Insect Pests on the Move: Climate, Soil, Land Use, and the Search for Contingent Generality

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Funding information
Canadian Natural Science and Engineering Research Council (NSERC) to JAN, RGPIN-2022-04581

Climate change is reshaping the geographic distributions of insect pests, with major consequences for agriculture, forestry, and ecosystem stability. Species distribution models (SDMs) are widely used to project these changes, yet most rely primarily on climatic predictors and implicitly assume a degree of generality in species responses that may not hold across diverse taxa. Here, we evaluate how 62 globally important insect pest species respond to climate change and to non-climatic predictor variables, asking whether their responses exhibit global generality, idiosyncrasy, or intermediate forms of contingent generality. We constructed correlative SDMs using multiple algorithms and predictor sets (climate only; climate + land use; climate + soil; climate + land + soil) and projected distributions under two emissions scenarios (SSP1–2.6 and SSP5–8.5) and two future time horizons (2020s and 2080s). Climate change produced strong aggregate trends, including poleward shifts and declining similarity between future and historical distributions, but species-level responses were highly heterogeneous in both magnitude and direction. Trait-based analyses revealed patterns of contingent generality structured by taxonomic order, feeding guild, and habitat association. Adding land-use variables consistently improved model performance more than adding soil variables, while combining both predictors was typically subadditive. Further analyses showed that land-use effects reorganize climate-response predictions for specific subsets of species, whereas soil effects were weaker and more context-dependent. Together, these results demonstrate that insect pest responses to climate change and model complexity are neither uniform nor random, but structured by ecologically meaningful contingencies. Recognizing and explicitly incorporating contingent generality can improve the interpretation, performance, and policy relevance of

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Abbreviations: SDM, Species Distribution Model; SSP, shared socioeconomic pathways; TSS, True Skill Statistic; AUC, Area Under the Curve; OR5, 5% omission rate; EPPO, European and Mediterranean Plant Protection Organization; GBIF, Global Biodiversity Information Facility; LUH2, Land-Use Harmonization v2.

SDMs under global change.

KEYWORDS
insect pests; climate change; species distribution models; contingent generality; land use; trait-based analysis

1 | INTRODUCTION

Climate change is reshaping species distributions worldwide, altering community composition, ecosystem function, and the risks posed by economically and ecologically important taxa [see e.g., 1]. Insects—particularly insect pests—have become a focal group in this research because their distributions respond rapidly to environmental change and because their impacts on agriculture and forestry can scale nonlinearly with range expansion and redistribution. Anticipating these shifts remains a central objective of global change ecology and applied biogeography [2].

Species distribution models (SDMs) are the primary tool for projecting these responses. By relating species occurrences to environmental predictors, most often climatic variables, SDMs generate spatially explicit forecasts of potential distributions under future scenarios. Across taxa and regions, such models frequently reveal directional patterns, including poleward and upslope shifts, high-latitude expansions, and declining overlap between future and historical ranges. These patterns are commonly summarized using mean effect sizes or ensemble averages, which play a central role in synthesis, meta-analysis, and policy-relevant interpretation.

Yet an exclusive focus on mean directional change obscures a defining feature of SDM outputs: responses are often highly heterogeneous across species. Species exposed to similar climatic forcing can differ markedly in both the magnitude and direction of projected change. Although this heterogeneity is well documented, it is typically treated as residual variation around a central tendency rather than as a primary target of inference.

1.1 | From mean responses to structured heterogeneity

The key inferential question is therefore not whether species respond identically to climate change—few researchers expect that—but whether heterogeneity itself is structured in biologically meaningful ways. Mean responses summarize one dimension of change, but they do not indicate whether deviations from the mean are random, weakly constrained, or systematically associated with species traits, ecological roles, or modelling context.

This distinction is critical. If heterogeneity is largely *unstructured*, mean responses provide an adequate basis for inference and decision-making. If heterogeneity is *patterned*—such that species sharing particular traits respond more similarly to one another than to other species—then mean-based summaries risk conflating qualitatively different ecological trajectories. This situation is analogous to interpreting a main effect in the presence of strong interactions: the mean effect remains well defined, but it no longer represents a single underlying process and may obscure the conditional structure that governs individual responses.

The concept of *contingent generality* provides a framework for resolving this tension. Under this view, generality is neither sought at the level of all species nor rejected in favour of pure idiosyncrasy. Instead, regularities emerge conditionally, holding for subsets of species defined by shared traits, taxonomic relationships, or ecological contexts. Contingent generality thus reframes heterogeneity from a nuisance to be averaged away into a source of explanatory structure.

1.2 | Climate change, model complexity, and sources of contingency

Most large-scale SDM studies emphasize climate as the primary driver of species distributions, reflecting its dominant influence on insect physiology, development, and survival. Climate-only models often produce clear directional signals, but of course, climatic suitability alone does not guarantee ecological suitability. Pest distributions are also constrained by host availability, habitat structure, and local environmental conditions, which are shaped by land use and soil properties.

Accordingly, land-use and soil predictors are increasingly incorporated into SDMs to improve performance and ecological realism [e.g., 3, 4, 5]. However, adding predictors does more than refine predictions. It can reorganize inferred species–environment relationships, alter the relative importance of climatic variables, and affect species differently depending on their ecological characteristics. These effects are unlikely to be uniform, suggesting that model complexity itself may generate contingent patterns of response.

Despite this, evaluations of added predictors typically focus on average improvements in performance metrics, again emphasizing mean effects while downplaying heterogeneity across species [e.g., 6, 7, 8]. Whether such improvements are driven by particular ecological dimensions, specific taxa, or systematic reorganization of predictor importance remains poorly resolved.

1.3 | Insect pests

Insect pests are among the most significant biotic threats to primary production systems worldwide. The Food and Agriculture Organization estimates that pests and diseases reduce global crop yields by up to 40% annually, resulting in more than \$220 billion in direct economic losses (FAO, 2019). Forestry systems face comparable risks, as climate-driven outbreaks of bark beetles (Scolytinae) and invasive species such as the emerald ash borer (*Agrilus planipennis*) are projected to reduce timberland values by tens of billions of dollars across North America [10, 11].

Beyond these direct costs, pest outbreaks can alter nutrient cycling, hydrology, and habitat structure, undermining the long-term resilience of agricultural and forested landscapes. Anticipating where and when pest pressures will intensify is therefore essential for safeguarding food and fibre supplies and for guiding adaptive management under rapid environmental change.

1.4 | Climate as a primary driver of insect pest dynamics

Climate exerts a dominant influence on insect pests by shaping the thermal and moisture regimes governing development [e.g., 12], voltinism [e.g., 13], overwintering survival [e.g., 14], and dispersal [e.g., 15]. Because many pest species operate within relatively narrow thermal performance windows, even modest warming can accelerate development, increase generational turnover, extend growing seasons, and relax cold-temperature constraints on geographic ranges [e.g., 16].

Precipitation regimes also indirectly influence pest dynamics by affecting host plants. Changes in soil moisture and rainfall timing affect leaf flush, sap flow, and canopy humidity, thereby modifying plant nutritional quality and microclimatic conditions that facilitate pest feeding and pathogen transmission. Extreme events such as droughts and heatwaves can amplify these effects by synchronizing dispersal or increasing host susceptibility through physiological stress.

Anthropogenic climate change intensifies these processes through sustained warming, altered precipitation patterns, and increased climatic variability. These pressures drive poleward and upslope range expansions, facilitate biological invasions, and, in some cases, cause range contractions when thermal or moisture limits are exceeded.

The work of projecting pest distributions under future climates depends heavily on correlative SDMs, which estimate species' realized niches by statistically linking occurrence data to spatially explicit environmental predictors. Their widespread use reflects pragmatic advantages—modest data requirements, scalability, and transferability across regions and scenarios—especially relative to mechanistic models that require detailed physiological or demographic data not readily available for most species [17, 18, 16, 19]. As a result, correlative SDMs have become the *de facto* standard for large-scale projections, despite relying on the assumption that inferred species–environment relationships remain valid under novel conditions.

1.5 | Land use and soil roles in pest species distributions

Although climate constrains the physiological limits of herbivorous insects, their distributions are often more proximally shaped by host-plant availability [20], which in turn depends on land use and soil conditions. These dependencies can be incorporated into SDMs either explicitly, by modelling host and pest distributions jointly [e.g., 21, 22], or implicitly, by including land-use and soil variables as predictors [e.g., 23, 24].

Land-use patterns and soil properties jointly structure the ecological contexts in which pests establish and persist [25, 26]. Homogeneous cropland landscapes dominated by monocultures provide stable and predictable host resources that favour specialist pests, whereas heterogeneous landscapes can suppress or facilitate pests depending on feeding breadth and mobility [e.g., 27, 28, 29]. Soil characteristics further influence pest distributions by affecting host performance and belowground life stages, including oviposition, larval development, and overwintering [e.g., 30, 31, 21].

Together, land-use and soil conditions govern the spatial coincidence of hosts and suitable microhabitats. Adding these predictors to climate-based SDMs may therefore increase both predictive power and biological realism, distinguishing physiologically suitable areas from those that are ecologically viable.

1.6 | Research questions and approach

Here, we use a diverse assemblage of globally important insect pests to move beyond mean-centric summaries and ask whether heterogeneity in SDM projections is structured in ways that support contingent generality. Specifically, we ask:

1. **How will suitable areas for these species shift under climate change?** Here, we ask whether projected pest distributions change under future climate scenarios when summarized by common distributional metrics.
2. **Is there generality in insect pest responses to climate change?** Here, we ask to what extent species deviate from these mean directional trends, and whether those deviations are structured by ecological traits.
3. **Does adding land-use and/or soil variables improve SDM performance?** Here, we ask whether adding land-use and soil predictors improves SDM performance uniformly, contingently, or idiosyncratically.
4. **Is there generality in species responses to the addition of land and soil variables?** Here, we ask whether responses to increased model complexity reveal recurring, trait-structured patterns of explanatory importance.

By combining multi-algorithm SDMs with trait-based analyses and detailed assessments of predictor importance and robustness, we treat heterogeneity not as noise around an average response but as the central phenomenon to be explained. In doing so, we argue that contingent generality provides a more informative basis for synthesis and prediction than either mean directional change or species-specific idiosyncrasy alone.

2 | METHODS

2.1 | Pests and Species Occurrence Data

The primary source for the catalogue of quarantine pest species is the European and Mediterranean Plant Protection Organization (EPPO) A1/A2 List of Pests Recommended for Regulation, including 133 species in the A1 list and 75 species in the A2 list [32, 33]. Based on the species names in the catalogue, we obtained the distribution information for each species and its synonyms, as provided in EPPO, using the `R` package `rgbif` [34]. The `R` package provides access to species distribution data to the Global Biodiversity Information Facility (GBIF, `https://www.gbif.org/`). We excluded duplicates, incorrect records, and those species with fewer than 30 occurrence records. This left us with 62 species across five orders, each with between 30 and 1393 occurrence records (see Table 1 and Table S1).

TABLE 1 Status and traits for insect pest species considered in this study.

Species	**Order**	**Family**	**Feeding guild**	**Host specificity**	**Primary habitat**	**Invasive**
1. *Acleris variana*	Lepidoptera	Tortricidae	Foliar feeder	Oligophagous	Forest	No
2. *Agrilus anxius*	Coleoptera	Buprestidae	Wood/stem borer	Oligophagous	Forest	No
3. *Agrilus bilineatus*	Coleoptera	Buprestidae	Wood/stem borer	Oligophagous	Forest	No
4. *Anastrepha obliqua*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes
5. *Anoplophora chinensis*	Coleoptera	Cerambycidae	Wood/stem borer	Polyphagous	Both	Yes
6. *Anthonomus bisignifer*	Coleoptera	Curculionidae	Fruit/flower feeder	Oligophagous	Agricultural	No
7. *Bactericera cockerelli*	Hemiptera	Triozidae	Sap feeder	Oligophagous	Agricultural	Yes
8. *Bactrocera dorsalis*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes
9. *Bactrocera tryoni*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes
10. *Bactrocera zonata*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes
11. *Bemisia tabaci*	Hemiptera	Aleyrodidae	Sap feeder	Polyphagous	Agricultural	Yes
12. *Cacoecimorpha pronubana*	Lepidoptera	Tortricidae	Foliar feeder	Polyphagous	Agricultural	Yes
13. *Cacyreus marshalli*	Lepidoptera	Lycaenidae	Wood/stem borer	Oligophagous	Agricultural	Yes
14. *Ceratitis capitata*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes
15. *Ceratitis rosa*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes
16. *Chionaspis pinifoliae*	Hemiptera	Diaspididae	Sap feeder	Oligophagous	Forest	Yes
17. *Chloridea virescens*	Lepidoptera	Noctuidae	Fruit/flower feeder	Polyphagous	Agricultural	No
18. *Choristoneura conflictana*	Lepidoptera	Tortricidae	Foliar feeder	Oligophagous	Forest	No
19. *Choristoneura fumiferana*	Lepidoptera	Tortricidae	Foliar feeder	Oligophagous	Forest	No
20. *Choristoneura rosaceana*	Lepidoptera	Tortricidae	Fruit/flower feeder	Polyphagous	Both	No
21. *Chrysobothris femorata*	Coleoptera	Buprestidae	Wood/stem borer	Polyphagous	Both	No
22. *Dacus ciliatus*	Diptera	Tephritidae	Fruit/flower feeder	Oligophagous	Agricultural	Yes
23. *Dendroctonus ponderosae*	Coleoptera	Curculionidae	Wood/stem borer	Oligophagous	Forest	No
24. *Dendroctonus rufipennis*	Coleoptera	Curculionidae	Wood/stem borer	Oligophagous	Forest	No
25. *Dendroctonus valens*	Coleoptera	Curculionidae	Wood/stem borer	Oligophagous	Forest	Yes
26. *Dendrolimus superans*	Lepidoptera	Lasiocampidae	Foliar feeder	Oligophagous	Forest	No
27. *Diabrotica undecimpunctata*	Coleoptera	Chrysomelidae	Root feeder	Polyphagous	Agricultural	No
28. *Diabrotica virgifera zeae*	Coleoptera	Chrysomelidae	Root feeder	Polyphagous	Agricultural	No
29. *Exomala orientalis*	Coleoptera	Scarabaeidae	Root feeder	Polyphagous	Agricultural	Yes
30. *Frankliniella occidentalis*	Thysanoptera	Thripidae	Sap feeder	Polyphagous	Agricultural	Yes
31. *Grapholita packardi*	Lepidoptera	Tortricidae	Fruit/flower feeder	Polyphagous	Agricultural	No
32. *Helicoverpa armigera*	Lepidoptera	Noctuidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes
33. *Helicoverpa zea*	Lepidoptera	Noctuidae	Fruit/flower feeder	Polyphagous	Agricultural	No
34. *Heteronychus arator*	Coleoptera	Scarabaeidae	Root feeder	Polyphagous	Agricultural	Yes
35. *Ips pini*	Coleoptera	Curculionidae	Wood/stem borer	Oligophagous	Forest	No

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Species	**Order**	**Family**	**Feeding guild**	**Host specificity**	**Primary habitat**	**Invasive**
36. *Leptinotarsa decemlineata*	Coleoptera	Chrysomelidae	Foliar feeder	Oligophagous	Agricultural	Yes
37. *Liriomyza trifolii*	Diptera	Agromyzidae	Foliar feeder	Polyphagous	Agricultural	Yes
38. *Lycorma delicatula*	Hemiptera	Fulgoridae	Sap feeder	Polyphagous	Both	Yes
39. *Lymantria mathura aurora*	Lepidoptera	Erebidae	Foliar feeder	Polyphagous	Forest	No
40. *Malacosoma disstria*	Lepidoptera	Lasiocampidae	Foliar feeder	Polyphagous	Forest	No
41. *Metamasius hemipterus*	Coleoptera	Curculionidae	Wood/stem borer	Polyphagous	Agricultural	Yes
42. *Monochamus alternatus*	Coleoptera	Cerambycidae	Wood/stem borer	Oligophagous	Forest	No
43. *Monochamus carolinensis*	Coleoptera	Cerambycidae	Wood/stem borer	Oligophagous	Forest	No
44. *Monochamus notatus*	Coleoptera	Cerambycidae	Wood/stem borer	Oligophagous	Forest	No
45. *Monochamus scutellatus*	Coleoptera	Cerambycidae	Wood/stem borer	Oligophagous	Forest	No
46. *Naupactus leucoloma*	Coleoptera	Curculionidae	Root feeder	Polyphagous	Agricultural	Yes
47. *Neocerambyx raddei*	Coleoptera	Cerambycidae	Wood/stem borer	Oligophagous	Forest	No
48. *Orgyia leucostigma*	Lepidoptera	Erebidae	Foliar feeder	Polyphagous	Both	No
49. *Orgyia pseudotsugata*	Lepidoptera	Erebidae	Foliar feeder	Oligophagous	Forest	No
50. *Popillia japonica*	Coleoptera	Scarabaeidae	Root feeder	Polyphagous	Both	Yes
51. *Rhynchophorus ferrugineus*	Coleoptera	Curculionidae	Wood/stem borer	Oligophagous	Agricultural	Yes
52. *Rhynchophorus palmarum*	Coleoptera	Curculionidae	Wood/stem borer	Oligophagous	Agricultural	Yes
53. *Saperda candida*	Coleoptera	Cerambycidae	Wood/stem borer	Oligophagous	Both	Yes
54. *Spodoptera eridania*	Lepidoptera	Noctuidae	Foliar feeder	Polyphagous	Agricultural	Yes
55. *Spodoptera frugiperda*	Lepidoptera	Noctuidae	Foliar feeder	Polyphagous	Agricultural	Yes
56. *Spodoptera littoralis*	Lepidoptera	Noctuidae	Foliar feeder	Polyphagous	Agricultural	Yes
57. *Spodoptera litura*	Lepidoptera	Noctuidae	Foliar feeder	Polyphagous	Agricultural	Yes
58. *Spodoptera ornithogalli*	Lepidoptera	Noctuidae	Foliar feeder	Polyphagous	Agricultural	No
59. *Spodoptera praefica*	Lepidoptera	Noctuidae	Foliar feeder	Polyphagous	Agricultural	Yes
60. *Thrips palmi*	Thysanoptera	Thripidae	Sap feeder	Polyphagous	Agricultural	Yes
61. *Zeugodacus cucumis*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	No
62. *Zeugodacus cucurbitae*	Diptera	Tephritidae	Fruit/flower feeder	Polyphagous	Agricultural	Yes

2.2 | Environmental data

To characterize climatic conditions, we obtained 19 bioclimatic variables (bio1–bio19) from CHELSA v2.1 for the 1970–2000 period to represent baseline historical climate [35]. For future projections, we considered two contrasting shared socioeconomic pathways (SSPs): SSP1–2.6 (sustainability-focused) and SSP5–8.5 (fossil fuel–intensive), for mid-century (2011–2040, aka the "2020s") and late-century (2071–2100, aka the "2080s") periods. To reduce model-specific uncertainty, we averaged projections from five general circulation models: GFDL-ESM4 [36], IPSL-CM6A-LR [37], MPI-ESM1-2-HR [38], MRI-ESM2-0 [39], and UKESM1-0-LL [40].

Land-use data were derived from the Land-Use Harmonization v2 (LUH2) dataset (`http://luh.umd.edu`) at 0.25° resolution [41]. For historical conditions, we used LUH2 v2h (850–2015) and averaged 1981–2010 values to align with the historical climate baseline. For future scenarios, we used LUH2 v2f (2015–2100) under SSP1–2.6 and SSP5–8.5, averaging data for 2011–2040 and 2071–2100. From the 14 available land-use variables, we selected 12 and aggregated several to obtain seven land-cover classes: `forests`, `non-forests`, C_3 `crops`, C_4 `crops`, C_3 `nitrogen-fixing crops`, `pastrrange`, and `secondary mean biomass density`.

Soil data were obtained from the SoilGrids database (`https://www.soilgrids.org` ; `https://www.isric.org/explore/soilgrids`), which provides global soil attributes at 250 m resolution [42]. We extracted 11 variables (at 5–15 cm depth) for use in both historical and future predictions, reflecting the core environmental conditions of the soil, particularly for taxa in our study who have life stages in the soil [43, 44].

Because these environmental datasets differ in native spatial resolution, we resampled all layers to 10 × 10 km using bilinear interpolation implemented in the `terra` package in `R` [45]. To minimize multicollinearity among predictors, we applied a variance inflation factor (VIF) analysis [46] across 62 species and five predictor sets. All retained variables had VIF values < 5, indicating acceptable levels of collinearity [46] (See Table S2, S3 for the environmental variables used for each species).

2.3 | Species Distribution Modelling

We used the `R` package `biomod2` [47] to model potential species distributions under historical and future climates. Within `biomod2`, we selected six algorithms commonly used in species distribution models: generalized linear models (GLM), gradient boosting machines (GBM; boosted trees), multivariate adaptive regression splines (MARS), classification tree analysis (CTA), random forests (RF), and flexible discriminant analysis [FDA, 6]. We generated pseudo-absences using multiple strategies and partitioned occurrences (presences and pseudo-absences) into training and testing sets using checkerboard, spatial, and environmental blocking. Model replication and validation followed Zou et al. (2024).

We evaluated performance across six model sets: `climate`, `land`, `soil`, `climate+land`, `climate+soil`, and `climate+land+soil`, using the true skill statistic [TSS; 48],the area under the receiver operating characteristic (ROC) curve (AUC) [AUC; 49], and the 5% omission rate [OR5; 50]. These metrics capture complementary aspects of model performance. *Threshold-dependent accuracy*, measured by the TSS, evaluates predictive performance after a continuous suitability surface has been converted into binary presence–absence predictions, combining sensitivity and specificity in a way that is sensitive to the chosen threshold. *Discrimination capacity*, expressed as the AUC, reflects the ability of the model to distinguish between sites where the species is present versus absent, independent of any threshold. Finally, the *false-negative error*, quantified by the OR5, indicates the proportion of observed presences that the model fails to predict, thereby highlighting instances where suitable habitat is incorrectly classified as unsuitable [51].

To enhance projection reliability, ensembles were constructed from base models satisfying the OR5 criterion ($\text{OR5} \leq 0.05$) and averaged their predictions to historical and future distributions. The continuous suitability was then dichotomized (aka threshholded) to maximize the TSS [52].

2.4 | Analyses

2.4.1 | Model Comparison

We compared four predictor sets per species: `climate`, `climate+land`, `climate+soil`, and `climate+land+soil`. For each species-set combination, we computed TSS, AUC, and OR5. Where multiple algorithms or resampling replicates were available, replicate-level metrics were averaged to a single per-species estimate.

For the TSS evaluation, we used the same hold-out partitions as for model fitting; the classification threshold was chosen on the training fold (TSS-maximizing) and applied to the corresponding test fold. AUC was computed on held-out data without a threshold. For OR5, we used the 5% *training* omission threshold to score omission on the test fold.

For each of the 62 species, we calculated differences from the climate-only baseline:

$$\begin{aligned} \Delta\text{TSS} &= \text{TSS}_{\text{target}} - \text{TSS}_{\texttt{climate}}, \\ \Delta\text{AUC} &= \text{AUC}_{\text{target}} - \text{AUC}_{\texttt{climate}}, \\ \Delta\text{OR5} &= \text{OR5}_{\texttt{climate}} - \text{OR5}_{\text{target}}, \text{(so that improvement is positive).} \end{aligned} \tag{1}$$

We summarized the proportion of species with $\Delta > 0$ and with gains exceeding *a priori* thresholds (+0.05 for TSS, +0.02 for AUC, 0.05 for OR5), reporting Wilson 95% confidence intervals [53]. To compare variable additions, we ran paired Wilcoxon signed-rank tests for `soil` *vs* `land` and `land+soil` *vs* the per-specigreater importance, implying that the model relies more strongly on that predictor in its predictionss with 95% CIs, p-values, and effect sizes $\theta = Z/\sqrt{N}$ (sign following the median difference).

2.4.2 | Variable importance

For each species s and predictor combination

$$c \in \{\texttt{climate}, \texttt{climate+land}, \texttt{climate+soil}, \texttt{climate+land+soil}\}, \tag{2}$$

we computed total variable importance $I_{s,c}$ from `biomod2`. In `biomod2`, variable importance is estimated using a permutation procedure: the values of a given predictor are randomly permuted while keeping all other predictors unchanged, and the resulting decrease in model predictive performance is quantified (as defined by the `biomod2` implementation). Larger decreases indicate higher importance, implying that the model relies more strongly on that predictor for prediction. Because this importance metric is relative and model-specific, it can be affected by correlations among predictors.

We used the climate-only model ($c = \texttt{climate}$) as the baseline and summarized the relative change (in %) in total variable importance as

$$\Delta_{s,c}(\%) \;=\; 100 \times \frac{I_{s,c} - I_{s,\texttt{climate}}}{I_{s,\texttt{climate}}}\,. \tag{3}$$

This yielded three contrasts against the climate baseline:

$$\begin{aligned}\Delta_{\texttt{land}} &= \Delta_{s,\texttt{climate+land}}\\ \Delta_{\texttt{soil}} &= \Delta_{s,\texttt{climate+soil}}\\ \Delta_{\texttt{land+soil}} &= \Delta_{s,\texttt{climate+land+soil}}.\end{aligned}$$

2.4.3 | Change in area

To identify distribution range changes in the future compared with historical, we compare current and future (2030s and 2050s) potential distribution area under two climate scenarios (SSP1-2.6 and SSP5-8.5) for each species as follows:

$$\text{Area Change} = \frac{\text{Future} - \text{Historical}}{\text{Historical}}. \tag{4}$$

2.4.4 | Change in distribution latitude and longitude

To detect future direction change patterns in the potential distribution area, we employed centroid-tracking analysis to quantify the spatio-temporal dynamics of each species' distribution. Using the `R` package `rgeos` [54], we derived the geometric centroid for the suitable areas. This process was applied iteratively across each species in different time periods and climate change scenarios. The resulting longitudinal and latitudinal coordinates were used to calculate the magnitude and direction of potential shifts in the distribution area over time.

2.4.5 | Jaccard similarity index

The Jaccard similarity index is a commonly used measure of similarity between two sets, ranging from 0 (no overlap) to 1 (identical sets). It is calculated as the size of the intersection divided by the size of the union of the two sets, that is, $J = \frac{|A\cap B|}{|A\cup B|}$ [55]. In the context of species distributions, the Jaccard index quantifies the degree of spatial overlap between a historical distribution and a projected future distribution. A high Jaccard value indicates that most areas suitable historically are also suitable in the future, implying relative stability in the species' range, whereas a low value indicates the potential for substantial turnover, with losses from historically occupied areas, gains in novel areas, or both. As such, the Jaccard index provides an intuitive summary of how similar future species distributions are to their historical baselines in terms of shared geographic occupancy.

2.4.6 | Evidential strength and effect sizes

Throughout this paper, we use the Shannon Information Index [56], defined as:

$$S = -\log_2(p), \tag{5}$$

where p is the p-value associated with the test in question. We use this as a measure of evidential strength rather than effect size. Interpreted literally, S quantifies the amount of information[1] gained against a null hypothesis, measured in bits: an S-value of 1 corresponds to the surprise associated with a single fair coin landing heads once, while $S = 10$ would produce the same amount of surprise as a fair coin landing heads 10 times in a row. Larger values thus correspond to increasingly unlikely outcomes under the null expectation. This framing provides an intuitive and scale-free way to assess how strongly the data support a given effect, independent of its magnitude. Unlike conventional p-values, which are bounded between 0 and 1 and often difficult to compare across analyses, the Shannon Information Index is unbounded above and additive,[2] making differences in evidential weight easier to interpret.

In this study, we use S alongside the effect-size measure partial η^2 (denoted: η_p^2) to distinguish between patterns that are biologically substantial and those that are merely statistically well supported.

$$\eta_p^2 = \frac{\mathrm{SS}_{\text{effect}}}{\mathrm{SS}_{\text{effect}} + \mathrm{SS}_{\text{error}}}. \tag{6}$$

High S-values indicate robust evidence that a trait or predictor contributes to structuring species responses, while η_p^2 indicates how much variation that factor explains across species. Considering these two quantities jointly allows us to identify cases of contingent generality that are both evidentially secure and ecologically meaningful, and to avoid conflating strong statistical support with large explanatory power.

The Shannon Information Index used here serves a distinct purpose from information criteria such as AIC or BIC. While information criteria compare competing models by balancing fit against complexity, the Shannon Information Index quantifies evidence against a specific null hypothesis within a given framework. AIC and BIC address which model is preferable; S addresses how surprising the observed association would be if no real effect were present. In this study, we use information criteria implicitly through ensemble model construction, but rely on the Shannon Information Index to assess the evidential weight of trait–response associations across species. This separation avoids conflating model selection with inference about generality.

3 | RESULTS

3.1 | How will the suitable areas for these species shift under climate change?

For the metrics described in Section 2.4, we subjected the results from all 62 species to an analysis of variance. Species were treated as independent analytical units. Although phylogenetic relatedness can induce statistical non-independence, our aim was not to infer evolutionary effects but to characterize cross-species patterns in projected responses. Similar responses among closely related species, therefore, constitute a meaningful ecological signal rather than a violation of model assumptions.

Figure 1 summarizes how projected climate change alters the potential geographic distributions of the 62 insect pest species under two future time horizons (2020s vs. 2080s) and two emissions scenarios (SSP1–2.6 and SSP5–8.5). Panels A–C show cumulative distributions of species responses for changes in proportional suitable area, latitudinal shift, and longitudinal shift, respectively, while Panel D shows changes in Jaccard similarity between future and historical distributions. In each panel, steeper curves indicate that a larger fraction of species exhibit similar magnitudes of change, whereas horizontal separation among curves reflects systematic differences among times or scenarios.

Across responses, time consistently emerges as a dominant driver. Proportional changes in suitable area (Panel A) show modest but significant effects of both time and scenario, as well as their interaction, indicating that losses and gains in climatically suitable area become more pronounced by the 2080s and diverge between low- and high-emissions pathways. Latitudinal shifts (Panel B) exhibit very strong effects of time, scenario, and their interaction, with most species projected to shift poleward, and substantially larger shifts under SSP5–8.5 by the late century. In contrast, longitudinal shifts (Panel C) show no consistent effects, suggesting that east–west redistribution is comparatively weak and idiosyncratic across species.

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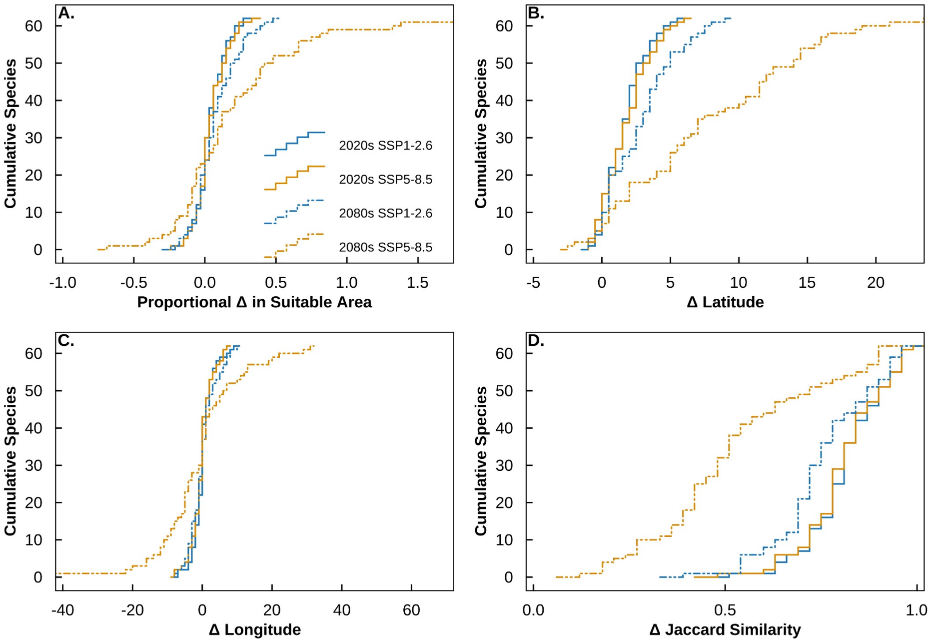
[1] In information theory, “surprise” is defined as $-\log_2(p)$ and measures how unlikely an observed event is under a specified expectation; rarer events are more surprising because they eliminate a larger set of alternatives.

[2] Because $0 < p \leq 1$, $S \in [0, \infty)$. Importantly, S is additive: for independent tests with p-values p_1 and p_2, the combined evidential weight is $S = -\log_2(p_1 p_2) = S_1 + S_2$.



E. Two-way repeated-measures ANOVAs

Response	Effect	df	F	p	S	partial η²
A. Proportional area	Time	1,61	12.246	8.8×10^{-4}	10.15	0.167
A. Proportional area	Scenario	1,61	7.747	7×10^{-3}	7.13	0.113
A. Proportional area	Time × Scenario	1,61	7.467	8×10^{-3}	6.93	0.109
B. Δ latitude	Time	1,61	87.046	2.4×10^{-13}	41.94	0.588
B. Δ latitude	Scenario	1,61	80.937	8.7×10^{-13}	40.07	0.57
B. Δ latitude	Time × Scenario	1,61	84.15	4.3×10^{-13}	41.07	0.58
C. Δ longitude	Time	1,61	0.199	6.57×10^{-1}	0.61	0.003
C. Δ longitude	Scenario	1,61	1.156	2.87×10^{-1}	1.8	0.019
C. Δ longitude	Time × Scenario	1,61	0.279	6.00×10^{-1}	0.74	0.005
D. Jaccard similarity	Time	1,61	324.542	4.2×10^{-26}	84.31	0.842
D. Jaccard similarity	Scenario	1,61	337.279	1.5×10^{-26}	85.74	0.847
D. Jaccard similarity	Time × Scenario	1,61	342.422	1×10^{-26}	86.31	0.849

FIGURE 1 The effects of climate change alone on the distributions of 62 insect pests. A. shows the cumulative distribution of the changes in the suitable area. B. shows the changes in latitude. C. shows the changes in longitude. D. shows the changes in Jaccard similarity. E. shows ANOVA tables for each panel. A rule of thumb is that a $\eta_p^2 > 0.14$ is a "large effect" but because they are contingent on the model, they are not comparable between models [57].

Jaccard similarity (Panel D) highlights the cumulative effects of these changes for range turnover. Similarity between future and present distributions declines strongly with time and differs markedly between scenarios, with the lowest similarities projected for the 2080s under SSP5–8.5. The large S-values for time, scenario, and their interaction underscore that temporal horizon and emissions pathway jointly structure how much future pest assemblages diverge from contemporary ones, whereas longitudinal displacement contributes relatively little to this divergence.

3.2 | Is there generality in the responses of insect pest distributions to climate change?

Perhaps the most important conclusion from Figure 1 emerges from simple inspection: despite clear differences in mean metric values, species responses exhibit substantial heterogeneity across the 62 species, both in magnitude and in direction. For example, in Panel A, between 58% and 68% of species are predicted to increase their proportion of suitable habitat, whereas 32% to 42% are predicted to experience a decrease (see Table S4). And in Panel D, in the 2080s under SSP5–8.5 for example, the Jaccard similarity ranges from a minimum of 0.11 (near complete dissimilarity: *Monochamus notatus*) to a maximum of 0.98 (near complete similarity: *Liriomyza trifolii*) (see Table S5).

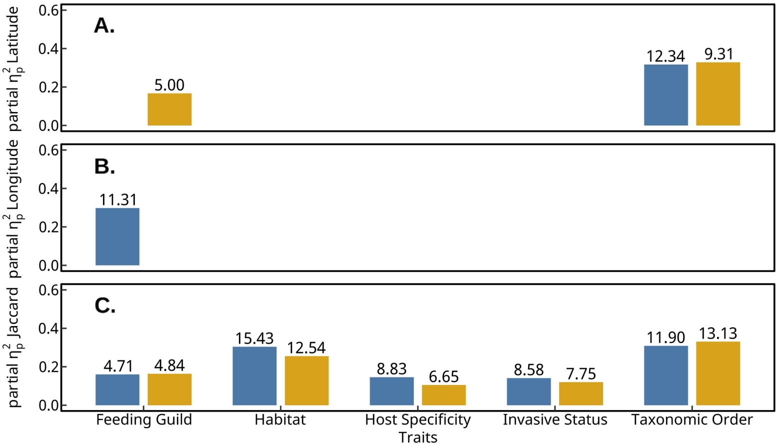


FIGURE 2 The effect sizes (η_p^2) and associated S-values for those traits that seem to account for at least a modest amount of the variation in the response variable (i.e, $p < 0.05$, $S > 4.32$). Changes in ares are not shown because they did not seem to relate to any of the traits we considered. Blue bars denote the 2020s and yellow bars the 2080s. A rule of thumb is that a $\eta_p^2 > 0.14$ is a "large effect" but because they are contingent on the model, they are not comparable between models [57].

Not surprisingly, these results indicate a clear absence of *global generality*: species do not respond to climate change to the same degree, nor even in the same direction. To search for the presence of *contingent generality*, we compared species responses to climate change while accounting for the traits listed in Table 1. Figure 2 summarizes this trait-based search for contingent generality. Partial η^2 (Equation 6) quantifies explanatory strength, indicating the proportion of between-species variation associated with each trait, while the Shannon Information index (numbers above bars; Equation 5) quantifies the strength of statistical evidence supporting each trait–response association. Larger S-values correspond to greater evidential support.

Interpreted jointly, these metrics distinguish qualitatively different forms of contingency. Traits exhibiting both high η_p^2 and high S identify axes along which species responses are not only strongly structured but also robustly supported by these species' responses, and therefore represent the clearest cases of contingent generality. Traits with high S but low η_p^2 reflect statistically well-supported yet biologically modest structuring, indicating consistent but minor differentiation among trait groups. Conversely,

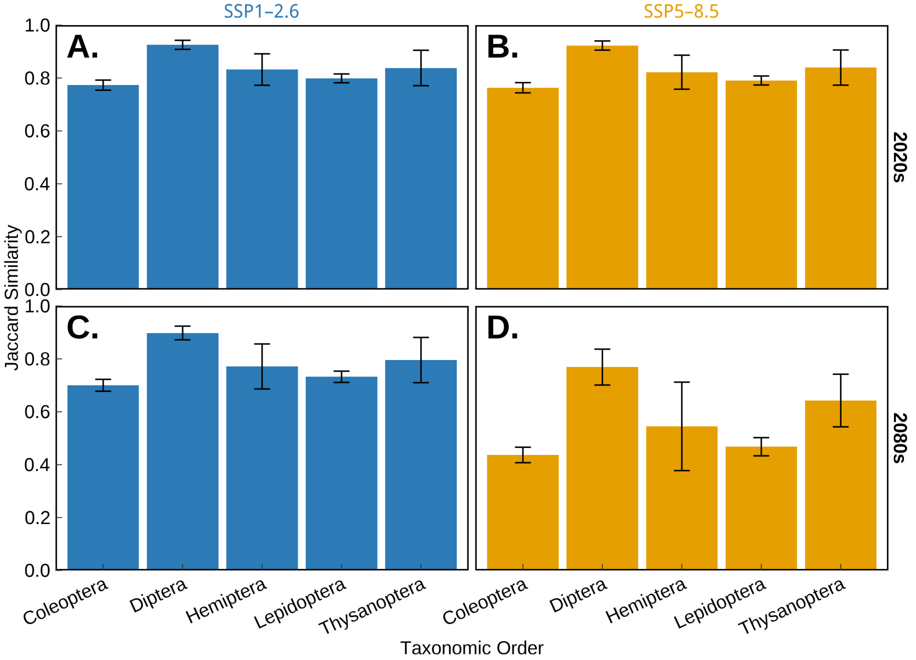


FIGURE 3 Mean Jaccard similarity (±SEM) in projected species distributions summarized by insect order, shown for two time horizons (2020s, 2080s) and two climate scenarios (SSP1–2.6 and SSP5–8.5). Higher values indicate greater similarity between projected and baseline distributions, while lower values indicate greater divergence. Short-term projections in the 2020s show consistently high similarity across orders and scenarios, whereas 2080s projections reveal increasing divergence that is both scenario-dependent and taxonomically structured. Differences among orders become most pronounced under the high-emissions SSP5–8.5 scenario, illustrating contingent generality in climate responses: similarity is neither globally uniform nor idiosyncratic, but instead depends jointly on taxonomic grouping, time horizon, and climate forcing.

traits with relatively large η_p^2 but low S suggest potentially important sources of variation whose support is limited or unstable, pointing to patterns that may be sensitive to sampling or model specification. Together, these contrasts show that contingent generality in insect responses to climate change arises from a small number of trait dimensions whose explanatory power is both biologically meaningful and evidentially secure, rather than from any universal or globally consistent response pattern.

Based on both η_p^2 and S, the most prominent patterns are associated with *taxonomic order*, indicating that higher-level phylogenetic structure captures substantial and well-supported differences in how species respond to climate change. *Feeding guild* shows similarly strong evidential support, especially for latitudinal shifts and changes in distributional similarity under SSP 5-8.5, suggesting that trophic strategy constitutes a broadly applicable axis along which responses are organized. *Habitat* also meets this joint criterion in Jaccard, though with greater variability across response metrics and scenarios, pointing to a form of contingent generality that is explicitly context-dependent rather than universal. By contrast, *host specificity* and *invasive status* are generally characterized by smaller effect sizes and weaker or less consistent evidential support, implying that these traits contribute to climate responses in more conditional or idiosyncratic ways. Overall, these results indicate that contingent generality in insect responses to climate change is concentrated along a limited number of trait dimensions—most notably higher-level taxonomy, feeding strategy, and, to a lesser extent, habitat.

This interpretation is illustrated directly by Figure 3, which summarizes distributional similarity at the level of taxonomic order.

Jaccard similarity varies substantially among orders, and these differences become more pronounced with stronger warming and longer projections. In the 2020s, similarity remains relatively high across most orders under both scenarios, consistent with broadly conserved distributions over short time scales. By the 2080s, however, this coherence erodes in a strongly order-dependent manner under SSP5–8.5, with some orders (e.g., Diptera and Thysanoptera) retaining comparatively high similarity while others (notably Coleoptera and Lepidoptera) exhibit marked divergence. The key result is therefore not that any order responds uniformly across all conditions, but that taxonomic grouping provides partial and conditional predictive power: species within the same order tend to respond more similarly to one another than to species in other orders, but most strongly at the end of the century under the highest emissions. In this way, the figure exemplifies contingent generality, in which biologically meaningful structure emerges at intermediate levels of organization without implying a universal or scenario-invariant response to climate change.

3.3 | Does adding land-use and/or soil variables improve the models?

3.3.1 | Model evaluation

The Area Under the Curve (AUC) and the True Skill Statistic (TSS) are two widely used metrics for assessing the quality of species distribution models. AUC measures a model's ability to differentiate between presence and absence across all possible thresholds, yielding a threshold-independent score that ranges from 0.5 (indicating random performance) to 1 (indicating perfect performance). In contrast, the TSS is threshold-dependent: it combines sensitivity (true positive rate) and specificity (true negative rate) into a single statistic that ranges from -1 (indicating perfect failure) to $+1$ (indicating perfect prediction).

While AUC is useful for evaluating overall discrimination and allows comparisons of models without threshold selection, it can be sensitive to factors such as prevalence and spatial extent. On the other hand, TSS directly balances omission and commission errors and is less biased by prevalence, but its value depends on the chosen threshold. Together, AUC and TSS offer complementary insights into model performance.

TABLE 2 Changes in the goodness of fit metrics True Skill Statistic (TSS) and Area Under the Curve (AUC) that result from adding predictive variables about land-use, soil, or both. The 95% confidence interval for each estimate, calculated using the Wilson score interval [53], is shown in brackets as a range.

Variables	**ΔTSS**		**ΔAUC**	
	% Improvement	% ≥ 0.05	% Improvement	% ≥ 0.02
`+land`	58 [46, 70]	45 [33, 57]	58 [46, 70]	47 [35, 59]
`+soil`	31 [21, 43]	18 [10, 29]	26 [17, 38]	18 [10, 29]
`+land+soil`	48 [36, 61]	35 [25, 48]	47 [35, 59]	39 [28, 51]

Adding environmental predictors generally improved model performance, but both the frequency and magnitude of gains depended strongly on the type of variables included (Table 2). Models augmented with `land` predictors showed the most consistent improvements, with more than half exceeding the improvement thresholds for both TSS and AUC. In contrast, `soil` predictors produced smaller and less frequent gains, with only about 18–31% of models meeting the more stringent criteria for improvement. Models including both predictor sets (`+land+soil`) exhibited sub-additive improvement rates, as the gains in two performance metrics were lower than those achieved by `+land`, rather than being amplified.

These patterns are reinforced by the paired contrasts in Figure 4. Across all 62 species, adding `land` predictors consistently outperforms adding `soil` predictors alone, with median differences in both ΔTSS and ΔAUC strongly favouring `land` and narrow confidence intervals well below zero for the `soil` − `land` comparison. Moreover, when the combined model is compared to each species' best single-addition model, median differences remain negative, indicating that adding `soil` to `land` rarely enhances performance and often slightly diminishes it. Together, the table and figure show that `land` variables constitute the most infor-

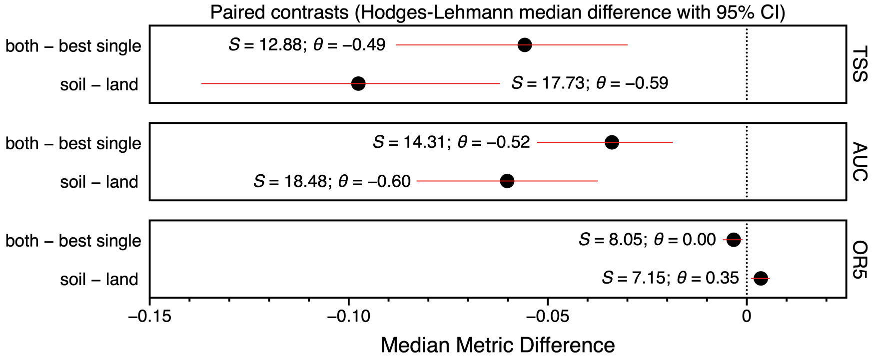


FIGURE 4 Paired contrasts in species-level performance deltas relative to the climate baseline. Each panel shows one metric: ΔTSS, ΔAUC, and ΔOR5 (defined as $\mathrm{OR5}_{\mathrm{clim}} - \mathrm{OR5}_{\mathrm{target}}$, so improvement is positive). Rows display two paired contrasts per species: `soil`− `land` and `both`− best single, where *best single* is the per-species maximum of $\Delta_{\mathtt{soil}}$ and $\Delta_{\mathtt{land}}$. Points give Hodges–Lehmann (HL) median differences; horizontal bars denote 95% confidence intervals; the dashed vertical line marks no difference (0). All estimates come from paired Wilcoxon signed-rank tests across $N = 62$ species; labels report: $S = -\log_2(p)$; $\theta = Z/\sqrt{N}$. Positive values favour the left-hand (first) model in each contrast, negative values favour the right-hand (second) model. Negative estimates for `soil`− `land` indicate that `land` generally yields larger gains than `soil`, and negative estimates for `both`− best single indicate sub-additivity of the combined model relative to the best single addition. *Abbreviations:* TSS, True Skill Statistic; AUC, Area Under the Curve; OR5, omission rate at the 5% training-omission threshold; CI, confidence interval.

mative and reliable non-climatic predictors, that `soil` variables provide weaker and more context-dependent benefits, and that combining the two tends to be sub-additive rather than synergistic—likely reflecting shared underlying structure, given that land use is partly determined by soil properties.

3.3.2 | Variable importance

Table 3 shows that adding `land` and/or `soil` predictors produces heterogeneous but generally modest shifts in variable importance, with no universal improvement across all 62 species but clear patterns within specific ecological groups. Most species fall into the “marginal positive” or “marginal negative” change categories regardless of whether `land`, `soil`, or both predictors are added, demonstrating that non-climatic variables typically adjust—rather than transform—the relative weighting of predictors in SDMs. A small number of species exhibit large (*Exomala orientalis*; *Orgyia pseudotsugata*; *Agrilus anxius*) or very large (*Orgyia pseudotsugata*) positive effects, highlighting cases where `land` or `soil` information meaningfully enhances explanatory power. Conversely, a minority of species, particularly certain soil-associated root feeders (e.g., *Diabrotica undecimpunctata*, *Diabrotica virgifera zeae*; *Naupactus leucoloma*), show consistent negative effects when these predictors are added, indicating possible mismatches between soil layers or land-use categories and the ecological drivers of their distributions (Table S6). Taken together, the table emphasizes that while most species experience only incremental changes, the direction and magnitude of those changes often align with ecological traits—especially for wood-boring forest beetles, which tend to benefit, and for some belowground herbivores, which do not (Table S6).

TABLE 3 Species counts by relative-change bins of variable importance and addition type. Relative change denotes the impact of adding additional variables to the best model based on climate variables alone. For example, 20 species had a marginal improvement in model fit ("marginal positive change") from adding land-use variables to the model, while 28 species showed a marginal decrease in model fit from adding land-use variables ("marginal negative change"). In general, we see no clear pattern across *all* species from including either land-use variables, soil variables, or both. There are, however, some patterns in subgroups. For example, the xylophagous beetles *Agrilus anxius*, *Agrilus bilineatus*, *Anoplophora chinensis*, *Cacyreus marshalli*, *Dendroctonus ponderosae*, *Dendroctonus rufipennis*, *Dendroctonus valens*, *Monochamus alternatus*, *Monochamus scutellatus*, *Neocerambyx raddei*, *Saperda candida* all show model improvement ("positive change") when adding `land` and/or `soil` variables. On the other hand, adding `soil` and `land` variables degrades the model fits ("negative effect") for a group of soil-associated root feeders: *Diabrotica undecimpunctata*, *Diabrotica virgifera zeae*, *Naupactus leucoloma*.

Relative change (%)		`+land`	`+soil`	`+land+soil`
very large positive effect	>100	–	–	1[a]
large positive effect	(60,100]	2[b]	1[c]	1[d]
positive effect	(20,60]	6[e]	9[f]	8[g]
marginal positive effect	(0,20]	20	30	28
no effect		–	–	–
marginal negative	(-20,0]	28	17	18
negative	(-60,-20]	6[h]	5[i]	6[j]

[a] *Orgyia pseudotsugata*.

[b] *Exomala orientalis*; *Orgyia pseudotsugata*.

[c] *Agrilus anxius*.

[d] *Exomala orientalis*.

[e] *Bactericera cockerelli*; *Ceratitis rosa*; *Dendroctonus rufipennis*; *Grapholita packardi*; *Ips pini*; *Lycorma delicatula*.

[f] *Anthonomus bisignifer*; *Exomala orientalis*; *Ips pini*; *Leptinotarsa decemlineata*; *Orgyia pseudotsugata*; *Rhynchophorus ferrugineus*; *Rhynchophorus palmarum*; *Saperda candida*; *Zeugodacus cucurbitae*.

[g] *Agrilus anxius*; *Cacyreus marshalli*; *Ceratitis rosa*; *Ips pini*; *Lycorma delicatula*; *Saperda candida*; *Spodoptera praefica*; *Zeugodacus cucurbitae*.

[h] *Anoplophora chinensis*; *Heteronychus arator*; *Metamasius hemipterus*; *Monochamus notatus*; *Naupactus leucoloma*; *Popillia japonica*.

[i] *Heteronychus arator*; *Metamasius hemipterus*; *Monochamus notatus*; *Popillia japonica*; *Spodoptera litura*.

[j] *Heteronychus arator*; *Lymantria mathura aurora*; *Metamasius hemipterus*; *Monochamus alternatus*; *Naupactus leucoloma*; *Popillia japonica*.

3.4 | Is there generality in insect responses to the addition of land and soil variables?

3.4.1 | Dimension-level robustness of land-use and soil effects

To evaluate whether the influence of `land` and `soil` predictors exhibits *contingent generality*, we aggregated individual predictors into ecologically interpretable dimensions and quantified, for each species and predictor set, the strongest robust signal expressed along each dimension. This framing reflects the level at which our hypotheses are posed—whether land use or soil—as conceptual dimensions rather than collections of individual, often highly correlated variables that contribute systematically to species' responses to climate change.

Specifically, for species i, predictor set g, and ecological dimension d, we defined the *dimension-level robustness maximum*:

$$M_{i,g,d} = \max_{v \in d} \left(\text{hit proportion}_{i,g,v} \right), \tag{7}$$

where hit proportion is the proportion of retained final models in which a predictor's importance exceeded the threshold $\tau = 0.20$ (a hit if Var.imp $\geq \tau$). This summary captures whether a given dimension contains *at least one* predictor that consistently exerts a strong and defensible influence, rather than requiring explanatory strength to be evenly distributed across all constituent variables. Averaging across predictors within a dimension would obscure such structure, particularly when variables serve as partially redundant proxies for shared ecological processes, and would penalize dimensions represented by larger numbers of correlated predictors. By contrast, the dimension-level maximum identifies the strongest recurring signal that survives repeated model fitting and exceeds the importance threshold, providing a conservative and interpretable measure of dimension-level explanatory potential aligned with our focus on contingent generality.

Land-use predictors were grouped into (i) agricultural intensity and cropping (`C3`, `C4`, `N-fixing C3 crops`), (ii) grazing pressure (`pasture/rangeland`), and (iii) vegetation structure and biomass (`forest cover`, `non-forest natural cover`, `secondary mean biomass`). Soil predictors were grouped into (i) texture and physical structure (`sand`, `silt`, `clay`, `bulk density`, `coarse fragments`), (ii) chemical fertility (`CEC`, `total N`, `pH`), and (iii) carbon storage and pools (`SOC`, `organic carbon density`, `organic carbon stocks`).

Rank–frequency curves of $M_{i,g,d}$ reveal the form of contingent generality within each predictor set (Figure 5). Across dimensions, the distributions are characteristically right-skewed: many species exhibit near-zero robustness maxima for a given dimension, while a smaller subset shows moderate to high values. This pattern indicates that `land` and `soil` predictors do not exert uniform influence across the assemblage; instead, when a dimension matters, it does so robustly for a contingent subset of species.

3.4.2 | Decomposing contingent generality with fingerprint contrasts

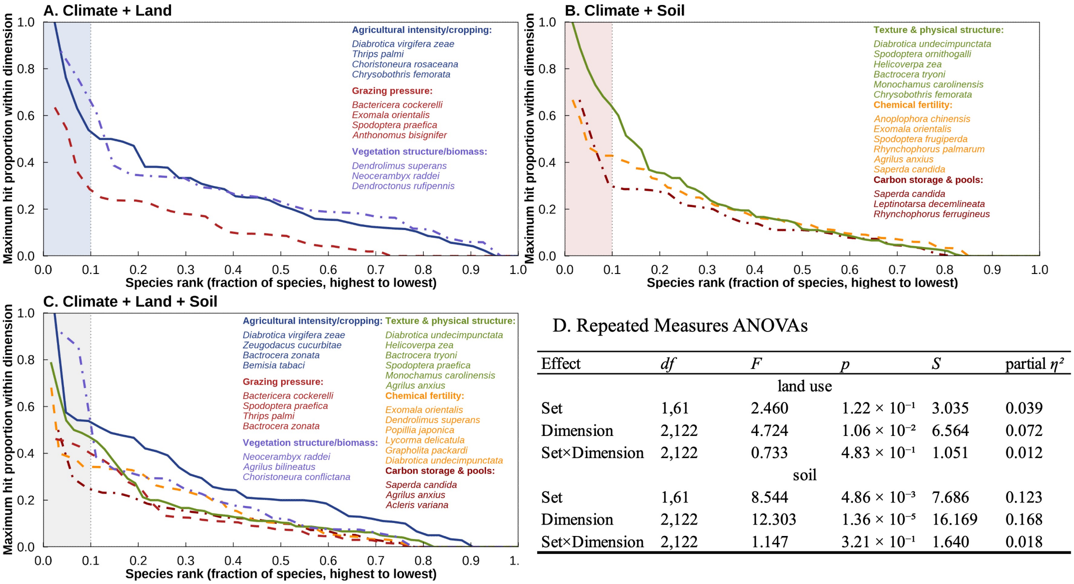
The preceding analyses treated predictor-set context as a contrast (e.g., `climate+land` versus `climate+land+soil`) and asked whether species exhibit structured differences across trait dimensions. Here we extend that logic by constructing *fingerprints* that separate (i) *intrinsic* structure within `land` and `soil` predictors, (ii) *climate-conditioning* of those structures, (iii) *addition* when the complementary predictor class is added in the presence of climate, and (iv) *reorganization of climate predictors themselves* as `land` and/or `soil` predictors are added. These fingerprints allow us to distinguish effects that are present even in the absence of climate predictors from those that emerge only in particular predictor contexts.

Reliability-weighted importance score.

For each species i, predictor set g, and predictor variable v, the SDM summaries provide a hit proportion $H_{i,g,v}$ (fraction of retained final models in which Var.imp $\geq \tau$ with $\tau = 0.20$) and a retention count $F_{i,g,v}$ (number of randomized fits in which the variable was retained in the final model). We combined these into a reliability-weighted importance score

$$C_{i,g,v} = \left(\frac{F_{i,g,v}}{N_g} \right) H_{i,g,v}, \tag{8}$$

where N_g is the number of randomized fits for predictor set g. High $C_{i,g,v}$ therefore requires both frequent retention and robust importance conditional on retention.



D. Repeated Measures ANOVAs

Effect	*df*	*F*	*p*	*S*	partial η^2
		land use			
Set	1,61	2.460	1.22×10^{-1}	3.035	0.039
Dimension	2,122	4.724	1.06×10^{-2}	6.564	0.072
Set×Dimension	2,122	0.733	4.83×10^{-1}	1.051	0.012
		soil			
Set	1,61	8.544	4.86×10^{-3}	7.686	0.123
Dimension	2,122	12.303	1.36×10^{-5}	16.169	0.168
Set×Dimension	2,122	1.147	3.21×10^{-1}	1.640	0.018

FIGURE 5 Rank–frequency curves for dimension-level robustness maxima ($M_{i,g,d}$) within each predictor set. For each ecological dimension, species are ordered from highest to lowest $M_{i,g,d}$, where $M_{i,g,d}$ is the maximum hit proportion among variables belonging to that dimension (hit if Var.imp $\geq \tau = 0.20$ with $\tau = 0.20$). Curves with heavier upper tails indicate dimensions that yield robust predictor-importance signals for a larger contingent subset of species, while near-zero plateaus indicate dimensions that rarely produce robust hits. Species listed in each panel are in the top 10% $M_{i,g,d}$ for each trait group.

Four fingerprint types.

Using the $C_{i,g,v}$ matrices, we defined four types of fingerprints (Figure 6).

1. **Intrinsic fingerprints** describe the land-only and soil-only structures:

$$\mathbf{C}_i^{\texttt{land}} = \{C_{i,\texttt{land},v}\}_{v \in \texttt{land}}, \tag{9}$$

$$\mathbf{C}_i^{\texttt{soil}} = \{C_{i,\texttt{soil},v}\}_{v \in \texttt{soil}}. \tag{10}$$

2. **Climate-conditioned fingerprints** quantify how land and soil profiles change when climate predictors are introduced:

$$\Delta_{i,v}^{\texttt{land}|\texttt{climate}} = C_{i,\texttt{climate+land},v} - C_{i,\texttt{land},v}, \tag{11}$$

$$\Delta_{i,v}^{\texttt{soil}|\texttt{climate}} = C_{i,\texttt{climate+soil},v} - C_{i,\texttt{soil},v}. \tag{12}$$

3. **Addition fingerprints** quantify how land (soil) profiles change when soil (land) predictors are added *given climate*:

$$\Delta_{i,v}^{\texttt{soil}|\texttt{+land}} = C_{i,\texttt{climate+land+soil},v} - C_{i,\texttt{climate+land},v}, \tag{13}$$

$$\Delta_{i,v}^{\texttt{land}|\texttt{+soil}} = C_{i,\texttt{climate+land+soil},v} - C_{i,\texttt{climate+soil},v}. \tag{14}$$

4. **Climate-variable reorganization fingerprints** quantify how the climate predictor profile itself shifts as land-use and/or soil

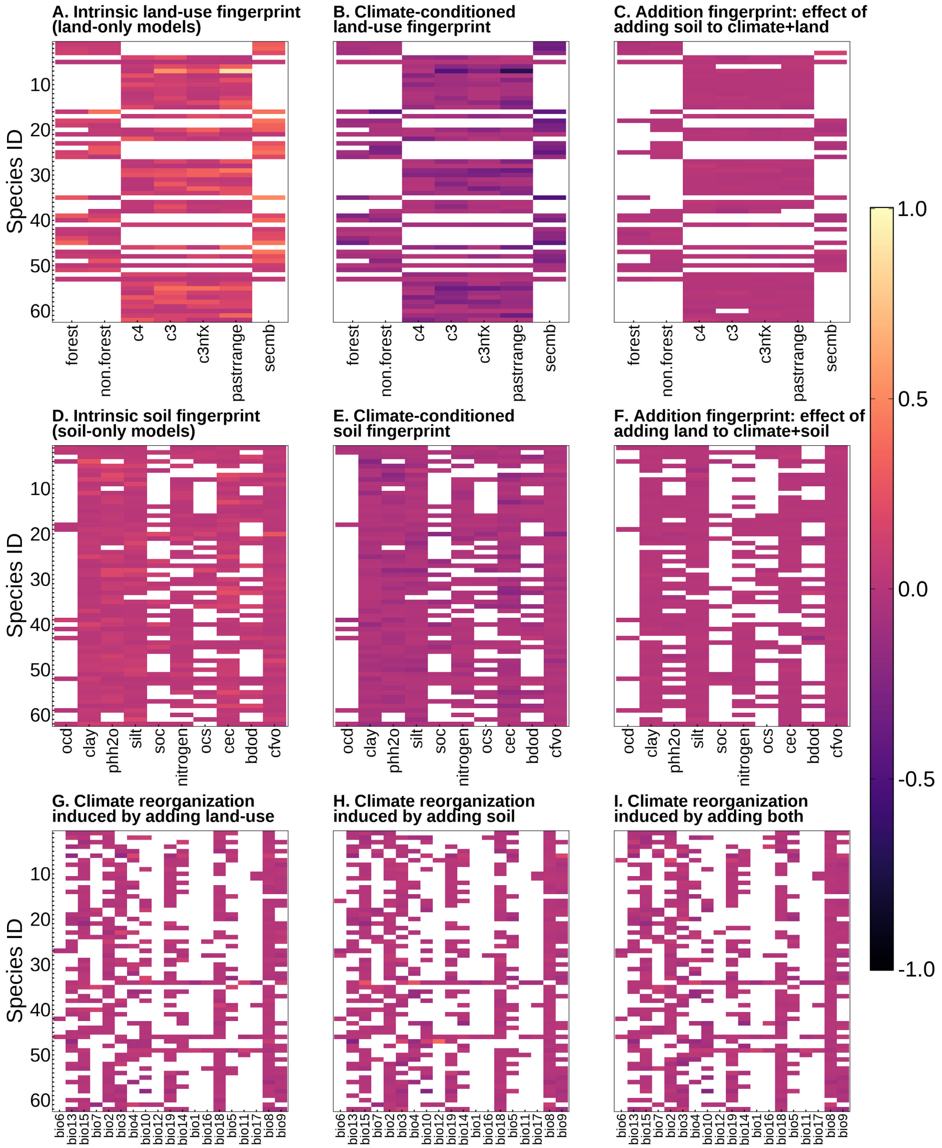


FIGURE 6 Fingerprints summarizing intrinsic and context-dependent structure in predictor importance across species. Panels A–C show land-use fingerprints, D–F soil fingerprints, and G–I climate-variable fingerprints. For land and soil, panels show intrinsic structure (A, D), climate-conditioned changes when climate predictors are added (B, E), and addition fingerprints when the complementary predictor class is added in the presence of climate (C, F). Climate panels show reorganization of climate-predictor importance when land (G), soil (H), or both (I) are added. Rows (species) are ordered alphabetically with the numbers corresponding to species names, see Table 1, and columns are predictors; values indicate reliability-weighted changes (or baseline levels for intrinsic panels) in predictor importance.

predictors are added:

$$\Delta_{i,c}^{\texttt{climate}|+\texttt{land}} = C_{i,\texttt{climate+land},c} - C_{i,\texttt{climate},c}, \tag{15}$$

$$\Delta_{i,c}^{\texttt{climate}|+\texttt{soil}} = C_{i,\texttt{climate+soil},c} - C_{i,\texttt{climate},c}, \tag{16}$$

$$\Delta_{i,c}^{\texttt{climate}|+\texttt{land+soil}} = C_{i,\texttt{climate+land+soil},c} - C_{i,\texttt{climate},c}. \tag{17}$$

In each case, the fingerprint is a multivariate vector for each species, summarizing either (*i*) the baseline structure of robust explanatory recurrence (**C**) or (*ii*) a context-specific change in that structure (Δ).

Visualizing response types and testing trait-structured similarity.

For each fingerprint type, we visualized the species-by-variable matrices as clustered heatmaps (hierarchical clustering on fingerprints; Figure 6). We also summarized multivariate similarity among species using PCoA, computed from Euclidean distances on column-Z-scored fingerprints (Figure 7). To test whether fingerprints are structured by traits or taxonomy, we used one-factor PERMANOVA on each fingerprint distance matrix, reporting evidential support as S-values (Table 4).

Across fingerprint types, trait-structured similarity was most evident for the *intrinsic land-only* fingerprints (strongest association with host specificity, primary habitat, and invasive status) and for *climate-conditioned land* fingerprints (strongest association with the same three variables), indicating that robust land-use structure is both present in the absence of climate predictors and further reorganized when climate predictors enter the model. Addition fingerprints showed moderate structure (most clearly for land-use fingerprints when soil predictors are added, aligned with primary habitat), consistent with the interpretation that adding the complementary predictor class induces substantial reorganization for a subset of species rather than uniformly across the assemblage. Climate-variable reorganization fingerprints showed weaker-to-moderate structuring, with the clearest evidence emerging when land-use predictors are added to climate predictors (aligned with primary habitat), indicating that part of the contingency induced by land-use predictors is expressed as a redistribution of robust explanatory recurrence among the climate predictors themselves.

TABLE 4 PERMANOVA tests linking trait groupings to species similarity in fingerprint profiles. Distances are Euclidean on column-Z-scored fingerprints. p-values were obtained by permutation (n = 1999 permutations) and converted to S-values ($S = -\log_2 p$).

Fingerprint	Domain	Grouping	k	pseudo-F	p	S	R^2	Panel
Intrinsic	Land-only	Host specificity	2	6.730	0.001	10.966	0.101	A
Intrinsic	Land-only	Primary habitat	3	13.899	0.001	10.966	0.320	A
Intrinsic	Land-only	Invasive status	2	6.031	0.001	10.966	0.091	A
Intrinsic	Land-only	Feeding guild	5	2.078	0.004	7.966	0.127	A
Intrinsic	Land-only	Taxonomic order	5	1.918	0.027	5.238	0.119	A
Climate-conditioned	Land variables	Host specificity	2	6.378	0.001	10.966	0.096	B
Climate-conditioned	Land variables	Primary habitat	3	11.564	0.001	10.966	0.282	B
Climate-conditioned	Land variables	Invasive status	2	5.849	0.001	10.966	0.089	B
Climate-conditioned	Land variables	Feeding guild	5	1.959	0.005	7.644	0.121	B
Climate-conditioned	Land variables	Taxonomic order	5	1.835	0.021	5.608	0.114	B
Addition	Land variables	Host specificity	2	7.482	0.001	10.966	0.111	C
Addition	Land variables	Primary habitat	3	8.826	0.001	10.966	0.230	C
Addition	Land variables	Feeding guild	5	2.119	0.001	9.966	0.129	C
Addition	Land variables	Invasive status	2	4.368	0.001	10.966	0.068	C
Addition	Land variables	Taxonomic order	5	1.449	0.070	3.847	0.092	C

Fingerprint	Domain	Grouping	k	pseudo-F	p	S	R^2	Panel
Intrinsic	Soil-only	Invasive status	2	1.987	0.022	5.540	0.032	D
Intrinsic	Soil-only	Primary habitat	3	1.281	0.167	2.582	0.042	D
Intrinsic	Soil-only	Taxonomic order	5	1.111	0.279	1.844	0.072	D
Intrinsic	Soil-only	Feeding guild	5	0.863	0.740	0.435	0.057	D
Intrinsic	Soil-only	Host specificity	2	0.742	0.723	0.469	0.012	D
Climate-conditioned	Soil variables	Primary habitat	3	1.703	0.013	6.322	0.055	E
Climate-conditioned	Soil variables	Invasive status	2	1.909	0.021	5.573	0.031	E
Climate-conditioned	Soil variables	Taxonomic order	5	1.410	0.034	4.878	0.090	E
Climate-conditioned	Soil variables	Feeding guild	5	1.046	0.388	1.366	0.068	E
Climate-conditioned	Soil variables	Host specificity	2	1.139	0.322	1.637	0.019	E
Addition	Soil variables	Primary habitat	3	2.005	0.004	7.966	0.064	F
Addition	Soil variables	Invasive status	2	1.824	0.022	5.506	0.030	F
Addition	Soil variables	Host specificity	2	1.831	0.026	5.265	0.030	F
Addition	Soil variables	Taxonomic order	5	1.319	0.086	3.548	0.085	F
Addition	Soil variables	Feeding guild	5	1.191	0.159	2.657	0.077	F
Climate reorganization	Climate variables (+land)	Primary habitat	3	2.427	0.001	10.966	0.076	G
Climate reorganization	Climate variables (+land)	Invasive status	2	3.110	0.001	10.966	0.049	G
Climate reorganization	Climate variables (+land)	Host specificity	2	2.205	0.003	8.381	0.035	G
Climate reorganization	Climate variables (+land)	Feeding guild	5	1.063	0.336	1.573	0.069	G
Climate reorganization	Climate variables (+land)	Taxonomic order	5	1.051	0.375	1.415	0.069	G
Climate reorganization	Climate variables (+soil)	Invasive status	2	3.266	0.001	10.966	0.052	H
Climate reorganization	Climate variables (+soil)	Primary habitat	3	1.807	0.008	7.059	0.059	H
Climate reorganization	Climate variables (+soil)	Feeding guild	5	1.277	0.061	4.047	0.084	H
Climate reorganization	Climate variables (+soil)	Taxonomic order	5	1.331	0.070	3.847	0.087	H
Climate reorganization	Climate variables (+soil)	Host specificity	2	1.421	0.103	3.279	0.024	H
Climate reorganization	Climate variables (+land+soil)	Invasive status	2	2.799	0.001	10.966	0.045	I
Climate reorganization	Climate variables (+land+soil)	Host specificity	2	2.085	0.007	7.158	0.034	I
Climate reorganization	Climate variables (+land+soil)	Taxonomic order	5	1.454	0.036	4.816	0.093	I
Climate reorganization	Climate variables (+land+soil)	Primary habitat	3	1.509	0.037	4.756	0.049	I
Climate reorganization	Climate variables (+land+soil)	Feeding guild	5	1.189	0.157	2.676	0.077	I

4 | DISCUSSION

The central aim of this study was to evaluate whether insect pest responses to climate change and to increasing SDM complexity exhibit global generality, idiosyncrasy, or intermediate forms of contingent generality. By combining multi-scenario climate projections with trait-based analyses and a detailed examination of how land-use and soil predictors alter model structure, we show that none of these responses are uniform across species. Instead, consistent patterns emerge at intermediate levels of biological organization and predictor structure. In this section, we synthesize these results, interpret their ecological and methodological implications, and situate them within broader debates about SDM inference and prediction under global change.

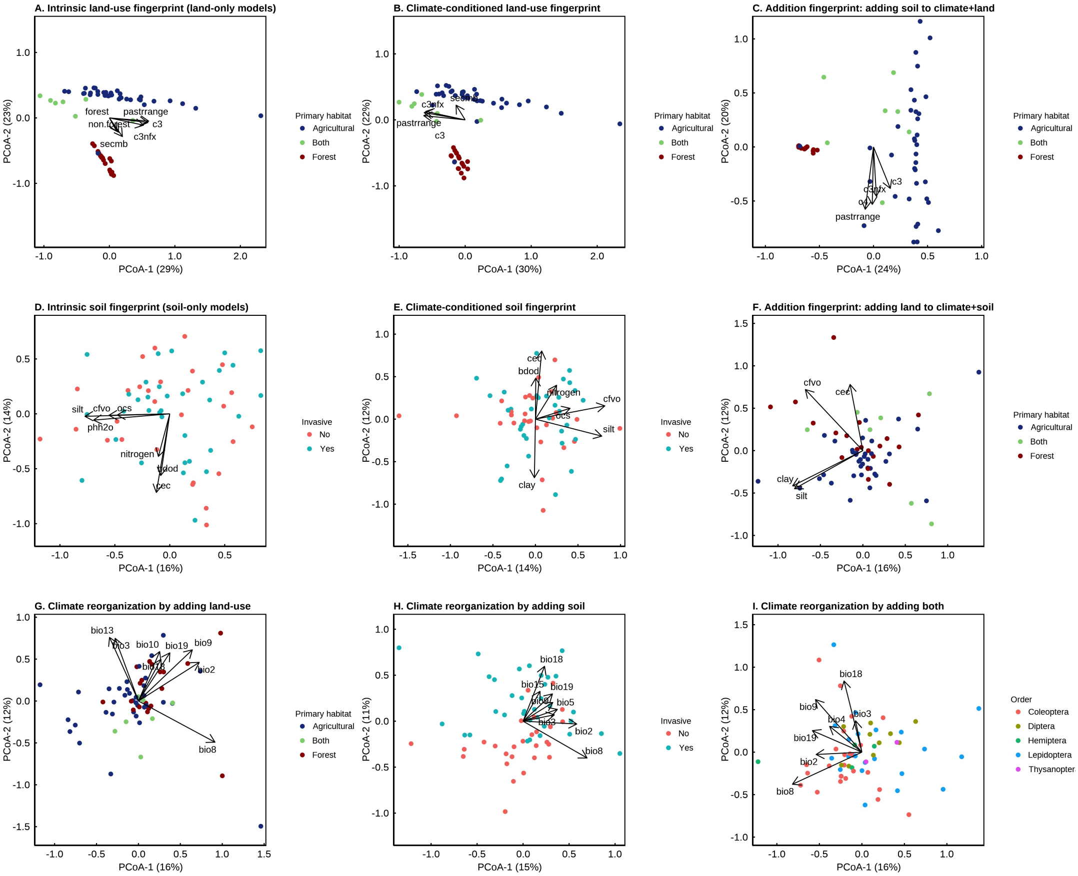


FIGURE 7 Principal coordinates analyses (PCoA) summarizing species-level fingerprint structures derived from land-use, soil, and climate predictors, and their interactions. Panels A–C show land-use fingerprints: (A) intrinsic land-use structure from land-only models, (B) land-use fingerprints conditioned on climate, and (C) addition fingerprints capturing changes when soil predictors are added to climate + land models. Panels D–F show the corresponding soil fingerprints: (D) intrinsic soil structure from soil-only models, (E) soil fingerprints conditioned on climate, and (F) addition fingerprints capturing changes when land-use predictors are added to climate + soil models. Panels G–I depict climate reorganization fingerprints, showing how the relative positions of species in climate space shift when (G) land-use variables, (H) soil variables, or (I) both are added to climate-only models. Points represent species and are coloured by dominant habitat association (agricultural, forest, or both). Axis labels report the percentage of variation explained by each PCoA axis. Arrows indicate predictor variables significantly fitted to the ordination using permutation-based vector fitting (`envfit`; `vegan` package in `R` [58]; $p < 0.05$); only significant variables are shown.

4.1 | How will the suitable areas for these species shift under climate change?

Across all four response metrics examined—proportional area change, latitudinal shift, longitudinal shift, and Jaccard similarity—climate change produces strong aggregate trends but substantial interspecific heterogeneity (Section 3.1; Figure 1). The most robust signal is the dominance of time horizon and emissions scenario, with later projections and higher forcing consistently associated with larger range shifts and lower similarity to historical distributions. These results align with previous large-scale SDM studies showing that the strength of the climatic change, and hence its effects, are strongly time- and scenario-dependent, particularly for ectothermic organisms whose performance is tightly constrained by temperature.

At the same time, the results demonstrate that these aggregate trends conceal wide variation in both the direction and magnitude of species-level responses. For example, although poleward shifts dominate on average (Figure 1B), individual species exhibit minimal movement or even equatorial shifts, and changes in suitable area span strong expansions and contractions within the same scenario and time horizon (Figure 1A). Correspondingly, Jaccard similarity declines sharply with time and emissions intensity (Figure 1D), but values range from near-complete overlap to almost complete redistribution across species under identical climatic conditions.

These patterns underscore an important limitation of interpreting climate-driven SDM outputs solely through mean responses or ensemble summaries. Climate change clearly restructures the potential distributions of insect pests at a global scale, but it does so in ways that are not uniformly experienced across taxa. The ecological significance of these projections, therefore, lies not in their central tendencies alone but in the structured heterogeneity they reveal.

4.2 | Is there generality in the responses of insect pest distributions to climate change?

The results in Section 3.2 demonstrate that—not surprisingly—global generality is absent: species do not respond to climate change in a consistent or directionally uniform way. However, this absence of universality does not imply that responses are unstructured or purely idiosyncratic. Instead, trait-based analyses reveal multiple forms of contingent generality, where species sharing particular characteristics respond more similarly to one another than to species lacking those traits.

This conclusion is most clearly supported by the joint interpretation of effect sizes (η_p^2) and evidential strength (S-values) in Figure 2. A small subset of traits—most notably taxonomic order and feeding guild—consistently exhibit both moderate-to-large explanatory power and strong evidential support across several response variables. These traits, therefore, define axes along which climate responses are repeatedly and robustly structured, even though no single trait explains a majority of the variation across all metrics or scenarios.

Figure 3 illustrates this form of contingent generality concretely. At short time horizons (2020s), differences among orders are muted, with high Jaccard similarity across scenarios. By the 2080s, and especially under SSP5–8.5, divergence among orders becomes pronounced, indicating that taxonomic grouping gains predictive relevance as climatic forcing intensifies. Importantly, this pattern is itself conditional: taxonomic order does not determine a fixed response, but rather modulates the rate and extent of distributional reorganization under particular climatic contexts.

Traits such as habitat association also meet the joint criterion of evidential support and explanatory strength in some cases, though less consistently than taxonomy or feeding guild. In contrast, host specificity and invasive status tend to exhibit weaker and more context-dependent effects, suggesting that these traits influence climate responses in more conditional or indirect ways. Together, these results support a view of climate responses that is neither universally general nor irreducibly species-specific, but instead structured by a limited number of biologically meaningful traits whose influence depends on scenario and time horizon.

4.3 | Does adding land-use and/or soil variables improve the resulting models?

The results in Section 3.3 show that adding non-climatic predictors can improve SDM performance, but that these improvements are neither uniform nor symmetric across predictor types. Land-use variables consistently yield larger and more frequent gains in model performance than soil variables, as reflected in both threshold-dependent (TSS) and threshold-independent (AUC) metrics (Table 2; Figure 4). More than half of the species show meaningful improvements when land predictors are added, whereas soil predictors produce smaller and less consistent gains.

Paired contrasts (Figure 4) make this asymmetry explicit. Across species, the median improvement from adding land exceeds that from adding soil for all three evaluation metrics, with strong evidential support. Moreover, combining land and soil predictors is typically subadditive: adding the complementary predictor class to the best single addition does not further improve performance and often slightly reduces it. This result suggests redundancy or partial collinearity in the ecological information captured by land-use and soil variables, which is not surprising, since land-use is, to some extent, determined by soil type.

These findings have direct methodological implications. Climate-only models systematically omit ecologically relevant land-use structures, particularly vegetation and habitat configuration, and their performance can often be improved by incorporating this information. However, indiscriminately adding predictor classes—especially those with diffuse or indirect links to species' realized niches—does not guarantee further gains and may complicate interpretation without enhancing predictive accuracy.

4.4 | Is there generality in insect responses to the addition of land and soil variables?

While land-use variables improve model performance on average, Section 3.4 demonstrates that responses to predictor addition are themselves heterogeneous, and that this heterogeneity is structured rather than random. Dimension-level robustness analyses (Figure 5) show that land-use and soil predictors rarely exert uniform influence across all species. Instead, robust effects are concentrated in the upper tails of rank–frequency distributions, indicating that particular ecological dimensions matter strongly for some species but not for most.

For land-use predictors, dimensions related to vegetation structure and biomass produce the most consistent and robust signals, particularly when climate predictors are included. Repeated-measures ANOVAs reveal strong evidential support for structured differences among land-use dimensions and for interactions between predictor-set context and dimension (Figure 5D). Soil dimensions, by contrast, exhibit weaker and less consistent structure, reinforcing the conclusion that soil effects are more diffuse and contingent.

Fingerprint analyses extend this interpretation by decomposing how predictor importance changes across modelling contexts (Section 3.4.2; Figure 6). Intrinsic land-use fingerprints already show clear structure in the absence of climate predictors, and this structure is further reorganized when climate is introduced. Addition fingerprints indicate that adding `soil` to `climate+land` models induces substantial reorganization for a subset of species, but not universally. Climate reorganization fingerprints (Figure 6G–I; Figure 7) show that part of the effect of adding land-use predictors is expressed as a redistribution of importance among climate variables themselves.

Trait-based PERMANOVA tests (Table 4) reinforce these conclusions. Climate-conditioned land-use fingerprints show strong and consistent structuring by primary habitat, host breadth, invasive status, taxonomic order and feeding guild, whereas soil-related fingerprints show much weaker trait associations. Together, these results indicate that contingent generality in responses to predictor addition is most evident for land-use effects, particularly when they interact with climate and species' ecological roles.

4.5 | Conclusions

Taken together, our results demonstrate that neither insect pest responses to climate change nor their responses to additional predictor variables can be described as either globally general or purely idiosyncratic. Climate change produces strong, scenario- and time-dependent aggregate trends, but these trends are expressed through highly heterogeneous species-level responses. Similarly, adding land-use and soil predictors improves model performance *on average*, but the magnitude, direction, and explanatory structure of those improvements depend on species traits and ecological context.

The concept of contingent generality provides a unifying framework for interpreting these patterns. Generality emerges, but only at intermediate levels of organization—such as taxonomic order, feeding guild, habitat association, and specific predictor dimensions—and only under particular climatic and modelling contexts. Recognizing this contingency has practical implications for pest risk assessment and ecological forecasting: SDMs are most informative when their assumptions about generality are made explicit, their predictor sets are chosen with ecological intent rather than maximal inclusion, and their outputs are interpreted in terms of structured heterogeneity rather than average response alone.

Future work should build on this approach by integrating mechanistic information where available, refining trait classifications to capture functional rather than taxonomic similarity, and explicitly testing how management-relevant decisions depend on the forms of contingent generality assumed. In the context of rapidly changing climates and expanding pest pressures, embracing rather than obscuring contingency may be essential to producing robust, actionable ecological predictions.

| Acknowledgements

This work was carried out on the shared traditional territory of the Neutral, Anishnaabe, and Haudenosaunee peoples. We recognize, honour, and respect these Nations as the traditional stewards, since time immemorial, of the lands and water on which Wilfrid Laurier University is now present. This acknowledgement represents our responsibility and commitment to learn about and confront colonial legacies and to earnestly engage in the unfinished work of reconciliation. This work was supported by a grant from the Canadian Natural Science and Engineering Research Council (NSERC; RGPIN-2022-04581) to JAN. We used ChatGPT 5.1 and 5.2 to test some of our ideas and Grammarly to improve the writing in some places. All AI-assisted content was reviewed and verified by the authors. We also thank Deborah Arnal for administrative support.

| Conflicts of Interest

The authors declare no conflicts of interest.

| Data Availability Statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.6hdr7srfd

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