relation to photoperiod, temperature, and latitude (Sasaki et al. 2002, Zeng and Zhu 2014, Rosetti and Remis 2018). Variation in climate can also shape the distribution of insect body size along latitudinal gradients (Masaki 1967). A necessary step in understanding these relationships is tearing apart environment effects on morphological traits and their influence on fitness. For example, different morph frequencies may confer differential survival according to local climatic conditions (Forsman 1999). For insect pests, such information offers a starting point for characterizing species resilience under shifting climatic conditions.

Here, we examine how morphological traits vary along environmental gradients in a widespread agricultural pest, the wingless grasshopper, *Phaulacridium vittatum* (Sjöstedt), an endemic species to Australia. Adult grasshoppers exhibit morphological variation in three key traits: wing presence/absence, stripe polymorphism (Fig. 1; three distinct morphs; Dearn 1984, Key 1992), and body size (both within and between sexes; Key 1992). Body size of males (ranging from 6 to 9 mm) is smaller than females (average size of 6–13 mm; Key 1992). *Phaulacridium vittatum* has nonoverlapping generations, with eggs undergoing diapause in winter, and the first hatchlings emerging in spring between October and November (Clark 1967). Development involves five instar stages, and adults survive until late March and April. Prior to European colonization of Australia, *P. vittatum* was restricted to savannah woodlands or grasslands, but with forest clearing for pasture and agriculture, suitable breeding habitat increased dramatically, contributing to the species' current widespread distribution and high abundance that can reach pest proportions (Dearn 1984). Adult grasshoppers cause damage to pasture, gardens, economically important crops (Clark 1967, Roberts 1972), and juvenile eucalyptus trees (Loch and Floyd 2001) and can compete with livestock for pasture (Bailey et al. 1994). Severe outbreaks can be cyclic and have been documented every 4 or 5 yr in areas with suitable habitats and weather conditions (Milner et al. 1994).

Several selective forces may be responsible for maintaining morphological polymorphisms in *P. vittatum*. For example, stripe polymorphism in *P. vittatum* appears to be maintained by disassortative mating (i.e., increased frequency of matings between striped and unstriped individuals) as documented by Dearn (1980, 1984). Another potential selective force maintaining stripe morph in *P. vittatum* is frequency-dependent selection exerted by predators (Dearn 1984) as reported in other species (Losey et al. 1997, Gray and McKinnon 2007).
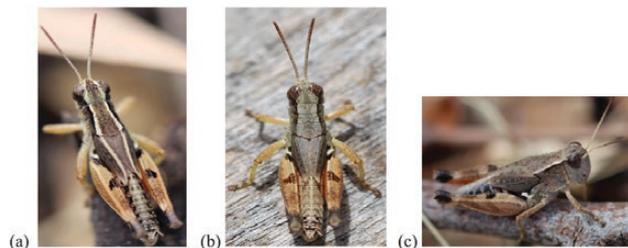

Fig. 1. Stripe polymorphism in *Phaulacridium vittatum*: (a) fully striped morph with two full longitudinal white stripes, (b) unstriped morph, (c) partially striped morph with two partial white stripes (photographs by S. Yadav).

Evidence also suggests that morphological variation in *P. vittatum* is influenced by latitude, climatic variables, and habitat type. Latitudinal cline in stripe pattern polymorphism has been suggested in previous studies (Dearn 1981). Radiation seasonality and rainfall best explained latitudinal clines in *P. vittatum* body size (Harris et al. 2012). Furthermore, thermoregulatory effects of melanism have been shown in this species, where darker colored individuals (without stripes) maintained a higher body temperature than lighter color individuals (Harris et al. 2013a,b). In terms of habitat type, unstriped morphs were present at a higher frequency in more forested habitats, perhaps a result of camouflage advantage (Dearn 1984). In addition, a higher frequency of winged individuals was observed in shrub-dominated areas, forest margins, and gardens than in open pastures (Clark 1967). Despite these early studies, little is known of the broader spatial distribution of morphological variation or abundance of *P. vittatum* in relation to local environmental variables, which is important for understanding the ecology and potential spread and persistence of this agricultural pest.

With morphological, environmental, and site relative abundance data collected for *P. vittatum* across 36 sites spanning an eight degree latitudinal gradient (from 29.18° S to 36.50° S) along the east coast of Australia, we examine 1) the effect of latitude and environmental variables (i.e., soil moisture, precipitation, wind speed, solar radiation, and foliage projective cover [FPC]) on site relative abundance and the frequency of morphological traits (body size, wing presence/absence, and stripe polymorphism) and 2) evidence for density-dependent selection on morphology by examining the interaction between site relative abundance and the frequency of morphological traits.

Materials and Methods

Sampling

Phaulacridium vittatum grasshoppers were sampled from late January to early February of 2017 when most individuals had reached maturity. In total, 36 sites were sampled across the east coast of New South Wales spanning ~900 km, covering eight degrees of latitude (from 29.18° S to 36.50° S), a mean annual temperature gradient of 4.6–17.4°C, and an elevation gradient of 133–1,966 m asl (Supp Table S1 [online only], Fig. 2). Sites were located approximately 50–60 km apart, and sample sizes ranged from 6 to 34 individuals per site (mean = 28.49 ± 0.17). The elevation, latitude, and longitude of each site were recorded using a Garmin e-Trex 20 handheld GPS. Most sites were situated adjacent to or within open pastures, along roadside edges, and some sites were situated inside national parks within eucalyptus woodlands and other native shrubs. A site was declared absent of *P. vittatum* after searching for a minimum of ~15 min by three people (total search time = 45 min) without any sightings or captures.

Samples were collected either using a sweep net or by hand using small plastic containers. Habitat type does not have a large effect on spotting and catching grasshoppers as captures are largely cued by the obvious hopping activity of the grasshoppers. Similarly, stripe pattern did not introduce sampling bias as stripes are not readily visible from afar and do not influence capture rates. All collected specimens were stored on ice until processed and preserved in 90% ethanol. The following details were recorded on live samples during sample processing: sex (male/female), morphology: (winged/wingless), (striped/partially striped/unstriped), and femur length (mm), the latter being measured with digital calipers to the nearest 0.01 mm as a proxy for body size in grasshoppers (Masaki 1967).
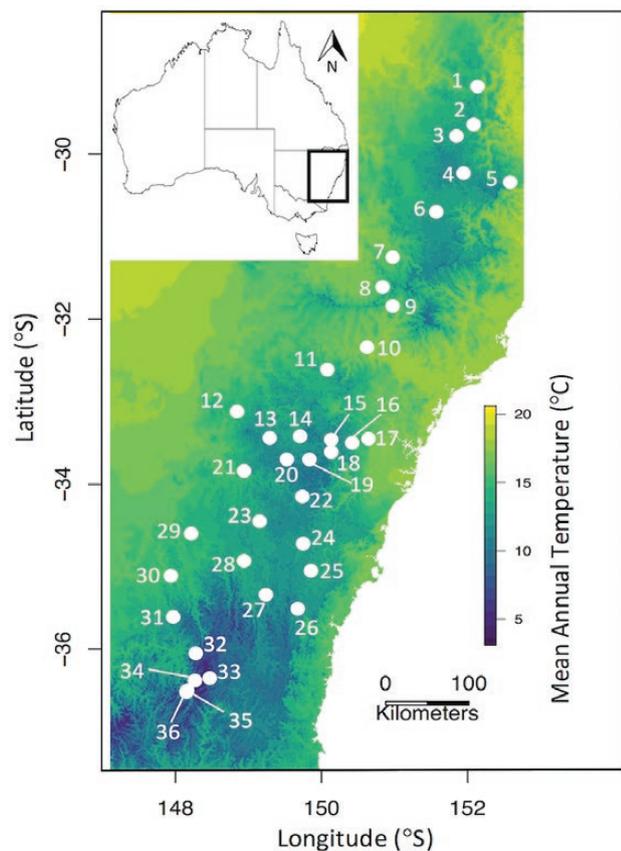
Fig. 2. Sample sites (*n* = 36) indicated by filled circles over a map of mean annual temperature (°C, BIO1) along the east coast of New South Wales, Australia.

The relative abundance of *P. vittatum* at each site was measured via capture rate per minute, calculated as the number of grasshoppers captured divided by the number of people searching multiplied by the number of minutes spent searching (Lancaster et al. 2015). All procedures were performed in accordance with the animal ethics guidelines of Macquarie University, Australia, and sampling permissions were obtained from local government authorities and national parks (license number: SL101832).

Environmental Data

Environmental variables were selected based on field observations and findings of previous studies on the ecology of *P. vittatum*. Latitude and environmental variables such as radiation seasonality and rainfall are known to influence body size variation in *P. vittatum* (Harris et al. 2012). Foliage cover is important for egg laying in this species, as eggs are laid in open areas with bare ground between vegetation patches (Clark 1967). In addition, soil properties such as soil moisture and soil type have been shown to influence density (Miao et al. 2018), oviposition, and therefore further offspring viability in grasshoppers (Herrmann et al. 2010). Wind speed was chosen because wind is beneficial for passive dispersal of insects (Drake 1994, Venette and Ragsdale 2004) and may aid in the colonization of new areas by facilitating long-distance dispersal (Anderson et al. 2010, Colombari and Battisti 2016).

Mean annual temperature (BIO1) and mean annual precipitation (BIO12) were extracted per sampling site from WorldClim v1.4 (Hijmans et al. 2005). Mean annual wind speed and mean annual solar radiation were extracted from WorldClim v2.0 (Fick and

Hijmans 2017). All data from WorldClim were used at a spatial resolution of 1 km². FPC % was extracted from a buffered area of 100 m surrounding each of the sites from the TERN AusCover database (2011) with a spatial resolution of 5 m². Data for each of 36 sites were extracted (Supp Table S1 [online only]) using the *raster* package (Hijmans and Van Etten 2014) in R v3.3.2 (R Core Team 2014).

Soil type data were downloaded from the New South Wales Office of Environment and Heritage (OEH 2017) and obtained for each sample site using QGIS v2.18 (QGIS Development Team 2009). Soil type data were then used to classify soil moisture for each site and was categorized based on the clay content and water holding capacity of the soil, as defined in the Australian Soils Classification (ASC) and Great Soil Group guidelines (GSG; Raymond 2016). Soils with high to intermediate water holding capacity based on ASC and GSG classifications were scored as 1 (high moisture), whereas soils with low water holding capacity were scored as 0 (low moisture; Supp Table S4 [online only] for site-based information).

A Pearson's correlation matrix was obtained between all environmental variables measured at each site (Supp Table S2 [online only], Supp Text S1 [online only]). After removing variables with very high correlation ($r > 0.80$), a total of six variables were used for further analyses, i.e., 1) solar radiation, 2) wind speed, 3) soil moisture, 4) FPC, 5) BIO12, and 6) latitude. Despite the high correlation between latitude and solar radiation ($r = 0.81$), we retained latitude to examine its influence on site relative abundance. Nonetheless, both variables were not used together in the same model.

Statistical Approach

All statistical analyses were performed in R v3.3.2. We analyzed our data (*n* = 954 individuals) using multiple regression, and generalized linear mixed-effects model (GLMM) and linear mixed-effects model (LMM). The statistical significance of models was examined using likelihood ratio tests within ANOVA by comparing fitted models with the null model including only the response variable, random effects (in case of the mixed model), and intercept. Insignificant fixed effects were removed from the model by applying the "analysis of deviance test" using the *drop1()* command with a chi-square test. The model was refitted after dropping insignificant fixed effects. We performed a nonlinear transformation on the response variable wherever possible (relative abundance and femur length) by using log-transformation. Site ID was included as a random effect in mixed modeling to account for nonindependence between sampling sites. To examine the goodness of fit of the GLMM and LMM, conditional R^2 statistics were calculated using the MuMIn R package (Barton 2018).

Relative Abundance

Multiple linear regression modeling was used to examine the influence of latitude, FPC, soil moisture, and wind speed on the relative abundance of *P. vittatum* at each site. In addition, the relative importance of each fixed effect and confidence intervals for relative importance were determined using the *boot.relimp()* and *booteval.relimp()* functions of the relaimpo v2.2-2 R package (Grömping 2006) by implementing 1,000 bootstraps.

Wing Polymorphism

Wing polymorphism was divided into two categories: winged individuals were categorized as 1 and wingless individuals were categorized as 0. We tested for the association of solar radiation, wind speed, FPC, soil moisture, relative abundance, body size, and stripe pattern on wing presence using GLMM in the lme4 R package

(Bates et al. 2015) and the function *glmer()*. The final model was refitted after dropping insignificant fixed effects and using site relative abundance as the random effect to account for its influence on the relationship and to provide additional explanatory power to the model.

Stripe Polymorphism

Stripe polymorphism in *P. vittatum* appears to be genetically controlled by three alleles at an autosomal locus (C^S = full stripe, C^I = partial stripe, C^P = plain) following a hierarchical dominance pattern ($C^S > C^I > C^P$; Dearn 1983). As previously done by Dearn (1978, 1981), and due to a low number of partially striped individuals in our data set, partially striped morphs were combined with striped morphs into an "any striped" category, pooling C^S and C^I genotypes. Stripe polymorphism was classified into two categories: any striped individuals were coded as 1 and unstriped individuals were coded as 0. We constructed a GLMM, using stripe polymorphism as a response variable and solar radiation, wind speed, FPC, soil moisture, relative abundance, body size, and wing polymorphism as fixed effects. After dropping, insignificant fixed-effects model was refitted using site relative abundance as the random effect.

Body Size

We fitted an LMM to examine the influence of environmental variables on body size of males and females combinedly using the *lmer()* function within the lme4 R package (Bates et al. 2015) with the fixed-effects solar radiation, BIO12, FPC, soil moisture, wind speed, and relative abundance. The final model was refitted using significant fixed effect. We conducted type II Wald chi-square tests using the "car" R package (Fox and Weisberg 2011) to obtain *P* values for the fitted model. In addition, a linear model was fitted for body size of both males and females individually with significant fixed effect.

Results

Environmental Correlations with Relative Abundance

We found a significant positive association of relative abundance with latitude ($P = 0.001$), soil moisture ($P ≤ 0.001$), and wind speed ($P ≤ 0.001$), whereas FPC showed significant negative association ($P ≤ 0.001$), with total variance explained by the model = 23% (Fig. 4, Table 1). FPC had the highest relative importance among other fixed effects followed by wind speed, soil moisture, and latitude (Fig. 3, Supp Table S3 [online only]). Several sites in our study with elevation above 1,000 m (*n* = 12 sites) had greater FPC (mean = 23.27 ± 5.92; Supp Fig. S4 [online only]), compared with sites of elevation below 1,000 m (*n* = 24 sites, mean = 10.01 ± 2.73). In the case of soil moisture, out of 36 sites, 17 were categorized as having intermediate to high soil moisture and had an average relative abundance of 0.36 (± 0.06), compared with 19 sites with low soil moisture that had an average relative abundance of 0.29 (± 0.05).

Environmental Correlations with Morphology

In total, 72 out of 954 (7.55%) individuals were winged, and 882 out of 954 (92.45%) were wingless. Within each of the 36 sample sites, the proportion of winged individuals ranged from 0 to 0.73 (mean = 0.10 ± 0.02) and wingless from 0.27 to 1.00 (mean = 0.90 ± 0.02). A positive correlation was found between FPC and wing presence (GLMM estimate = 0.03, *P* = 0.03 conditional R^2 = 0.41; Supp Fig. S2 [online only]). However, other variables did not show any significant correlation with wing presence or absence (Table 2). The addition of site relative abundance as a random effect increased the fit of the model (random effect variance: 1.94, SD 1.39).

In total, 15.6% of individuals were striped, 8.1% partially striped, and 76.2% unstriped. Within each of the 36 sample sites, the proportion of fully striped individuals ranged from 0 to 0.36 (mean = 0.15 ± 0.01), partially striped individuals ranged from 0 to 0.40 (mean = 0.09 ± 0.01), and unstriped individuals ranged from 0.58 to 0.93 (mean = 0.76 ± 0.01). The proportion of both fully and partially striped morphs in each site was positively associated with solar radiation (GLMM estimate = 0.31, *P* ≤ 0.001, conditional R^2 = 0.042). No other significant associations were observed with stripe polymorphism (Table 2). Site relative abundance had no effect on the relationship and did not explain any of the variance.

Body size varied within males (range 5.36–10.63 mm; mean = 8.25 ± 0.03 mm) and females (range 7.41–12.28 mm; mean = 10.3 ± 0.03 mm) along the sampled gradient. A significant positive correlation was found between body size and solar radiation (LMM: χ^2 = 5.56, df = 1, *P* = 0.01, conditional R^2 = 0.079; Supp Fig. S1 [online only]). However, we did not find a significant association with other fixed effects (Table 3). Males were shown to have a stronger relationship (linear model *P* < 0.001) than females (linear model *P* = 0.03). Furthermore, site relative abundance had no influence on the relationship (random effect variance = 0.0).
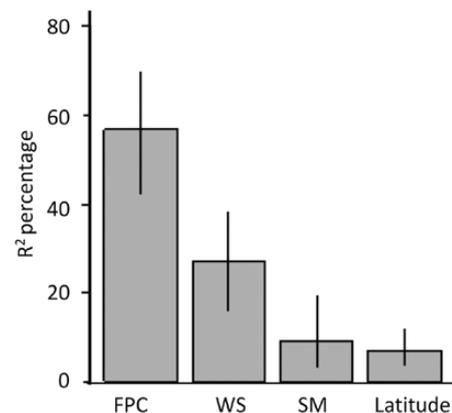

Fig. 3. Relative importance of four fixed effects on relative abundance in multiple regression analysis with bootstrapped 95% confidence intervals; FPC = foliage projective cover (%); WS = wind speed (m/s); SM = soil moisture.

Table 1. Summary of multiple linear regression analysis for site relative abundance with four fixed effects

Fixed effects	Estimate	SE	*t* value	Pr (>|*t*|)
Latitude	0.03	0.01	3.18	0.001
Soil moisture	0.22	0.03	5.99	<0.001
Wind speed	0.42	0.04	9.88	<0.001
Foliage projective cover (%)	−0.02	0.00	−14.78	<0.001

Table 2. Summary of the generalized linear mixed-effects model for wing polymorphism and stripe polymorphism

Fixed effects	Estimate	Pr (>z value)	Estimate	Pr (>z value)
	Wing polymorphism		Stripe polymorphism	
Solar radiation	0.58	0.06	**0.31**	**< 0.001**
Wind speed	−0.23	0.34	−0.08	0.66
Foliage projective cover (%)	**0.03**	**0.03**	−0.00	0.87
Soil moisture	−0.08	0.87	0.26	0.18
Relative abundance	−0.56	0.06	0.06	0.40
Body size	−0.00	0.96	−0.04	0.45
Stripe pattern	−0.07	0.82	—	—
Wing pattern	—	—	−0.05	0.85

Significant associations are shown in bold.

Table 3. Analysis of deviance table summary using type II Wald chi-square tests for linear mixed-effects model fit for body size

Fixed effects	Estimate	Df	χ^2	Pr (>χ^2)
Initial LMM				
Solar radiation	**0.03**	**1.00**	**6.66**	**0.01**
Mean annual precipitation	0.03	1.00	2.84	0.09
Foliage projective cover (%)	0.00	1.00	1.51	0.21
Soil moisture	0.02	1.00	2.42	0.11
Wind speed	−0.03	1.00	1.67	0.19
Relative abundance	0.02	1.00	0.40	0.52
Final model (after dropping insignificant fixed effects)				
Solar radiation	**0.01**	**1.00**	**5.56**	**0.01**

Significant results are indicated in bold. LMM (linear mixed-effects model).

Discussion

Our study reveals significant relationships between environmental variables, site abundance, and the distribution of morphological traits in an agricultural insect pest. We found site relative abundance was positively influenced by latitude, wind speed, and soil moisture and was negatively influenced by foliage cover. Solar radiation was the principal factor influencing stripe polymorphism and body size variation in *P. vittatum*. Furthermore, site relative abundance did not significantly associate with morphological traits, indicating no evidence for density-dependent processes governing morphological trait variation; however, this requires further investigation. Our study demonstrates how multiple environmental factors can influence the distribution of morphological variation and relative abundance of *P. vittatum*, and contributes knowledge toward our capacity to understand how widespread pests cope with heterogeneous environments via morphological variation.

Environmental Variables and Relative Abundance

Overall, higher numbers of *P. vittatum* were observed at southern latitudinal sites (Fig. 4a). Climatic variables that correlate with latitude can have strong effects on local abundance (Bale et al. 2002). For instance, in grasshoppers, climatic factors such as temperature and precipitation are critical in controlling population dynamics, both directly by influencing life-history traits and indirectly by controlling resource availability (Fielding and Brusven 1990, De Wysiecki et al. 2011, Jonas et al. 2015). However, identifying the influence of individual variables is challenging due to the complex interaction between them. For example, in our study sites, mean annual temperature is strongly correlated with mean annual precipitation ($r = -0.83$) and wind speed ($r = -0.90$; Supp Table S2 [online only]). Furthermore, some of our sites are located near or within the

Australian Alps (latitudinal range of 35–36° S), which have higher elevation (Supp Table S1 [online only]) and receive greater solar radiation (Supp Fig. S3 [online only]). These strong interactions make it difficult to effectively tease apart which variable is most significant in driving the variation in relative abundance of *P. vittatum*. Given that our model explains a modest 23% of the variance, additional factors are likely to be involved in regulating the abundance.

A decrease in relative abundance was observed with increased FPC (Fig. 4d). A higher percentage of FPC at high elevation sites in our study (Supp Fig. S4 [online only]) may hamper dispersal and connectivity among individuals, which in turn may reduce site relative abundances. Furthermore, this observed a negative association between relative abundance, and FPC is likely to be affected by site preference and resource availability. Open pastures and grazing areas are among the primary habitats of *P. vittatum*, where low FPC provides suitable sites for egg laying (Clark 1967). Furthermore, high vegetation cover negatively affects early instar survival due to a scarcity of preferable food resources that grow in more disturbed areas (i.e., prostrate and rosette-forming plants growing under pasture; Clark 1967). Last, in grasshoppers, basking is a crucial factor to regulate body temperature, facilitated by shuttling between sun and shade (Chappell and Whitman 1990), which is also exhibited by *P. vittatum* (Harris et al. 2015). Compromised thermoregulation due to high vegetation cover and reduction in suitable basking sites could influence fitness and decrease relative abundance (Kearney et al. 2009).

Sites with greater wind speed had higher relative abundance (Fig. 4c) suggesting a role of wind-assisted dispersal in the population dynamics of *P. vittatum*. In insects, wind can aid long-distance migration (Drake and Farrow 1988) and drive selection processes (Dudaniec et al. 2018), and for pest species, wind-assisted flight can lead to accelerated invasion to new areas, outbreaks, and major
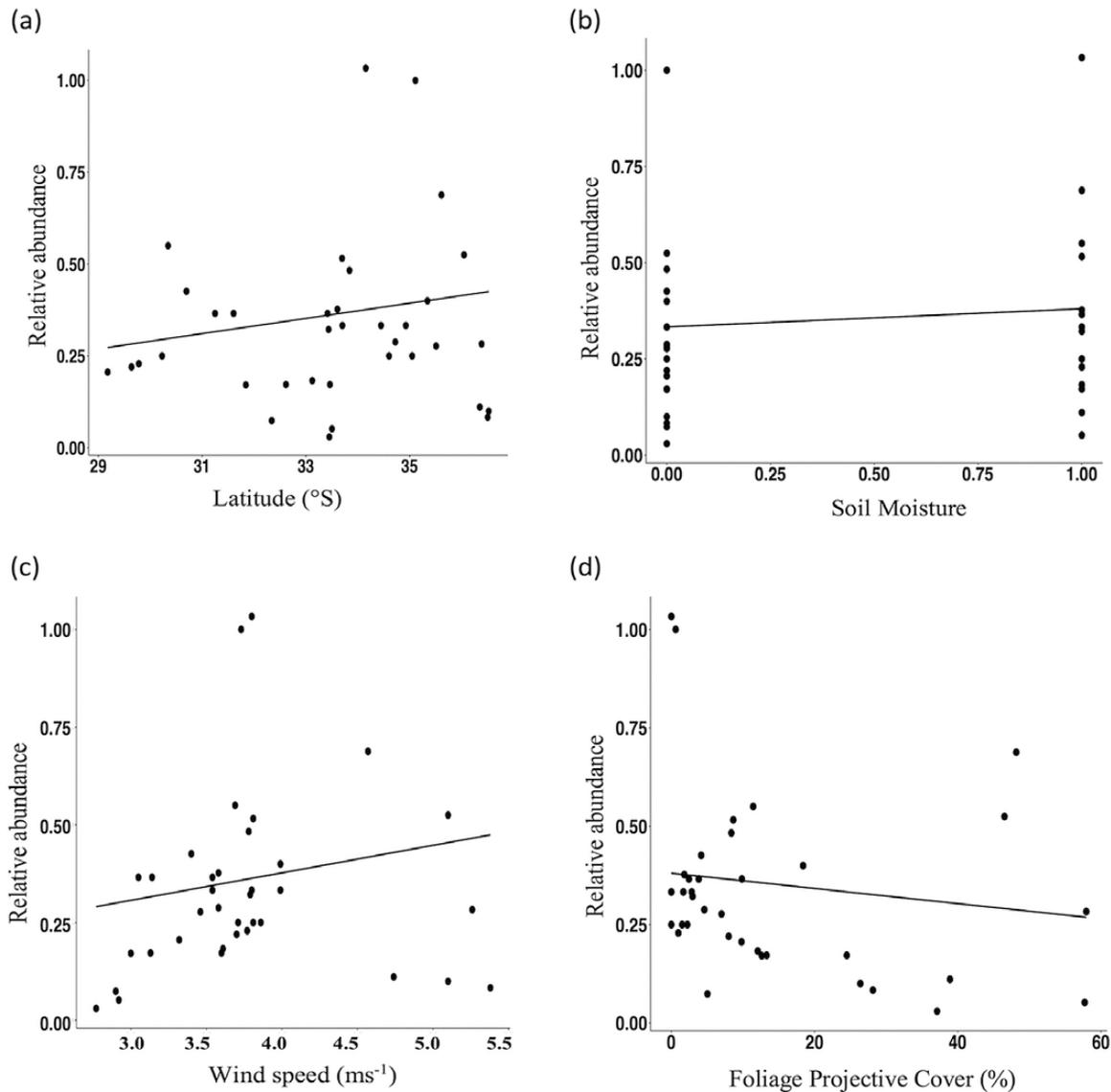
Fig. 4. The relationship between four significant fixed effects used in multiple regression analysis and relative abundance: (a) latitude: ($P = 0.001$); (b) soil moisture ($P < 0.001$); (c) wind speed ($P < 0.0001$); and (d) foliage projective cover (%; $P < 0.0001$).

crop losses (Drake 1994, Liebhold and Tobin 2008, Anderson et al. 2010). Wind speed and the presence of wings in *P. vittatum* are likely to facilitate both passive and active dispersal, respectively, facilitating its broad distribution. Wind speed can also regulate local ambient temperatures, and indeed, we found that wind speed was highly correlated with mean annual temperature ($r = -0.90$). Hence, a combined effect of wind speed and temperature is likely to be a key driver of relative abundance.

A significant effect of soil moisture on relative abundance is evident from our study (Fig. 4b). Soil can control insect abundances via influencing life-history traits of phytophagous insects, such as egg laying, nymphal development (as shown in the lubber grasshopper, *Romalea microptera* (Beauvois) (Orthoptera: Acrididae); Herrmann et al. 2010), or via regulation of habitat resources (McColloch and Hayes 1922) and controlling the growth of suitable food resources (Miao et al. 2018). Soil moisture content can support vegetation growth; this may compromise egg laying in *P. vittatum* because females preferentially lay egg pods in patches of bare ground (Clark 1967). However, high soil moisture content may facilitate food

resource availability after emergence, supporting higher relative abundances, as observed in our study. Therefore, soil moisture may influence the life stages of *P. vittatum* differentially with greater benefits after emergence than during egg and early instar phases. Furthermore, the local distributions of *P. vittatum* have been found to be influenced by the interaction between soil moisture and the occurrence of parasitic nematodes and entomopathogenic fungi (Milner and Prior 1994, Clift and Baker 1998), indicating evidence for an indirect effect of soil moisture.

Wing Polymorphism and Foliage Projective Cover
Wing polymorphism is a common phenomenon in several insects with ecological and evolutionary implications (Harrison 1980, Roff 1986). Winged and wingless morphs may be retained in different frequencies depending on environmental conditions such as temperature, precipitation (Sasaki et al. 2002, Rosetti and Remis 2018), and habitat type (Denno 1994). For instance, planthoppers (Homoptera: Delphacidae) are more likely to have wingless morphs in more stable habitats and dispersive, winged morphs in less stable

habitats (Denno et al. 1991). Our study found a larger proportion of winged individuals at sites with high foliage cover (Supp Fig. S2 [online only]), which supports the observations of a previous study on *P. vittatum* by Clark (1967), who found that the wingless form was abundant in pastures (>75% wingless adults) and the winged form was abundant in forested areas (60–70% winged individuals). Our concurrent finding that relative abundance also decreases significantly with increased FPC (Fig. 4d) indicates that high FPC sites are not the preferred habitat of this species. This suggests that high foliage sites are of lower habitat suitability for *P. vittatum* and may select for higher frequencies of traits that facilitate dispersal into new areas, such as wings (Denno et al. 1996).

The development of wings in insects can be a trade-off between dispersal and reproduction (Guerra and Pollack 2007, Guerra 2011, Steenman et al. 2015). For example, an analysis of life-history traits of 22 insect species by Roff (1986) showed wingless forms have higher fecundity and reproduce earlier than winged forms. Although wingless forms can show high fecundity and reproductive rates in stable, good-quality habitats, in unfavorable environments, winged forms may be favored for their high dispersal ability (Harrison 1980, Denno et al. 1991, Zera and Harshman 2001). The winged form of *P. vittatum* may be advantageous for dispersal during outbreaks to avoid competition with conspecifics and locate new resources. For example, in an outbreak in 1980/1981, the winged form of *P. vittatum* was found to successfully undertake dispersal distances of 100 to >500 m from the center of infested areas to favorable peripheral pastures (Farrow et al. 1982). Therefore, the presence of wings can provide additional benefit to this pest species to disperse to new areas, increasing widespread infestation. Last, population densities can also influence the frequency of winged and wingless individuals (Poniatowski and Fartmann 2009, Ríos Martínez and Costamagna 2018). Our results also indicate a possible influence of relative abundance on the presence of wings in this species, however further study on density-dependent effects of relative abundance on the frequency of wings in *P. vittatum* is needed to clearly disentangle this effect.

Stripe Polymorphism and Solar Radiation

Solar radiation is an important factor for the body temperature regulation in grasshoppers (Pepper and Hastings 1952), while melanism is important for the efficient use of solar radiation (Trullas et al. 2007). However, under high solar radiation, dark coloration might impose negative effects on fitness causing overheating of melanics, whereas lighter color morphs may benefit in such conditions (Trullas et al. 2007). We found a positive correlation between solar radiation and individuals with white stripes in *P. vittatum* (Fig. 5, Table 2), which may be involved in reducing heat absorption in sites with higher solar radiation. Likewise, darker individuals without stripes in cooler sites may benefit from increased heat absorption efficiency (True 2003), but this remains to be tested. Effects of melanism on the thermoregulatory behavior of *P. vittatum* have been examined by Harris et al. (2013a,b), who found darker morphs (unstriped morph) warm up rapidly and also have preferred high temperature as compared to lighter morphs. The presence or absence of stripes may therefore be under selection due to its important role in thermoregulation (Harris et al. 2013b).

Several other factors such as predator avoidance via crypsis, disassortative mating, or density-dependent selection exerted by predators (Dearn 1984) may also influence the maintenance and distribution of stripe polymorphism. Disassortative mating is beneficial for maintaining alleles responsible for a rare phenotypic trait
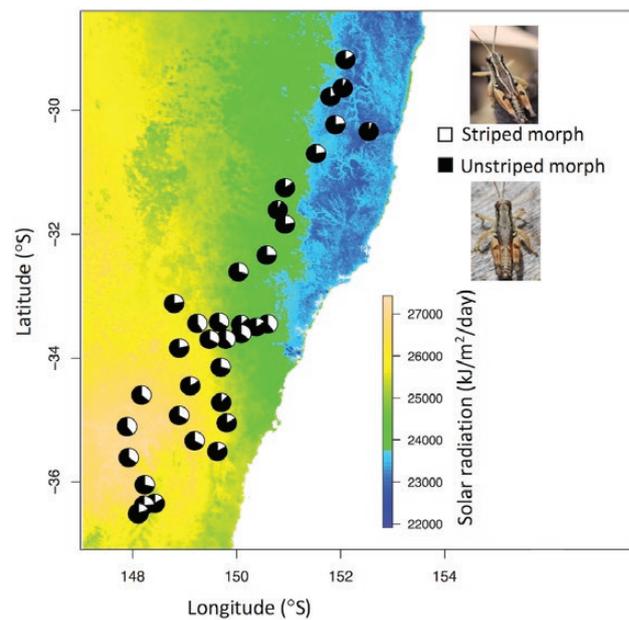

Fig. 5. The change in striped morph (striped and partially striped pattern) and unstriped morph frequency is shown along the solar radiation gradient. White corresponds to the proportion of striped morphs within a site, and black corresponds to the proportion of unstriped morph within a site.

(Follett et al. 2014). In *P. vittatum*, a strong selective constraint on striped individuals with homozygous C^S genotypes has been indicated previously via observations of their reduced viability (Dearn 1984). Strong viability selection on the homozygous genotype indicates a possible role of disassortative mating (observed in *P. vittatum* by Dearn 1980, 1984) in maintaining heterozygous genotypes for stripe pattern. The co-occurrence of striped and unstriped morphs within sites also suggests that balancing selection may be operating to maintain stripe polymorphism in this species, which may be driven by fitness advantages of different morphs under different environmental conditions (e.g., in relation to solar radiation). Further study is needed to identify, first, the role of disassortative mating and frequency dependence in maintaining stripe polymorphism and, second, whether genes associated with stripes are under environmental selection, which may help to unveil the traits' adaptive significance.

The relatively low frequency of striped and partially striped individuals observed in our study is consistent with observations made in previous studies (Dearn 1981, 1984; Harris et al. 2012). Furthermore, we did not find a significant association between foliage cover and stripe pattern as was observed by Dearn (1984). This is possibly due to our use of foliage cover as a continuous variable (%), as opposed to Dearn (1984), who applied a categorical approach (forest vs pasture) with a much smaller spatial scale with just two 50–100 km transects located approximately 100 km apart. This inconsistency with the observations made by Dearn (1984) suggests that the relationship between stripe polymorphism and forest habitat does not hold true at broader spatial scales. Furthermore, an increase in the frequency of striped individuals (including striped and partially striped) was found from north to south (ranging from 28° S to 38° S) in Dearn (1981). The significant positive correlation between stripe pattern and solar radiation we find in the current study suggests that solar radiation is likely to be one of the contributing variables shaping this latitudinal increase in stripe pattern morphs.

Body Size and Solar Radiation

Body size variation in insects is a vital life-history trait due to its relationship with physiology and fitness (Honĕk 1993, Nylin and Gotthard 1998) and exhibits clinal variation along latitudinal gradients in many ectotherms. Bergmann's rule states that body size increases with latitude, but the opposite of this (body size decreases with increase in latitude) has been found to apply in insects (Blackburn et al. 1999, Chown and Gaston 2010, but see Cushman et al. 1993, Kaspari and Vargo 1995). Factors such as temperature, seasonality, humidity, diet, and interactions among these factors can cause linear or nonlinear clines in ectotherm body size (Roff 1980, Kennington et al. 2003, Ho et al. 2009, Çağlar et al. 2014).

In *P. vittatum*, body size variation was previously explained by rainfall and radiation seasonality (Harris et al. 2012). Our study suggests that solar radiation is significantly associated with increased body size in both males and females (Supp Fig. S1 [online only], Table 3). Our finding of an insignificant relationship between annual precipitation and body size (Table 3) contrasts with previous observations made by Harris et al. (2012), which found this association to be significant. The number of study sites analyzed ($n = 61$) in Harris et al. (2012) was larger than in the present study ($n = 36$) and spans a latitudinal gradient that is approximately eight degrees wider. However, in the present study, we analyze nearly five times the number of individuals as in Harris et al. (2012; i.e., 198 individuals vs 954 individuals), allowing us to gain meaningful averages per site and higher data resolution.

Furthermore, the strong association between solar radiation and latitude in our study suggests other factors associated with latitude may also influence body size variation in *P. vittatum*. For example, the availability of a longer growing season at higher latitudes may extend growth and development periods and result in larger adult body size (Blanckenhorn 2000, Blanckenhorn and Demont 2004). Larger body size, in turn, can have further fitness advantage such as increased chances of survival and mating (e.g., Waller and Svensson 2017). Our study suggests that climatic and topographical variables are interacting selection pressures acting on the latitudinal variation in body size in *P. vittatum*. Further study using genetic analyses that examine signatures of selection along the sampled environmental gradient would be beneficial to elucidate this.

Conclusion

Environmental changes can drive an increased frequency of invertebrate pest outbreaks that bring economic costs and threaten food security (Macfadyen et al. 2018). Knowledge of how environmental conditions and habitat variation are correlated with morphological traits in invertebrate pests is therefore a necessary step for understanding pest responses and persistence under variable climatic conditions. Our study identifies a significant role of environmental and climatic variables on the relative abundance and distribution of morphological variation in *P. vittatum*, indicating that this species exhibits high variability, and potential adaptive responses that assist survival in different environments. We find that variation in body size, and in two discrete morphological traits, wing presence and stripe polymorphism can be maintained at large spatial scales, probably as a result of spatially varying selective pressures that are at least partially explained by environmental gradients. Notably, our study uses a data set collected in just one season and provides a snapshot of correlations that may or may not be upheld over longer temporal scales, perhaps due to shifts in weather and resources. The results of this study are informative for investigation into the genetic basis of selection on morphology and environment, and ultimately be informative for understanding the future spread and persistence of this agricultural pest.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

Acknowledgments

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