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Tong Qiu, Aaron J Bell, Jennifer J Swenson, James S Clark. Habitat–trait interactions that control response to climate change: North American ground beetles (Carabidae). *Global Ecology and Biogeography*, 2023, 32 (6), pp.1-15. 10.1111/geb.13670 . hal-04291399

HAL Id: hal-04291399

<https://hal.inrae.fr/hal-04291399>

Submitted on 17 Nov 2023

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Habitat–trait interactions that control response to climate change: North American ground beetles (Carabidae)

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Funding information

National Science Foundation, Grant/Award Number: Belmont Forum 1854976 and DEB-1754443; NASA, Grant/Award Number: AIST16-0052 and AIST18-0063

Handling Editor: Thomas W. Gillespie

Abstract

Aim: As one of the most diverse and economically important families on Earth, ground beetles (Carabidae) are viewed as a key barometer of climate change. Recent meta-analyses provide equivocal evidence on abundance changes of terrestrial insects. Generalizations from traits (e.g., body size, diets, flights) provide insights into understanding community responses, but syntheses for the diverse Carabidae have not yet emerged. We aim to determine how habitat and trait syndromes mediate risks from contemporary and future climate change on the Carabidae community.

Location: North America.

Time period: 2012–2100.

Major taxa studied: Ground beetles (Carabidae).

Methods: We synthesized the abundance and trait data for 136 species from the National Ecological Observatory Network (NEON) and additional raw data from studies across North America with remotely sensed habitat characteristics in a generalized joint attribute model. Combined Light Detection and Ranging (LiDAR) and hyperspectral imagery were used to derive habitat at a continental scale. We evaluated climate risks on the joint response of species and traits by expanding climate velocity to response velocity given habitat change.

Results: Habitat contributes more variations in species abundance and community-weighted mean traits compared to climate. Across North America, grassland fliers benefit from open habitats in hot, dry climates. By contrast, large-bodied, burrowing omnivores prefer warm-wet climates beneath closed canopies. Species-specific abundance changes predicted by the fitted model under future shared socioeconomic pathways (SSP) scenarios are controlled by climate interactions with habitat heterogeneity. For example, the mid-size, non-flier is projected to decline across much of the continent, but the magnitudes of declines are reduced or even reversed where canopies are open. Conversely, temperature dominates the response of the small, frequent flier *Agonoleptus conjunctus*, causing projected change to be more closely linked to regional temperature changes.

Main conclusions: Carabidae community reorganization under climate change is being governed by climate–habitat interactions (CHI). Species-specific responses to CHI are

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explained by trait syndromes. The fact that habitat mediates warming impacts has immediate application to critical habitat designation for carabid conservation.

KEYWORDS

Carabidae diversity, climate change, habitat, insect population change, LiDAR, response velocity, trait syndromes

1 | INTRODUCTION

Identifying the critical habitats needed for species recovery and persistence with climate change is a goal of conservation science. Recent syntheses disagree on the risks of climate change, such as regional or global declines reported for terrestrial insects in some studies (Brooks et al., 2012; Hallmann et al., 2020; van Klink et al., 2020) but not others (Crossley et al., 2020; Zajicek et al., 2021). At least three challenges contribute to divergent interpretations. First, meta-analysis is highly dependent on the uneven coverage of published literature across species and climate-habitat space. For example, the well-balanced coverage of trees available from North American monitoring data shows that every dominant species is increasing and decreasing somewhere (Clark et al., 2021; Fei et al., 2017; Stanke et al., 2021). Even in the limited cases where long time series can provide reliable estimates of trends from noisy data, their unrepresentative coverage of habitats and species in meta-analyses can suggest trends that differ from what could be inferred if observations were balanced over

geographic, climate, and habitat space (Rosenberg et al., 2019). Second, estimates of change are difficult to interpret where knowledge of habitat requirements is lacking (van Klink et al., 2020). The diverse ground beetles (family Carabidae includes 40,000 species globally, with 2,000 in North America, Figure 1) belong to nearly all major trophic guilds, and they vary widely in distribution, behaviour, and morphology (Lovei & Sunderland, 1996; Rainio & Niemelä, 2003). Many are nocturnal and hard to identify, with the result that life-history knowledge is thin and largely anecdotal. Finally, species are interdependent and must be modeled jointly, but a diverse group like the Carabidae is too large to interpret on a species-by-species basis; generalization benefits where species and traits can be analyzed together (Clark, 2016). The importance of habitat preference for climate responses makes it imperative to analyze their effects together, as climate-habitat interactions (CHI). To determine how CHI influences the joint response of species and traits, we analyze climate sensitivity and change in the Carabidae using data on all dominant species, with a balanced representation of climate and habitats. Rather than interpret trends

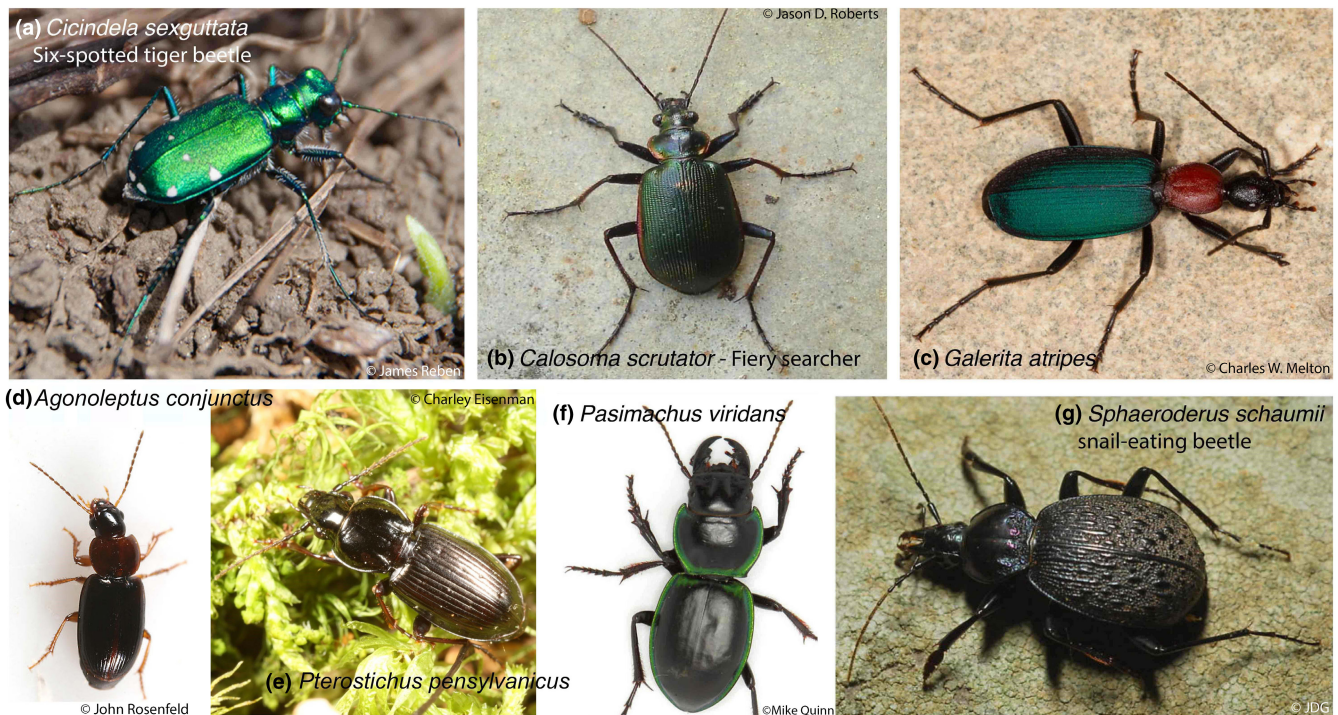


FIGURE 1 Ground beetles are abundant, important economically and ecologically, but poorly understood. This figure illustrates the diversity of trait attributes.

from noisy time series, we assess climate vulnerability by expanding on the notion of climate velocity (Loarie et al., 2009) to rates of the response given habitat change, or *response velocity* (Clark et al., 2021). Here we show that habitat interactions result in site-specific community reorganization in ways that could not be predicted by extrapolating trends from models that omit CHI.

The implications of climate change are difficult to evaluate for major insect groups due to a limited understanding of both biogeography and behaviour. Being one of the most diverse and economically important families on Earth, ground beetles are viewed as a barometer of climate change (Koivula, 2011; Rainio & Niemelä, 2003), so consequential that they were selected as one of the species groups for detailed monitoring in the National Ecological Observatory Network (NEON; Kao et al., 2012; NEON, 2021). For most species, identification at the species level requires an expert; citizen science data platforms exist (e.g., iNaturalist), but offer insights on a few species (Ribera et al., 2001; Zalewski et al., 2016). If the Carabidae are at risk of climate change, the biodiversity implications depend on how those impacts are distributed across habitat types and species that range widely in trophically important traits.

Where data are limited and noisy (e.g., abundances of insects), the notion of climate velocity (Loarie et al., 2009; Schliep et al., 2015) can be extended to provide insights through response velocity (Clark et al., 2021). Response velocity translates the effects of climate on species abundance that can be estimated from geographic and habitat variation (Gobbi et al., 2007;

Kotze et al., 2011; Niemela, 2001) into the rates at which climate changes influence habitat suitability. Through CHI, the impact of rapid climate change is modulated by habitat, which, in this study, includes canopy cover (gap fraction, G), understorey vegetation (normalized relative point density, NRD), surface roughness (Rough), fertility gradients (cation exchange capacity, CEC) and coarse woody debris (CWD) (Figure 2). For example, open habitats may be preferred by active runners and fliers that pursue prey on or near the ground (e.g., the genus *Cicindela*, Figure 1a; Hilmers et al., 2018). Canopy gaps affect microclimate, typically with elevated temperature and soil moisture (Beckage et al., 2008; Foggo et al., 2001; Ozanne et al., 2003). CWD can harbour invertebrate prey and, together with surface roughness and NRD, provide cover from vertebrate predators (Viterbi et al., 2013). Where the effects of temperature or moisture interact with these local habitat variables, then climate change alone represents only a main effect – the response velocity (abundance change per year) includes additional terms that come from the CHI.

The contribution of CHI to response velocity differs for each species. Mobile organisms, such as birds (Bateman et al., 2016; Jirinec et al., 2021; Rosenberg et al., 2019), large mammals (Berger, 2004; Tucker et al., 2018) and fish (Kleisner et al., 2017; Roberts et al., 2022), may locate distant habitats that become favourable as local conditions deteriorate, while sedentary organisms are left behind (Crous, 2019; Hoegh-Guldberg et al., 2007; Loarie et al., 2009; Ward et al., 2016). Species with wide habitat tolerances (niche breadth) are buffered as local habitats change relative

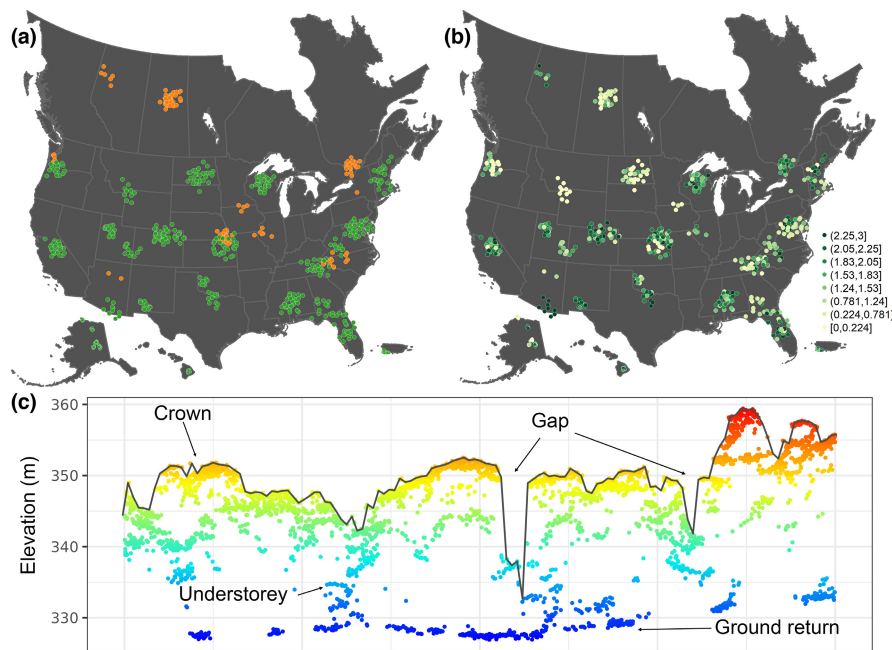


FIGURE 2 (a) Locations of Carabidae plots from the National Ecological Observatory Network (NEON, green) and published studies (orange), with jittered plot locations. (b) Species diversity is evaluated as the Shannon index, $-\sum_s p_s \log(p_s)$, where p_s is the fraction of species s at a plot. (c) Example habitat variables for gap, understorey density (normalized relative point density, NRD), and surface roughness (Table 2) derived from the NEON Airborne Observation Platform (AOP), which includes Light Detection and Ranging (LiDAR) point clouds. This LiDAR transect is from Mountain Lake Biological Station (MLBS, 2017), Virginia, USA. The black solid line shows the LiDAR-derived canopy height model (CHM). The colour ramp highlights elevation.

to species that are narrowly restricted to specific habitat types with less mobility (Eversham et al., 1996; Niemela, 2001). Habitat heterogeneity, represented by canopy structure, understorey, and soils, could affect mobility and define local refuges that buffer effects of climate change (Brooks et al., 2012; Niemela, 2001; Rainio & Niemelä, 2003; Woodcock, 2005). The community consequences depend on the mobility of each species.

In addition to mobility, diets and behaviours range widely in ground beetles, summarized here with the morphological traits (*body size and colour*), ecological performance traits (*habitat and trophic*) and physiological traits including *diurnal* (versus nocturnal), *flight, climbing, burrowing and running* (Fountain-Jones et al., 2015). Diets (*trophic*) include not only predation, but also detritus, seeds, pollen, and omnivory (Lovei & Sunderland, 1996). Some taxa are generalist feeders, while others target specific prey types, such as the caterpillar-specialist *Calosoma* (Figure 1b) and the snail-eating genus *Sphaeroderus* (Figure 1g). Some are active fliers (e.g., tiger beetles in the genus *Cicindela*, Figure 1a and *Agonoleptus*, Figure 1d), while others have fused elytra (*Pasimachus*, Figure 1f) or are functionally flightless (*Sphaeroderus*, Figure 1g). Some actively pursue prey in tree canopies (*Calosoma*, Figure 1b, and *Galerita*, Figure 1c), while others are slow-moving and fossorial (*Pasimachus*, Figure 1f and *Dyschirius*). These are the ambulatory traits *climbing, burrowing and running*. The ways in which these traits might control responses to CHI, and whether or not they predispose climate vulnerability in divergent ways, is unknown.

Evaluating the risks posed by climate change for species with divergent traits has to accommodate their interdependence. The response of one species to climate change depends on the other species with which it interacts, which are also responding to climate. Traits are likewise interdependent, because change in the abundance of any species affects the distribution of every trait in the community (Clark, 2016). For example, loss of an abundant predator shifts the community-weighted mean (CWM) trophic distribution toward herbivory. Efforts to identify the traits that might explain community responses often rely on aggregating responses of hundreds of taxa in ways that rarely offer estimates of uncertainty. Uncertainty is important, because much of the variation in noisy monitoring data is not meaningful.

The role of trait syndromes in responses to global warming and habitat degradation is complicated by the heterogeneous collection methods that are used and implemented sporadically in space and time (Crossley et al., 2020; van Klink et al., 2020). Presence-only data omit the effort needed to account for spatio-temporal bias in data collection. For example, Global Biodiversity Information Facility (GBIF) includes collections biased toward areas where experts live and work (e.g., universities and museums or targeted expeditions; Beck et al., 2014) and toward specific groups of taxonomic interest. Unlike eBird, where many observations come with records of observation time or distance, presence-only data further lack the observation effort that is needed to make observations comparable. Citizen-science efforts over-represent locations and habitats where species of broad

appeal are expected to be abundant (Scher & Clark, 2023; Tang et al., 2021). To avoid the diverse biases that challenge meta-analysis, data included in this study come from a consistent approach (pitfall traps at NEON), which includes sampling effort and an attempt at unbiased coverage of climate, habitats and species (within the Carabidae). Like all ecological studies employing pitfall traps, this analysis is subject to biases due to species differences in activity that influence collection efficiency (Niemela, 2001; Thomas et al., 1998; Woodcock, 2005).

This study aims to understand how habitat and trait syndromes mediate risks from contemporary and future climate change on the North American ground beetles. By combining response velocity, with its explicit decomposition for effects on the changes happening now, with future projections, we expect to identify risks that are linked to shared traits. We also expect that climate risks come not through the direct effects of temperate and moisture change, but rather through the indirect effects of climate change on the nature and distribution of habitats.

2 | METHODS

Our analysis includes two elements. To gauge habitat-trait combinations vulnerable to climate change, we first quantify community-wide responses to CHI for both species and traits. We then combine joint species abundance modeling with response velocity to quantify community change under future climate scenarios.

2.1 | Carabidae abundance and traits

Ground beetle count data were obtained from NEON (Kao et al., 2012) and 11 published studies (Bell et al., 2017; Browne et al., 2014; Chen et al., 2006; Dávalos & Blossey, 2006; Gagné & Fahrig, 2010; García-Tejero et al., 2018; Larsen et al., 2003; Maynard, 2007; McCravy & Willand, 2020; Riley & Browne, 2011; Unstad, 2012) that used the same collection methods. NEON data were downloaded from the data portal (product ID DP1.10022.001). Pitfall traps were deployed in all NEON domains, or sites, representing bioclimatic coverage, and plots-within-sites representing habitat diversity (Figure 2). Pitfall traps are arrayed 20m from the centre of NEON's distributed base plots. Sampling bouts occurred biweekly during the active season and ended when the temperature dropped below 4 °C. Ground beetles were identified to species or morphospecies by NEON technicians and expert taxonomists (NEON, 2021). The 11 published studies complement the biogeographic space available from NEON. We aggregated counts at a yearly temporal scale and analysed them as counts per effort (trap night). The diversity of ground beetles is summarized by the Shannon index (Figure 2b), with the Carabidae community being more diverse in the central, south-western and north-eastern United States compared to other regions.

Because rare species have low signal-to-noise ratios, we included in our analysis species with at least 20 non-zero observations

(Figure 2). This included 136 species sampled over 2,450 plot-years and 649 plots, 82% of which are from NEON. Traits include three categorical traits (i.e., habitat, body colour, trophic levels), one continuous trait (body size), one binary trait (diurnal versus nocturnal) and four ordinal traits (flight, burrowing, climbing and running) (Table 1). Trait values were compiled from the literature (Larochelle & Larivière, 2003; Ribera et al., 2001; Zalewski et al., 2016) and BugGuide (<http://bugguide.net>). Habitat preference was assigned as the dominant land cover type where a species is observed using the National Land Cover Database (NLCD).

2.2 | Climate

We used Daymet (<https://daymet.ornl.gov/Daymet>) version 4 daily air temperature and precipitation at 1-km resolution (Thornton et al., 2021). Moisture deficit quantifies water availability calculated as the difference between potential evapotranspiration and precipitation (i.e., PET – P). For active season temperature, we used mean temperature and cumulative moisture deficit from June to August. We used the deviance information criterion (DIC) for variable selection.

Climate scenarios were obtained from WorldClim (Fick & Hijmans, 2017) downscaled to a monthly interval from the Coupled Model Intercomparison Project Phase (CMIP6). We used the Canadian Earth System Model (CanESM; Swart et al., 2019), because it represents more extreme climate change in the future compared to other earth system models. We included a moderate emission scenario (shared socioeconomic pathways, SSP 2-4.5) and the highest emission scenario (SSP 5-8.5). We quantified abundance differences between future scenarios (2080–2100) and the historical baseline (2013–2021) as difference maps.

2.3 | Habitat characteristics

Gap fraction (G), understorey density (normalized relative point density, NRD), surface roughness (Rough), and canopy nitrogen

concentration (N) are derived from the NEON Airborne Observation Platform (AOP), which includes Light Detection and Ranging (LiDAR, DP1.30003.001) and hyperspectral imagery (DP1.30006.001) (Table 2). Although AOP campaigns include multiple years at a subset of NEON sites, many images were contaminated by clouds. We therefore selected the highest quality AOP data for each NEON site using the hyperspectral Quality (QA) layer (NEON, 2020) and visual inspection. For sites lacking AOP data (orange in Figure 2), we implemented inverse prediction from generalized joint attribute modeling (GJAM) (Clark et al., 2013, 2017) to impute missing observations.

Gap fraction (G) was quantified as the open canopy area above a height threshold divided by the total plot area (Silva et al., 2019). The height threshold was defined as the 90% quantile of the LiDAR-derived canopy height model (CHM) for the plot. The pit-free algorithm (Khosravipour et al., 2014), which triangulates multiple heights, was implemented to generate 1-m spatial resolution CHM from raw LiDAR point returns.

Understorey density was quantified as the NRD (Campbell et al., 2018), using

$$NRD = \frac{\sum_i z_i \in [0.15, 2]}{\sum_i z_i \in [0, 2]}$$

where z_i is the elevation of the LiDAR return points i . NRD thus summarized the number of LiDAR point returns that falls within understorey vegetation (between 0.15 and 2 m) divided by the total returns from the ground level (height of 0) to 2 m. Surface roughness comes from the LiDAR-derived digital terrain model (DTM, DP3.30024.001). Terrain elevation at 1-m spatial resolution was used to find anomalies from a fitted quadratic surface. The standard deviation of anomalies at each plot represents surface roughness (Rough).

Following Wang et al. (2020), we generated wall-to-wall maps of canopy nitrogen concentration (N) derived from NEON hyperspectral imagery and calculated the zonal mean value for each NEON plot. The calibrated parameters used to convert hyperspectral surface reflectance to canopy traits are available at the Ecological Spectral Model Library (<https://ecosml.org/>).

TABLE 1 Trait syndromes and their designations in the generalized joint attribute modeling (GJAM in Clark et al., 2017).

Traits	Type	Data type in GJAM
Habitat	Categorical data including forest, grass and others (shrub and wetland)	CAT
Body colour	Categorical data including black, brown and others (dark blue, dark purple, iridescent, and white)	CAT
Trophic	Categorical data including carnivore, omnivore and others (granivore and unknown)	CAT
Body size	Continuous (mm)	CA
Activity	Binary (diurnal versus nocturnal)	PA
Flight	Ordinal scale (0, 1 and 2)	OC
Burrowing	Ordinal scale (0, 1 and 2)	OC
Climbing	Ordinal scale (0, 1 and 2)	OC
Running	Ordinal scale (0, 1 and 2)	OC

TABLE 2 Habitat characteristics from Light Detection and Ranging (LiDAR) and hyperspectral imagery.

Habitat variable	Definition	Reference
Gap fraction (G, unitless)	Fraction of open canopy above height threshold	Silva et al. (2019)
Understorey density (NRD, unitless)	Normalized relative point density from LiDAR returns between 15 cm and 2 m above surface	Campbell et al. (2018)
Surface roughness (Rough, unitless)	Standard deviation of elevation anomalies from smoothed quadratic surface	
Canopy nitrogen concentration (N, mg/g)	Derived from hyperspectral imagery and used as a proxy for canopy productivity	Wang et al. (2020)
Coarse woody debris (CWD, m ²)	Volume of dead and downed trees	Woodall et al. (2008)
Cation exchange capacity (CEC, mmol _c /kg)	Soil fertility indicator for the depth range 0 to 30 cm	Hengl et al. (2017)

Coarse woody debris (CWD), defined as dead and downed trees above a minimum size (Woodall et al., 2008), was included for its known importance for wildlife (Harmon et al., 2004) and the fact that downed wood is a common habitat for ground beetles. We used NEON surveys, with a minimum diameter of 2 cm (DP1.10010.001). We calculated CWD volumes using diameter and length (Woodall et al., 2008).

Cation exchange capacity (CEC), a widely used indicator of soil fertility, was obtained from Hengl et al. (2017) at 250-m spatial resolution. We calculated the depth-weighted mean CEC using the uncertainty layers at three soil depths (0–5, 5–15 and 15–30 cm).

2.4 | Predictive traits model and response velocity

Generalized joint attribute modeling (GJAM) was used to jointly model species abundance as counts per effort (Clark et al., 2017), where effort is the number of pitfall traps per year. A predictive traits model (PTM; Clark, 2016) was used to quantify the response of traits to CHI. The community response matrix, which measures the similarities in trait responses, was used to define trait syndromes (Clark et al., 2017). Full technical details can be found in the Supporting Information.

The concept of climate velocity (Loarie et al., 2009) can be extended to response velocity $V(s)$ for a geographic location s , which combines climate sensitivity with the rate of climate change (Clark et al., 2021). Applying this concept to climate sensitivity, using temperature as an example, let $\beta_T = \frac{\partial w}{\partial T}$ represent the response of variable w (e.g., the abundance of a species) to temperature. The response velocity, $V_T(s) = \frac{\partial T(s)}{\partial t} \beta_T$ (change per year), combines the effects of climate with the rate of climate change at a location s . Where the effects of temperature interact with a habitat variable G , the response velocity shifts to

$$\frac{dw_s}{dt} = (\beta_T + \beta_{GT}G_s) \frac{dT_s}{dt} \quad (1)$$

where main effects of temperature and gap, β_T and β_G , combine with the interaction response β_{GT} (more details can be found in the Supporting Information). Thus, even if the habitat G is static (e.g., terrain), its effects are dynamic through its interaction with dynamic T .

Similarly, for a climate scenario that projects temperature change ΔT_s (°C), the abundance change is

$$\Delta w_s = (\beta_T + \beta_{GT}G_s) \Delta T_s \quad (2)$$

We evaluated both the response velocity and the projected change from CHI on abundance. We also evaluated future changes in community-weighted mean traits.

3 | RESULTS

3.1 | Trait syndromes emerge from CHI

The biogeographic responses of 136 species across North America can be summarized by four trait groups, or syndromes (Figure 4b), defined by similarities in the community response matrix (more details in the Supporting Information). Traits have positive correlation in (Figure 4b) if they share similar responses to predictors in the model (i.e., similar columns in the coefficient matrix of traits), especially for the variables with substantial variation across the data set (i.e., large covariance of the design matrix). Large-bodied, burrowing omnivores (LBO) occupy warm-wet climates beneath dense canopies and substantial understorey cover (green for T and NRD, brown for def and Gap in Figure 4a). Grassland fliers (GF) are characteristic of hot, dry and open habitats. Forest carnivores (FC) are most abundant beneath closed-canopy, wet, cool stands with surface relief (positive NRD). These predators tend to be active runners. A final group of others (O) includes cold, dryland forest species with heterogeneous diets and more likely than other groups to be brown in colour.

Taken over all species, the habitat variable canopy openness (G) is the most important source of variation in species abundance and trait syndromes (Figure 3). Consistent with sensitivity rankings in Figure 3, variable selection with DIC (Supporting Information Table S1) included climate, habitat and their interactions. Following Gap are the climate variables temperature and moisture deficit. Additional habitat variables are understorey vegetation density, canopy nitrogen concentrations, and CWD. Although significant for many species, surface roughness and soil fertility (CEC) account for lower overall variation in the community. The interaction between

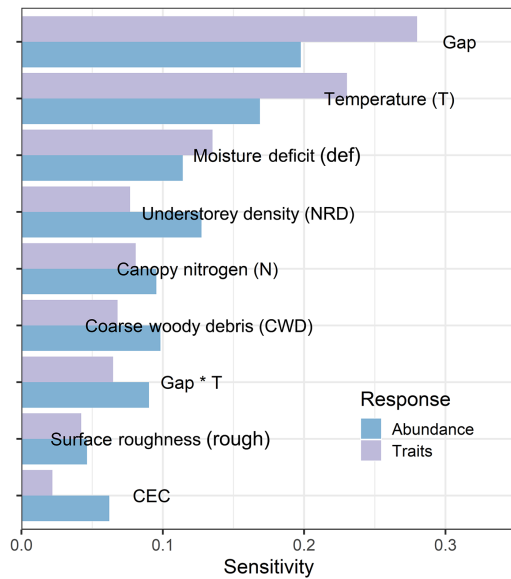


FIGURE 3 Community-wide sensitivity to climate and habitat variables and the important interaction, gap \times temperature from generalized joint attribute modeling (GJAM) analysis. The abundance bars are diagonal elements of f_w (joint sensitivity of abundance to predictors, more details in the Supporting Information). The trait bars are diagonal elements of f_u (joint sensitivity of traits to predictors). CEC is cation exchange capacity.

gap and temperature is an important predictor for species abundances and less so for trait variation.

Important interactions between temperature and gaps emerge for many species and trait groups (Figure 4). A negative $G \times T$ interaction for the LBO group means that a negative main effect of gaps can be amplified by high temperatures, as would be expected with heat stress. Equivalently, a positive main effect of temperature can be neutralized (or reversed) in open environments. The same negative interaction that amplifies the negative effect of gaps for LBO has the tendency to dampen the combined positive effects of temperature and gaps in the hot, dry climates characterized by the GF group (Figure 4). The negative main effect of gaps on FC in cool, moist climates does not have a consistent effect across trait types. High moisture availability in gaps may contribute to these interactions.

3.2 | Abundance changes vary by species and CHI

The synthesis of raw abundance data with fine spatial-scale remotely sensed habitat in GJAM reveals species-specific trends across a broad biogeographic scale (Figure 5). As an example, the small-bodied (3.2–4.3mm; Evans, 2010), frequent flier *Agonoleptus conjunctus* is projected to increase across much of the continent under future scenarios (Figure 5a,b). By contrast, abundance changes for the larger-bodied (9.5–12mm; Lindroth & Freitag, 1969), non-flier *Pterostichus pensylvanicus* are spatially heterogeneous, with no general tendency to increase or decline (Figure 5c,d). However, more locations show a declining trend under the high-emission scenario

SSP 5-8.5 (Figure 5d). The combination of negative direct temperature effects and positive gap interactions means that, for this species, gaps provide a buffer against warming, shown as warm colours in Figure 6d. By contrast, most of the large declines occur in the north-east and in the north-west where there is warming beneath a closed canopy (e.g., Figure 6a,c). Similarly, response velocity to the rate of recent warming (2000 to 2020 in Supporting Information Figure S2a) is governed by CHI (Supporting Information Figure S2d). Whereas rapid warming leads to a rapid decline in abundance of *P. pensylvanicus* in the north-east and north-west community, large gaps neutralize or even reverse the increasing trends caused by historical climate cooling in the central United States.

Contour surfaces for response velocity (Figure 7a) and abundance change for a climate change scenario (Figure 7b) place the mapped changes in climate space. For *P. pensylvanicus*, increasing temperatures induce declines (blue) where canopy cover is dense (low Gap in Figure 7a). The negative effects of warming on both response velocity (Figure 7a) and future abundance change (Figure 7b) are mitigated by an open canopy. For locations with recent cooling (e.g., the central United States), increased gap fraction has the opposite effect of reducing abundance (Figure 7a), but forecast scenarios are all increasing in temperature (Figure 7b).

The heterogeneous responses that result from habitat variation are shown at the landscape scale for the Pacific Northwest site Abby Road (ABBY; Figure 8), including both increases and decreases within the same regionally warming climate. Declines occur beneath closed canopies (blue dots), while increases occur in open environments (red dots). The combination of direct responses to climate and habitat, combined with their interactions, means that landscape heterogeneity has different consequences for each species.

Expanded to the full data set, results show that every species is increasing and decreasing somewhere across the study region. For both response velocity (Supporting Information Figure S3a) and future projection (Supporting Information Figure S3b), the whiskers for all 136 species include zero. More than half of all (52%) boxes include zero. While recent temperature trends that contribute to response velocity range from decrease to increase (Supporting Information Figure S2a), the projected temperatures in SSP2-4.5 increase across the entire map (Figure 6a). The heterogeneity of responses for every species combines climate effects across different parts of the range with the landscape scale responses to CHI.

3.3 | Changes in CWM traits

Variability in species responses to CHI is partially informed by traits. Large-bodied species most common in warm, moist climates (Figure 4) find future habitats in the north-east, Canada, and parts of the Central Plains (Figure 9a), where limited moisture declines (Supporting Information Figure S1) do not neutralize the positive effects of warming (Figure 6a). Diurnal species benefit on average from warming (positive β_T), but with a negative $G \times T$ interaction and weak sensitivity to moisture deficit (Figure 4). This group declines

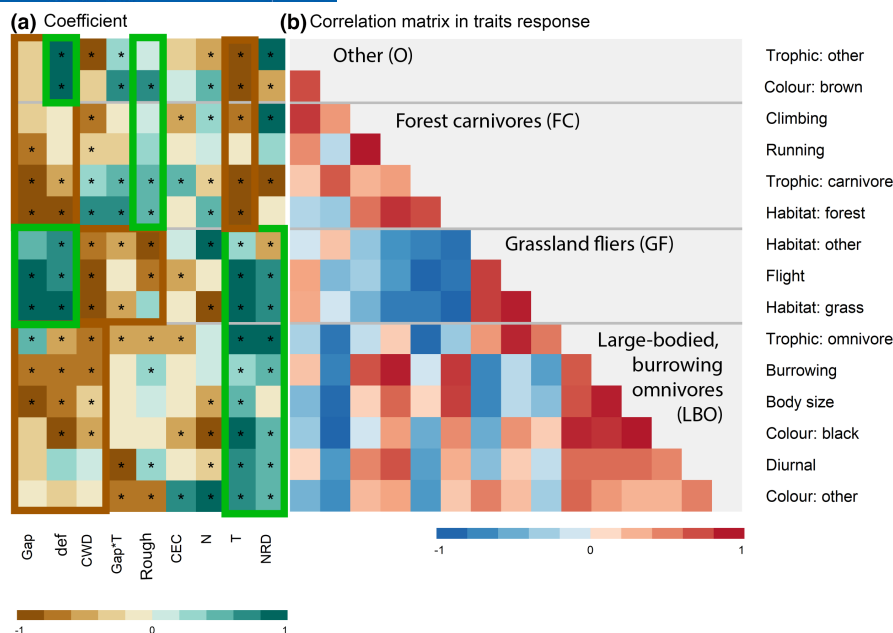


FIGURE 4 (a) Coefficients of trait response and (b) community response matrix (details in the [Supporting Information](#)). The coefficient in (a) measures the response of each trait to covariates. Bounding boxes in (a) highlight similarities within groups as brown (negative) and green (positive). Community response matrix in (b) quantifies similarities based on trait responses to all covariates. It is ordered by cluster analysis that yields four groups. For example, traits within the large-bodied, burrowing omnivore (LBO) group – diurnal, colour: other, colour: black, trophic: omnivore, burrowing, and body size – have positive responses to temperature (T) and understory density (quantified by normalized relative point density, NRD) in (a) (green) and negative responses to moisture deficit (def), coarse woody debris (CWD) and cation exchange capacity (CEC)(brown). Other predictors are terrain roughness (Rough) and canopy nitrogen (N).

in much of the continental interior, while benefiting in much of the north and east ([Figure 9b](#)). Non-fliers decrease in dry conditions ([Figure 4](#)) and suffer from warming over the entire map ([Figure 9c](#)). By contrast, carnivores that are most abundant in cold, wet climates ([Figure 4](#)), decline across most of the map ([Figure 9d](#)).

4 | DISCUSSION

4.1 | Effects of CHI on traits and abundance

The species-specific and spatially heterogeneous effects in [Figure 5](#) that respond to CHI ([Figure 6](#)) provide context for the aggregate trends reported by recent meta-analyses (Crossley et al., 2020; van Klink et al., 2020). The fact that climate change can mean both increases and decreases for the same species within the same landscape, depending on varying habitat, could be expected from the many ways in which habitat is known to mediate the effects of regional climate (Couper et al., 2021; Hamblin et al., 2017). For *P. pensylvanicus*, climate change tends to increase abundance under sparse canopies, while decreasing abundance in closed stands ([Figure 6](#)). For this example, direct effects of warming are negative ([Figure 6b](#)), but the full effects diverge due to habitat interactions. Canopy openness affects structural diversity (Hilmers et al., 2018; Seibold et al., 2019) in addition to microclimate, both of which might influence foraging efficiency and exposure to predators for a mid-sized carnivore like *P. pensylvanicus*

([Figure 6d](#)). By contrast, both direct and full effects of warming on *A. conjunctus* contribute to an increasing trend across the continent.

The response velocity used to quantify these CHI is a complement to, not a substitute for, time-series analysis of long-term community trends (Clark et al., 2020). Where spatially distributed, long-term data are sufficiently dense to balance habitat heterogeneity and penetrate the high noise levels in count data, time-series analyses have the potential to show abundance change (Rosenberg et al., 2019). Such dense, evenly distributed, uniformly sampled, long-term data do not exist for insects, even within the broad coverage offered by a uniform network like NEON, where our time-series analyses using gjamTime (Clark et al., 2020) detected few significant trends. However, even if such data were available, response velocity provides complementary insights. Climate velocity uses spatial temperature gradients to translate temperature change into the spatial implications of that change (Loarie et al., 2009). Response velocity generalizes this approach to variation in any predictor that affects abundance ([Equation 1](#)), even through interactions with static variables like canopy openness ([Figure 6c](#)). In response velocity, temperature change over distance is replaced by abundance change over the predictor variable ([Figure 6](#) and [Supporting Information Figure S2](#)), which is available, with full uncertainty, from the fitted model (Clark et al., 2021). The Interaction term $G \times T$ from the same fitted model show how change in a predictor like temperature varies across habitats ([Figure 6](#)). The effects from static variables G are still dynamic through its interaction with T ([Figure 6](#) and [Supporting](#)

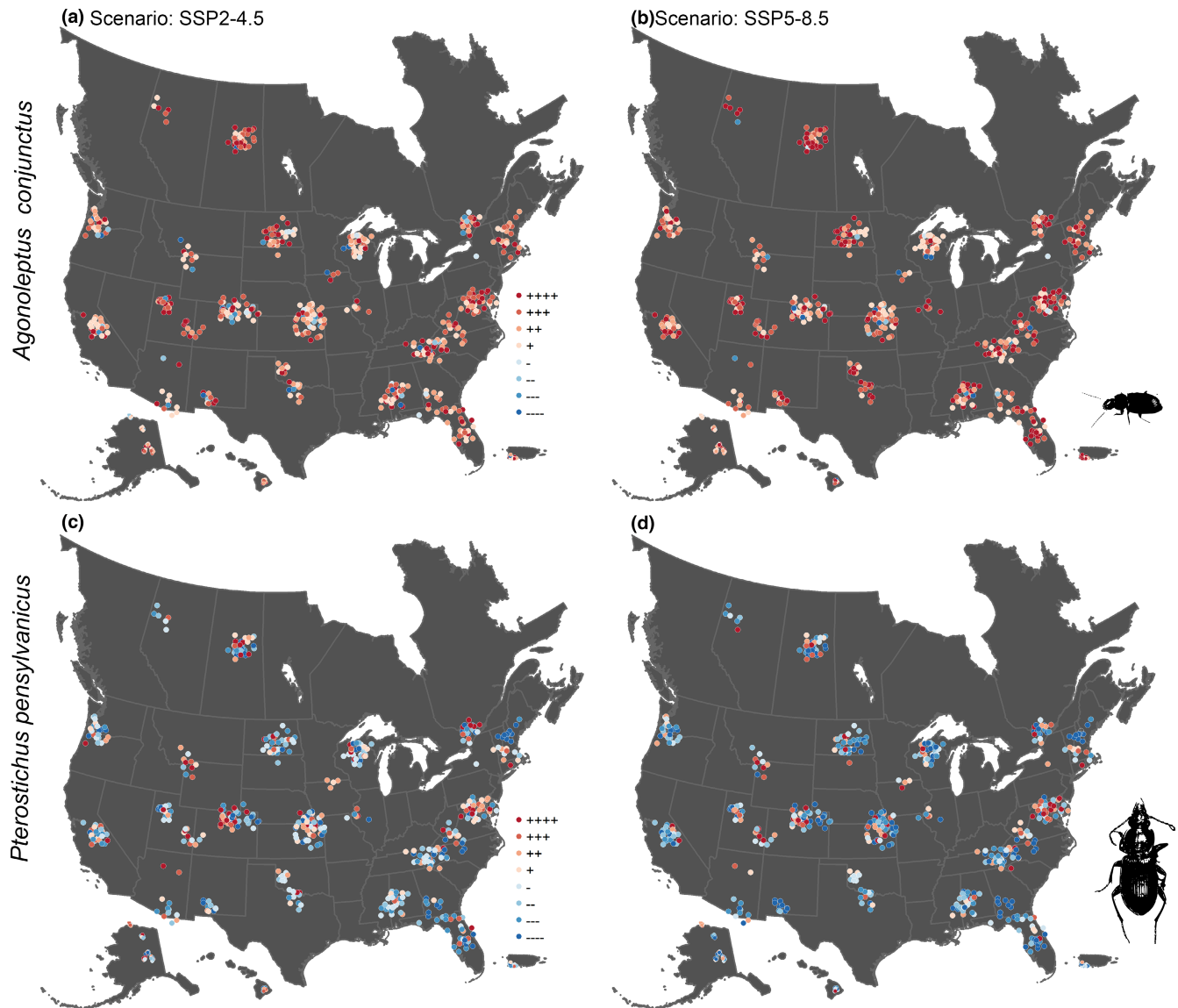


FIGURE 5 Differences of abundance in two common species [i.e., *Agonoleptus conjunctus* (a, b) and *Pterostichus pensylvanicus* (c, d)] between 2081–2100 and historical time interval under different scenarios, that is, shared socioeconomic pathways (SSP) 2-4.5 in left column and SSP 5-8.5 in right column.

Information Figure S2). The spatially heterogeneous G contributes to the variations of abundance change across a broad biogeographic gradient under climate change. The negative interaction means that sparse canopies can mediate or even revert the sign of the negative impacts of warming on response velocity (Supporting Information Figure S2).

The fact that every species is increasing and decreasing somewhere (Supporting Information Figure S3) suggests caution in the interpretation of meta-analysis. Trends detected in meta-analyses apply to the specific sites included in published data and are not expected to represent areas omitted from the analysis. While seemingly obvious, the fact that trends can diverge across habitats within the same landscape (Figure 8) means that results are more sensitive to the distribution of data than previously thought.

4.2 | Conservation implications

Despite local habitat variation, potential threats to carnivores and non-fliers posed by climate change appear to be general, transcending regional and habitat differences (Figure 9). Trait analysis integrates the responses of 136 species to CHI across North America (Figure 4). The tendency for large-bodied, burrowing omnivores (LBO) to occupy warm-wet environments supports the temperature–size rule (large size in warm climates; Atkinson, 1994), but adds the contributions of moisture and canopy/understorey cover (Figure 4a). Body size might respond to a number of environmental changes, beyond the climate and habitat variables considered here. For within-species change (which is not informed by our analysis), Tseng et al. (2018) found that body size declined with warming in museum specimens. Change in abundance at the species level (i.e., balanced over the full

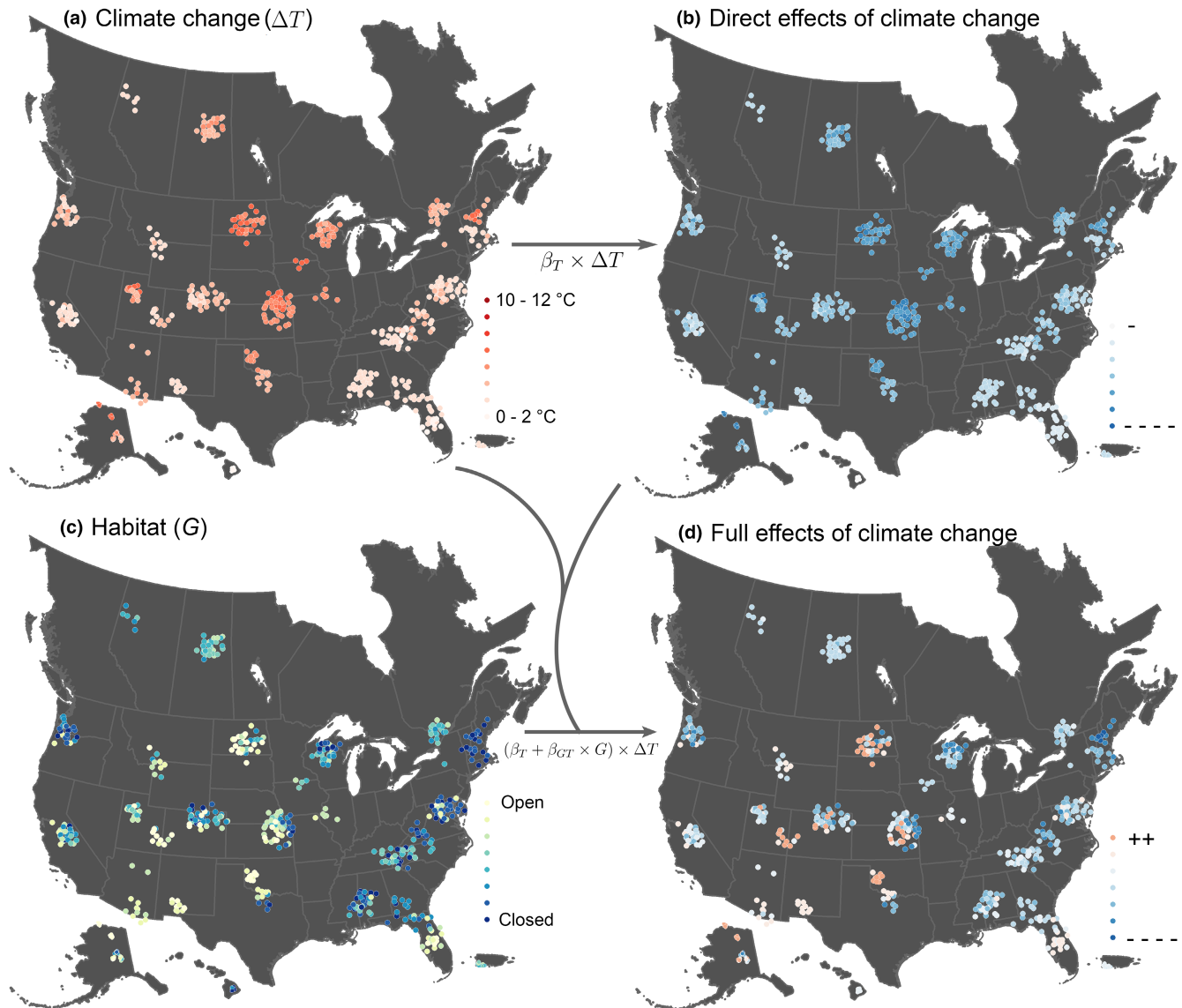


FIGURE 6 Response to direct effects of temperature (β_T) is multiplied by temperature change (ΔT) between 2081–2100 and historical baseline (or rate of temperature change if divided by the time interval) under scenario shared socioeconomic pathways (SSP) 2-4.5 (a) to give the direct effect (i.e., $\beta_T \times \Delta T$) in (b) for the common species *Pterostichus pensylvanicus*. Response to full effects is defined as the interaction coefficient with gap fraction (β_{GT}) multiplied by gap fraction in (c) and added by direct effect (i.e., $\beta_T + \beta_{GT} \times G$). Full effects from temperature in (d) comes from the response to full effects multiplied by ΔT in (a). Blue is negative and red is positive.

distribution) is not available from museum collections, due to uneven collection efforts by species, locations and over time. The forest carnivore (FC) trait syndrome that thrives in cool, wet forests (Figure 4a) is projected to decline (Figure 9d). The declines in non-flight and increases in diurnal traits come from the tendency for warm, dry conditions to favour flight and diurnal species in the LBO group (Figure 4a). These results add new insights to previous findings that species with poor dispersal ability were more likely to suffer from a higher rate of population decline in other insect species groups such as butterflies (Kotiaho et al., 2005) and moths (Mattila et al., 2006).

Habitat shifts that would reduce carnivore abundance (Figure 9d) are of concern due to their role as biological control agents: adults

hunt crop pests in soils, on the ground surface, and within vegetation canopies (Lovei & Sunderland, 1996; Snyder, 2019). The declining trends in carnivores with warming and drying (Figure 9d) may harm crop production, while also changing trophic interactions within food webs. Evidence of change within insect trophic guilds already underway includes more rapid declines in specialists compared with generalists (Habel et al., 2019; Wagner et al., 2021; Warren et al., 2021).

The fact that habitat dominates climate effects on Carabidae abundance and trait distributions highlights the important role of fine-scale habitat characteristics for climate response (Figure 2). Improved understanding of temperature and moisture impacts

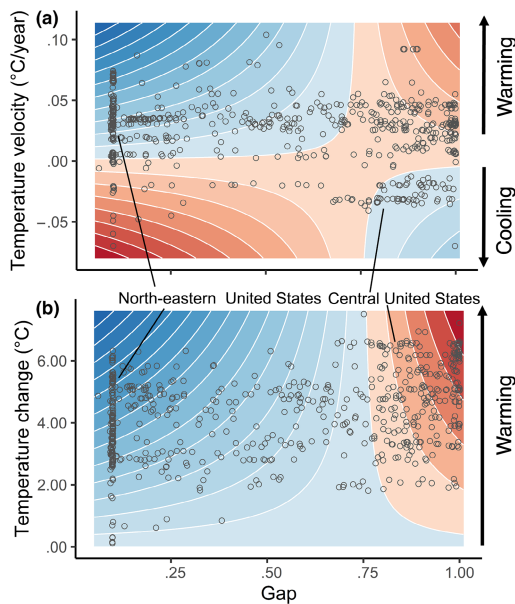


FIGURE 7 Full effects of temperature (i.e., $\beta_T + \beta_{GT}G$) on *Pterostichus pensylvanicus* multiplied by the current rate of temperature change (i.e., $\frac{dT}{dt}$) and temperature change for the shared socioeconomic pathways (SSP) 2-4.5 scenario (i.e., ΔT) on response velocity (a, Equation 1) and abundance change (b, Equation 2). The colour scale follows Figure 6 with red increases and blue declines. The scenario change for temperature is everywhere increasing (b), whereas current trends include both positive and negative rates (a). Contrasting climate–habitat combinations are indicated for the north-eastern (mostly closed canopy) and central United States (open canopy).

on insect communities (Gobbi et al., 2007; Lister Bradford & Garcia, 2018; Niemela, 2001; Seibold et al., 2019; Uhler et al., 2021) does not necessarily translate to the effects of climate change when there are CHI (Figure 8). The full context of global changes extends to agricultural intensification, urbanization, pesticide and fertilizer use, and introduced pathogens (Potts et al., 2010; Sánchez-Bayo & Wyckhuys, 2019). These predictors were not available for our sites, having not experienced nearby land conversion or agricultural use. Other future explorations include extending the model to accommodate environmental influenced movement, density-dependent and independent growth rate that depends on abundance of one species and its interaction with other species (gjamTime in Clark et al., 2020). The expanded model has the potential to capture the dynamic and nonlinear process in abundance change, especially when more years of data on Carabidae at NEON sites become available in the future. As a first effort to evaluate the response velocity of species and traits on a continental scale, our results confirm the dominant role of habitat and provide guidance for understanding and projecting changes in ground beetle communities under climate change. Methods can be applied to additional global changes as data become available in the future.

5 | CONCLUSIONS

Carabid responses to climate change are being governed by climate–habitat interactions (Figures 4, 6 and 7), an insight that depended on observations distributed across broad climate and

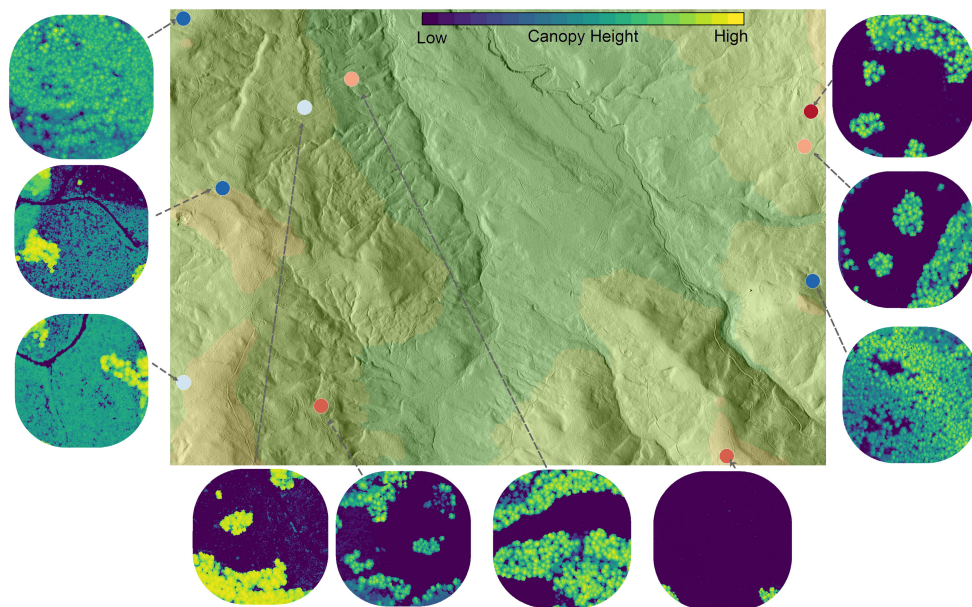


FIGURE 8 Climate–habitat interactions at Abby Road (ABBY), north-east of Vancouver, WA. Hillshading is used to visualize local terrain in the background map. Each inset plot (30×30m²) represents the plot-level canopy height model (CHM) from Light Detection and Ranging (LiDAR), where green and yellow colours indicate high values and purple colour represents low ones. Symbols of the points follow Figure 5 and represent abundance change in *Pterostichus pensylvanicus* between 2081–2100 and historical baseline under climate change scenario shared socioeconomic pathways (SSP) 2-4.5.

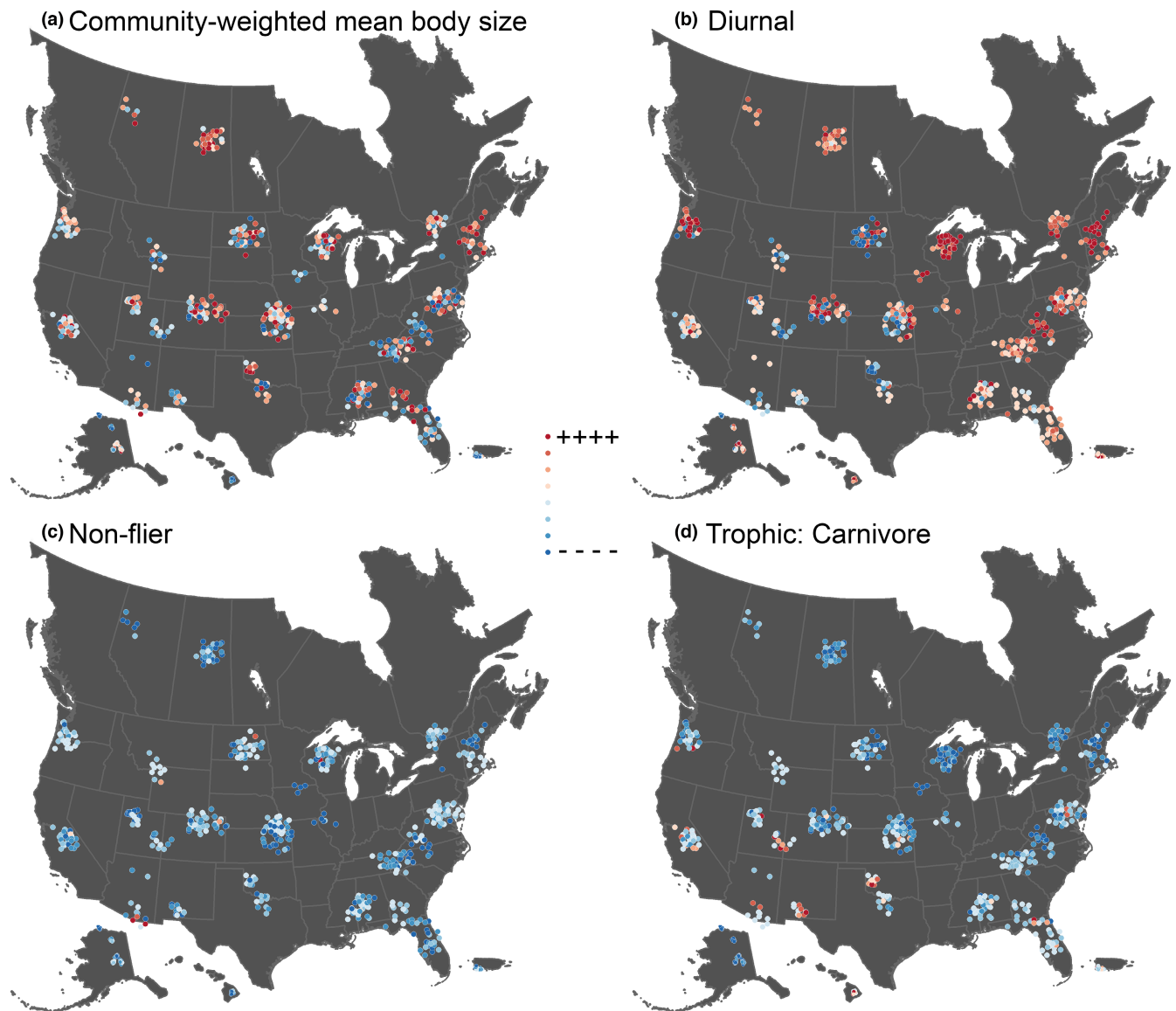


FIGURE 9 Prediction of community-weighted mean traits between 2081–2100 and historical baseline under future scenario shared socioeconomic pathways (SSP) 2-4.5, including (a) community-weighted mean body size and community-weighted fractions of (b) diurnal species, (c) non-fliers, and (d) carnivores in the community.

habitat space (Figure 2) and a joint analysis of species and traits. To supplement what can be extracted from published studies of aggregate variables (e.g., biomass in Hallmann et al., 2017; Seibold et al., 2019; van Klink et al., 2020), NEON monitoring can provide insights on responses of whole communities at a continental scale. Rather than uncertain trends from noisy time series, response velocity shows the effects of change that is in progress now.

Results of this study have immediate application to conservation. Abundances of some species are predicted to decline under future climate change while others do not (more examples at <http://pbjgjam.org>); nearly all species are increasing in some habitats while decreasing in others. Conservation efforts may benefit from the consideration of critical habitats defined at both the species and trait levels. Our analysis identifies where and in which directions the community shifts could happen in the future and which habitats could influence

those shifts. While climate change cannot be controlled by conservation management, the fact that canopy structure mediates warming offers insights needed to buffer the effects of climate change on Carabidae communities.

ACKNOWLEDGEMENTS

The authors acknowledge support from National Science Foundation DEB-1754443, the Belmont Forum (1854976), NASA (AIST16-0052, AIST18-0063), and the Programme d'Investissement d'Avenir under project Forecasting Biodiversity Change (FORBIC) (18-MPGA-0004) (Make Our Planet Great Again). We thank NEON for providing the Carabidae and Airborne Remote Sensing data. The NEON is a program sponsored by the NSF and operated under a cooperative agreement by Battelle Memorial Institute. We thank the comments from the two reviewers and the handling editor, which

greatly improved this work. T.Q. also acknowledges the support from the start-up funds provided by Pennsylvania State University.

FUNDING INFORMATION

This study is supported by National Science Foundation DEB-1754443, and by the Belmont Forum (1854976), NASA (AIST16-0052, AIST18-0063), and the Programme d'Investissement d'Avenir under project Forecasting Biodiversity Change (FORBIC) (18-MPGA-0004) (Make Our Planet Great Again).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are available within the article and its Supporting Information. Ground beetle count data can be downloaded from the NEON data portal (product ID DP1.10022.001). NEON LIDAR and hyperspectral data are available at DP1.30003.001 and DP1.30006.001, respectively. Cation exchange capacity data can be obtained from <https://soilgrids.org/>. Climate data can be extracted from Daymet at <https://daymet.ornl.gov/> and from WorldClim at <https://www.wcrp-climate.org/wgcm-cmip/wgcm-cmip6>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Qiu, T., Bell, A. J., Swenson, J. J., & Clark, J. S. (2023). Habitat–trait interactions that control response to climate change: North American ground beetles (Carabidae). *Global Ecology and Biogeography*, 32, 987–1001. <https://doi.org/10.1111/geb.13670>