Hyper-dominant species drive unexpected functional shifts in North American birds

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Abstract

Climate change has led to consistent intraspecific shifts in functional traits, yet the extent to which within-species trends predict community-level changes is unknown. We assessed how local community-weighted means of seven key traits have changed over the past 50 years across North American bird communities. Communities shifted toward larger body mass and smaller appendages over time, the opposite of widely documented within-species changes. These unexpected patterns arise from a small proportion (5%) of hyper-dominant species. Idiosyncratic changes in their abundances led to weak associations between functional shifts and climate but strong associations with human-induced land use changes. Our results reveal contrasting within-species responses to climate change and community-level responses to broader environmental dynamics, highlighting the importance of hyper-dominant species in shaping biodiversity under global change.

Main Text

Rapid climate change has driven widespread shifts in species' abundances and distributions (*1–3*), as well as changes in key functional or life history traits (*4*, *5*). Both shifts in species abundances across space and functional traits through time are expected to alter the taxonomic and functional diversity of ecological communities (*6*, *7*). Global change drivers are often general, such as broadly consistent increases in temperature and widespread human-mediated habitat degradation (*8*, *9*). Many of these changes could lead to similarly consistent responses among taxa; for example, as the world warms, thermoregulatory demands are likely to shift similarly across broad groups of species, driving parallel adaptations to facilitate heat dissipation (*10*). However, impacts of other global change factors, such as land use change, could be more idiosyncratic among species, potentially resulting in inconsistent responses (e.g., variable shifts in range (*11*), phenology (*12*), and morphology (*13*) across species). These inconsistencies may pose remarkable challenges for predicting how ecological communities will respond to global change from species-level responses.

Birds are a model system for relating species- and community-level responses to global change as they have comprehensive distributional (*14*), phylogenetic (*15*), behavioral (*16*), and functional trait (*17*) data, as well as long-term time series data on shifts in range, phenology, and morphology. There is reason to expect that responses to rapid environmental changes are general and directional among avian communities. Within species, shifts in key functional traits have been relatively uniform: broadly, species have become smaller and their appendages, such as beaks, tarsi, and wings, have become longer (*4*, *13*, *18–20*). These shifts are often interpreted within the context

of thermoregulation or adaptation to more fragmented habitats. There is growing evidence that some within-species responses to climate change (e.g., range shifts) have resulted in community-level changes. Bird species have generally shifted poleward and up in elevation, likely in response to the warming climate (*2*, *12*, *21*), and these distributional changes are thought to have contributed to consistent local changes in functional richness and evenness across large scales (*7*, *22*, *23*). Should within-species changes in morphology represent consistent selection favoring particular phenotypes (e.g., smaller body size), we may expect that species with that phenotype should be increasing in relative abundance, shifting the community-weighted mean (CWM) of that trait in parallel with the intra-specific trends. Alternatively, scaling up within-species trends to the community level may be more complex. Idiosyncratic responses of individual species to the broad array of environmental changes that are occurring contemporaneously may lead to inconsistencies between shared species-level responses to a single driver (e.g., climate change) and community-level functional shifts (*20*). Relatedly, within-species changes may be adaptive, but this micro-evolutionary response may not predict variation in fitness among species along the same trait axis. Finally, while many within-species changes have been associated with environmental change, it is unclear if these changes are adaptive or the result of plasticity, in which case they may be less likely to predict shifts in fitness among species. Evaluating the generality of these functional responses across the scales is important in predicting shifts in bird community structure and ecosystem function under rapid environmental changes.

Unexpected community-level shifts in functional traits

To compare community-level functional shifts with species-level evidence, we first characterized changes in functional traits of local communities within one-degree grids based on abundance data for 470 species spanning half a century of sampling in North America (Fig. 1A; (*24*); see materials and methods). We calculated community-weighted means (CWMs) of seven key morphological and demographic traits: beak size, wing size, body mass, relative beak length, relative wing length, clutch size, and generation length. CWMs are the average of functional trait values among species within a community, weighted by species abundances (*25*) and provide more mechanistic interpretations of functional shifts, more direct comparisons with species-level shifts, and are less biased by the presence of rare species than ordination-based approaches (*26*). To better compare with species-level expectations of functional shifts, we examined how shifts in CWMs are associated with time, major climatic attributes, and human-induced land use changes, which have greatly affected ecological communities (*9*, *27*).

We find that community-level shifts in key morphological traits are often in opposite directions from species-level expectations based on adaptations to warmer climates and human-influenced landscapes. CWM of body mass increases with both time and temperature of the warmest quarter, and the percentage of the area in local communities that is made up of settlements, which includes villages and urban areas (Fig. 1C; see table S1 for statistics). These results contrast with species-level studies that have found reductions in body size as the climate has warmed (*4*, *19*) and smaller body size in more human-dominated landscapes due to lower resource and habitat

requirements (*29*, *30*). CWMs of beak and wing sizes (the first PC axes from PCA of multiple bill and wing measurements, respectively; see materials and methods) are positively associated with temperature, while their lengths relative to body size (relative beak and wing lengths) show negative associations (Fig. 1C). While the increase in appendage length in the CWMs is consistent with some studies (*4*, *19*), they contrast with the more consistent within-species trends toward longer relative appendage size (*4*, *19*, *20*) that are often attributed to selection towards increased effective surface area and heat dissipation efficiency under warming (*10*). The percent area of settlements is positively associated with both wing PC1 and relative wing length, corresponding to the expectation that urban-adapted species should have larger wing-to-body ratios to assist with dispersal among fragmented habitats (*28*, *29*).

Environmental associations with key demographic traits also differ from species-level expectations. The CWMs of clutch size increase greatly with temperature but decrease with temperature seasonality (Fig. 1C). Both are contrary to species-level patterns: higher ambient temperature is associated with smaller clutch sizes often attributed to increased potential for hatching failure, and higher intra-annual fluctuations in temperature may select for larger clutch sizes as a bet-hedging strategy (*30*–*32*). Among human-induced land use changes, the percentage area of settlements is negatively associated with the CWMs of clutch size, again contrary to the expectation that urban-adapted species should have larger clutch sizes (*28*, *29*). Generation length represents the average age of parents in any population of a species (*33*, *34*); higher intra-annual fluctuations in temperature, stress, and habitat fragmentation should select for earlier reproduction (*28*, *29*, *33*, *35*). After correcting for the effect of body mass, we

observe increasing CWMs of generation length over temperature, temperature seasonality, and all three human-induced land use types, all of which are contrary to species-level expectations. Because temperature and precipitation seasonality only directly affect year-round residents (*33*), we re-analyzed the associations between climate seasonality and demographic traits separately for species that undertake long-distance seasonal migrations and those that do not according to (*36*) and found no difference in the signs of these associations (fig. S1-S2).

We found that across North America, community-level shifts in morphological and demographic traits generally contrast with species- and population-level expectations and studies. We did not consider how species traits may change across space or time, which is unlikely to alter results because the magnitudes of within-species trait changes are much smaller than typical among-species variation in these traits (*20*). In addition to advancing our understanding of how communities have shifted through time, our findings shed new light on the interpretation of well-documented functional shifts within species. If these changes in morphological and demographic traits are adaptive to environmental changes, then it is intuitive to expect that species with traits in these more adaptive directions would increase in abundance and lead to shifts in the CWMs of the trait that are aligned with intra-specific trends. However, the shifts we find at the community level are often contrary to the shifts that have been broadly observed within species, which we interpret in three possible ways. First, observed species-level functional shifts may not be adaptive, or may not have meaningful effects on fitness (*37*, *38*). Second, if observed intraspecific functional shifts are indeed adaptive, then our results indicate that microevolutionary processes may not necessarily predict relative

fitness differences among species (*39*). Third, factors that drive adaptive intraspecific changes in functional traits (e.g., climate change) may have weaker effects on relative abundance than other drivers that do not drive intraspecific trait evolution but do determine differential sensitivity to more significant population-level pressures (e.g., human-induced land use change; (*40*)). As such, inconsistencies between intraspecific trait changes and shifts at the community level demonstrate the complexities involved in scaling up from species to community level dynamics in the context of multifaceted global environmental change.

Nearly universal functional shifts across space

Continental-scale analyses of functional shifts may mask local and regional environmental factors. We explored the generality of functional shifts across local communities in North America by analyzing the temporal trajectory of each local community within a functional space constructed by a PCA that reduced the CWMs of the seven traits into two major axes (Fig. 2A). The first PC axis (which explains 71.2% of the variance) mostly represents variation in traits related to body size (beak and wing measurements, body mass, and mass-corrected generation length); the second PC axis (which explains 15.3% of the variance) mostly reflects variation in clutch size (Fig. 2A). We focus on the locations of the community in functional trait space at the start and end years (1970 and 2021), summarized by their positions in quadrants, and the overall direction (angle) of the shift for each community, summarized by the quadrant it points to (Fig. 2A).

Local communities across the continent generally shifted through time toward larger body mass, larger appendage sizes, smaller relative appendage sizes, and longer generation lengths, all contrary to expectations under a warming climate based on intra-specific trends (Fig. 2B; fig. S3). Despite these consistent general trends, we observe a major east-west divide based on clutch sizes for the start, end, and overall directions of shifts through time (Fig. 2B). From 1970 to 2021, local communities in the Eastern Forests and eastern parts of the Prairie regions have shifted towards smaller clutch sizes, whereas other major avifaunal biomes in the west and north have shifted towards larger clutch sizes; in contrast, the Southwest and southern Great Basin were characterized by transitions toward smaller clutch sizes (Fig. 2B; fig. S4; see fig. S5 for a map of avifaunal biomes). Overall, these local-level functional shifts are broadly consistent with the results from the continent-level temporal trends (Fig. 1C). The highly consistent community-level functional shifts that contrast with species-level expectations highlight that even when there are nearly universal changes in the environment over time that can drive consistent intraspecific functional trends among species (e.g. consistent size declines associated with increasing temperatures; (*4*)), these conserved trends may not scale simply to analogous functional shifts of local communities.

Functional shifts driven by a few hyper-dominant species

As a consequence of global environmental changes, shifts in the composition of a community may emerge due to consistent changes across many of the species in a community (e.g. consistent declines in the abundances of smaller species, resulting in an increase in the CWM of mass through time) or extreme shifts in the abundance of a

relatively small number of species that either become hyper-dominant while others are extirpated or decline rapidly transitioning away from being a hyper-dominant species (*41*). To better understand the mechanisms underlying the unexpected functional shifts on the community level, we quantified the contributions of each species to the temporal trends of CWMs within each local community, allowing us to determine the magnitude of the contributions of individual species to community-level functional shifts. For each trait, we ranked the species by the number of local communities in which they contribute greatly to the temporal trend (i.e., they are within the top 10% of species driving the community trend in that local community). We found 5.32% of species (25 out of 470) had overwhelmingly important contributions to functional shifts across North America (Fig. 3; fig. S6-S12). To illustrate the importance of these top contributors to community-level functional shifts, we calculated CWMs for two subcommunities: (1) only the "top contributors", and (2) the rest of the species (hereafter the "standard contributors"). We then repeated all the analyses of the temporal trends and environmental associations with CWMs and compared the results of each subcommunity with the results derived using the full set of species (the "complete communities").

In general, the unexpected associations between shifts in CWMs of the complete communities and bioclimatic variables can be explained by the idiosyncratic responses of top contributors to human-induced land use changes. Top contributors drive the unexpected positive association between body mass and temperature and negative associations between relative beak/wing lengths and temperature (Fig. 1C). These unexpected morphological shifts can be explained by a few large-bodied species that are increasingly abundant under human-induced land use changes, such as Canada

Goose (*Branta canadensis*) and Wild Turkey (*Meleagris gallopavo*; Fig. 3). Indeed, relationships between beak and wing sizes and proportions of agriculture and cultured lands are often contrary between the top contributors and the complete communities (Fig. 1C), indicating that these land use types may favor the increase of species with above-average appendage sizes (e.g., Canada Goose) or decrease of species with below-average appendage sizes (e.g., House Sparrow [*Passer domesticus*]). On the other hand, relative beak and wing lengths of the top contributors are strongly positively associated with proportions of settlements, whereas these associations are strongly negative for the standard contributors (Fig. 1C). The positive association for relative wing sizes may arise from the increase of long-winged songbirds, such as Blue-gray Gnatcatcher (*Polioptila caerulea*) and Red-eyed Vireo (*Vireo olivaceus*) in urban areas, while the positive association for relative beak sizes may arise from the decrease of small-beaked species such as House Sparrow and Northern Bobwhite (*Colinus virginianus*; Fig. 3).

The unexpected associations between CWMs of demographic traits and climatic variables are again driven by the top contributors, as indicated by their responses to land use changes. One of the most important contributors to the CWM of clutch size is Northern Bobwhite (*Colinus virginianus*; Fig. 3), which has a large clutch size and has been declining precipitously due to habitat degradation (*42*), corresponding to negative associations with agriculture and settlements (Fig. 1C). The strongly positive associations between CWMs of generation length and agriculture and cultured lands are also driven by the top contributors (Fig.1C), such as increasing abundances of Canada Goose and Northern Cardinal (*Cardinalis cardinalis*), both of which have above-

average generation lengths (Fig. 3). Overall, our analyses provide strong evidence that changes in the abundance of a few hyper-dominant species have been responsible for driving the functional shifts in North American avian communities. Contrary to expectations that climatic conditions drive consistent morphological changes among species, these unexpected functional shifts on the community level are driven by the highly idiosyncratic responses of individual species as they benefit or perish because of human-induced changes in land cover and habitats (*42–45*).

At the continental scale, most of the unexpected functional shifts and their strong associations with human-induced land use changes can be explained by the top contributors, which are often stronger than, or even opposite to, the associations of CWMs calculated with the standard contributors. To test the generality of this result among local communities, we repeated the analyses on the temporal trajectories for the top contributors and standard contributors. In 1970, subcommunities composed of the top contributors were mostly characterized by having larger body mass, appendage sizes, and longer generation lengths (quadrants 2 and 3; Fig. 2A-B); spatially, the Eastern Forests were mostly characterized by larger clutch sizes (quadrant 2) compared to other avifaunal biomes with smaller clutch sizes (quadrant 3; Fig. 2B; fig. S3). In 2021, subcommunities with top contributors have all shifted to larger clutch sizes (quadrant 3; Fig. 2B; fig. S3). Strikingly, spatial patterns of overall directions of functional shifts are nearly identical between complete communities and top contributors, indicating that the top contributors have driven most of the observed functional shifts of complete communities (Fig. 2B). In contrast, there were no widespread shifts in functional positions within the standard contributors between 1970

and 2021 (Fig. 2B; fig. S3). The uniform functional shifts of top contributors are further illustrated by the strong temporal decrease in spatial heterogeneity of functional positions, whereas spatial heterogeneity has increased for complete communities and standard contributors (Fig. 2C; table S2). Overall, our observations emphasize the hyper-dominance of a few species in driving nearly universal changes in CWMs of functional traits (*46*, *47*), indicating that environmental drivers may not induce shared responses across all species within communities. Together, our results highlight the importance of considering the role of a few key contributors in designing conservation and management strategies. Instead of the entire community, future studies should also consider analyzing species contributions in subcommunities with specific ecological roles, such as predators, herbivores, or scavengers, to better understand the effect of global change on biotic interactions and ecosystem functioning.

Conclusion

Rapid changes in global environments are driving species-level responses and are reshaping ecological communities, but are these community-level shifts emergent outcomes of general species-level processes? In North American avian communities, we find significant shifts in the functional traits of communities that are not driven by consistent responses among species, or by obvious climatic drivers, but instead are the outcome of the idiosyncratic rise and fall of a few highly impactful species in response to land use changes. These widespread, abundant, and often functionally distinctive species have undergone strong changes in relative abundance, leading to local and continental functional shifts that are not aligned with expectations derived from species-

level trends. Integration of functional ecology across scales will be essential to more accurately predict biotic responses to rapid global change.

Reference

1. C. Parmesan, N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. J. Tennent, J. A. Thomas, M. Warren, Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583 (1999).

2. M. W. Tingley, W. B. Monahan, S. R. Beissinger, C. Moritz, Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19637–19643 (2009).

3. I.-C. Chen, J. K. Hill, R. Ohlemüller, D. B. Roy, C. D. Thomas, Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* **333**, 1024–1026 (2011).

4. B. C. Weeks, D. E. Willard, M. Zimova, A. A. Ellis, M. L. Witynski, M. Hennen, B. M. Winger, Shared morphological consequences of global warming in North American migratory birds. *Ecology Letters* **23**, 316–325 (2020).

5. S. A. MacLean, S. R. Beissinger, Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis. *Global Change Biology* **23**, 4094–4105 (2017).

6. K. Zhu, Y. Song, J. C. Lesage, J. C. Luong, J. W. Bartolome, N. R. Chiariello, J. Dudney, C. B. Field, L. M. Hallett, M. Hammond, S. P. Harrison, G. F. Hayes, R. J. Hobbs, K. D. Holl, P. Hopkinson, L. Larios, M. E. Loik, L. R. Prugh, Rapid shifts in grassland communities driven by climate change. *Nat Ecol Evol* **8**, 2252–2264 (2024).

7. M. A. Jarzyna, W. Jetz, A near half-century of temporal change in different facets of avian diversity. *Global Change Biology* **23**, 2999–3011 (2017).

8. J. Rogelj, M. Meinshausen, R. Knutti, Global warming under old and new scenarios using IPCC climate sensitivity range estimates. *Nature Clim Change* **2**, 248–253 (2012).

9. E. C. Ellis, K. Klein Goldewijk, S. Siebert, D. Lightman, N. Ramankutty, Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* **19**, 589–606 (2010).

10. S. Ryding, M. Klaassen, G. J. Tattersall, J. L. Gardner, M. R. E. Symonds, Shape-shifting: changing animal morphologies as a response to climatic warming. *Trends in Ecology & Evolution* **36**, 1036–1048 (2021).

11. C. Moritz, J. L. Patton, C. J. Conroy, J. L. Parra, G. C. White, S. R. Beissinger, Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA, *Science*. **322** (2008)pp. 261–264.

12. M. H. C. Neate-Clegg, B. A. Tonelli, M. W. Tingley, Advances in breeding phenology outpace latitudinal and elevational shifts for North American birds tracking temperature. *Nat Ecol Evol*, 1–10 (2024).

13. S. Ryding, A. McQueen, M. Klaassen, G. J. Tattersall, M. R. E. Symonds, Long- and short-term responses to climate change in body and appendage size of diverse Australian birds. *Global Change Biology* **30**, e17517 (2024).

14. D. W. Gibbons, P. F. Donald, H.-G. Bauer, L. Fornasari, I. K. Dawson, Mapping avian distributions: the evolution of bird atlases. *Bird Study* **54**, 324–334 (2007).

15. E. J. McTavish, J. A. Gerbracht, M. T. Holder, M. J. Iliff, D. Lepage, P. C. Rasmussen, B. D. Redelings, L. L. Sánchez Reyes, E. T. Miller, A complete and dynamic tree of birds. *Proceedings of the National Academy of Sciences* **122**, e2409658122 (2025).

16. H. Wilman, J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, W. Jetz, EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027 (2014).

17. J. A. Tobias, C. Sheard, A. L. Pigot, A. J. M. Devenish, J. Yang, F. Sayol, M. H. C. Neate-Clegg, N. Alioravainen, T. L. Weeks, R. A. Barber, P. A. Walkden, H. E. A. MacGregor, S. E. I. Jones, C. Vincent, A. G. Phillips, N. M. Marples, F. A. Montaño-Centellas, V. Leandro-Silva, S. Claramunt, B. Darski, B. G. Freeman, T. P. Bregman, C. R. Cooney, E. C. Hughes, E. J. R. Capp, Z. K. Varley, N. R. Friedman, H. Korntheuer, A. Corrales-Vargas, C. H. Trisos, B. C. Weeks, D. M. Hanz, T. Töpfer, G. A. Bravo, V. Remeš, L. Nowak, L. S. Carneiro, A. J. Moncada R., B. Matysioková, D. T. Baldassarre, A. Martínez-Salinas, J. D. Wolfe, P. M. Chapman, B. G. Daly, M. C. Sorensen, A. Neu, M. A. Ford, R. J. Mayhew, L. Fabio Silveira, D. J. Kelly, N. N. D. Annorbah, H. S. Pollock, A. M. Grabowska-Zhang, J. P. McEntee, J. Carlos T. Gonzalez, C. G. Meneses, M. C. Muñoz, L. L. Powell, G. A. Jamie, T. J. Matthews, O. Johnson, G. R. R. Brito, K. Zyskowski, R. Crates, M. G. Harvey, M. Jurado Zevallos, P. A. Hosner, T. Bradfer-Lawrence, J. M. Maley, F. G. Stiles, H. S. Lima, K. L. Provost, M. Chibesa, M. Mashao, J. T. Howard, E. Mlamba, M. A. H. Chua, B. Li, M. I. Gómez, N. C. García, M. Päckert, J. Fuchs, J. R. Ali, E. P. Derryberry, M. L. Carlson, R. C. Urriza, K. E. Brzeski, D. M. Prawiradilaga, M. J. Rayner, E. T. Miller, R. C. K. Bowie, R.-M. Lafontaine, R. P. Scofield, Y. Lou, L. Somarathna, D. Lepage, M. Illif, E. L. Neuschulz, M. Templin, D. M. Dehling, J. C. Cooper, O. S. G. Pauwels, K. Analuddin, J. Fjeldså, N.

Seddon, P. R. Sweet, F. A. J. DeClerck, L. N. Naka, J. D. Brawn, A. Aleixo, K. Böhning-Gaese, C. Rahbek, S. A. Fritz, G. H. Thomas, M. Schleuning, AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters* **25**, 581–597 (2022).

18. J. A. Sheridan, D. Bickford, Shrinking body size as an ecological response to climate change. *Nature Clim Change* **1**, 401–406 (2011).

19. V. Jirinec, R. C. Burner, B. R. Amaral, R. O. Bierregaard, G. Fernández-Arellano, A. Hernández-Palma, E. I. Johnson, T. E. Lovejoy, L. L. Powell, C. L. Rutt, J. D. Wolfe, P. C. Stouffer, Morphological consequences of climate change for resident birds in intact Amazonian rainforest. *Science Advances* **7**, eabk1743 (2021).

20. C. Youngflesh, J. F. Saracco, R. B. Siegel, M. W. Tingley, Abiotic conditions shape spatial and temporal morphological variation in North American birds. *Nat Ecol Evol* **6**, 1860–1870 (2022).

21. C. S. Rushing, J. A. Royle, D. J. Ziolkowski, K. L. Pardieck, Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change. *Proceedings of the National Academy of Sciences* **117**, 12897–12903 (2020).

22. A. M. Schipper, J. Belmaker, M. D. de Miranda, L. M. Navarro, K. Böhning-Gaese, M. J. Costello, M. Dornelas, R. Foppen, J. Hortal, M. A. J. Huijbregts, B. Martín-López, N. Pettorelli, C. Queiroz, A. G. Rossberg, L. Santini, K. Schiffers, Z. J. N. Steinmann, P. Visconti, C. Rondinini, H. M. Pereira, Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. *Global Change Biology* **22**, 3948–3959 (2016).

23. J.-Y. Barnagaud, P. Gaüzère, B. Zuckerberg, K. Princé, J.-C. Svenning, Temporal changes in bird functional diversity across the United States. *Oecologia* **185**, 737–748 (2017).

24. J. R. Sauer, K. L. Pardieck, D. J. Ziolkowski Jr., A. C. Smith, M.-A. R. Hudson, V. Rodriguez, H. Berlanga, D. K. Niven, W. A. Link, The first 50 years of the North American Breeding Bird Survey. *The Condor* **119**, 576–593 (2017).

25. S. Lavorel, K. Grigulis, S. McIntyre, N. S. G. Williams, D. Garden, J. Dorrough, S. Berman, F. Quétier, A. Thébault, A. Bonis, Assessing functional diversity in the field – methodology matters! *Functional Ecology* **22**, 134–147 (2008).

26. S. Villéger, N. W. H. Mason, D. Mouillot, New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *Ecology* **89**, 2290–2301 (2008).

27. E. C. Ellis, N. Gauthier, K. Klein Goldewijk, R. Bliege Bird, N. Boivin, S. Díaz, D. Q. Fuller, J. L. Gill, J. O. Kaplan, N. Kingston, H. Locke, C. N. H. McMichael, D. Ranco, T. C. Rick, M. R. Shaw, L. Stephens, J.-C. Svenning, J. E. M. Watson,

People have shaped most of terrestrial nature for at least 12,000 years. *Proceedings of the National Academy of Sciences* **118**, e2023483118 (2021).

28. A. P. Møller, Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* **159**, 849–858 (2009).

29. M. H. C. Neate-Clegg, B. A. Tonelli, C. Youngflesh, J. X. Wu, G. A. Montgomery, Ç. H. Şekercioğlu, M. W. Tingley, Traits shaping urban tolerance in birds differ around the world. *Current Biology* **33**, 1677-1688.e6 (2023).

30. R. E. Ricklefs, Geographical Variation in Clutch Size among Passerine Birds: Ashmole's Hypothesis. *The Auk* **97**, 38–49 (1980).

31. W. Jetz, C. H. Sekercioglu, K. Böhning-Gaese, The Worldwide Variation in Avian Clutch Size across Species and Space. *PLOS Biology* **6**, e303 (2008).

32. C. B. Cooper, W. M. Hochachka, G. Butcher, A. A. Dhondt, Seasonal and Latitudinal Trends in Clutch Size: Thermal Constraints During Laying and Incubation. *Ecology* **86**, 2018–2031 (2005).

33. C. Youngflesh, K. Kapsar, A. Uscanga, P. J. Williams, J. W. Doser, L. Kounta, P. L. Zarnetske, Environmental Variability Shapes Life History of the World's Birds. *Ecology Letters* **28**, e70077 (2025).

34. J. P. Bird, R. Martin, H. R. Akçakaya, J. Gilroy, I. J. Burfield, S. T. Garnett, A. Symes, J. Taylor, Ç. H. Şekercioğlu, S. H. M. Butchart, Generation lengths of the world's birds and their implications for extinction risk. *Conservation Biology* **34**, 1252–1261 (2020).

35. W. M. Schaffer, Optimal Reproductive Effort in Fluctuating Environments. *The American Naturalist* **108**, 783–790 (1974).

36. K. V. Rosenberg, A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, P. P. Marra, Decline of the North American avifauna. *Science* **366**, 120–124 (2019).

37. A. Nord, E. Persson, J. K. R. Tabh, E. Thoral, Shrinking body size may not provide meaningful thermoregulatory benefits in a warmer world. *Nat Ecol Evol* **8**, 387–389 (2024).

38. C. Teplitsky, J. A. Mills, J. S. Alho, J. W. Yarrall, J. Merilä, Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences* **105**, 13492–13496 (2008).

39. C. P. terHorst, P. C. Zee, K. D. Heath, T. E. Miller, A. I. Pastore, S. Patel, S. J. Schreiber, M. J. Wade, M. R. Walsh, Evolution in a Community Context: Trait

Responses to Multiple Species Interactions. *The American Naturalist* **191**, 368–380 (2018).

40. T. Dias, N. P. Lemoine, S. W. Yanco, M. Zimova, R. A. Bay, B. C. Weeks, Long-term increases in wing length occur independently of changes in climate and climate-driven shifts in body size. *Proceedings of the Royal Society B: Biological Sciences* **292**, 20242556 (2025).

41. C. H. Trisos, C. Merow, A. L. Pigot, The projected timing of abrupt ecological disruption from climate change. *Nature* **580**, 496–501 (2020).

42. F. Hernández, L. A. Brennan, S. J. DeMaso, J. P. Sands, D. B. Wester, On reversing the northern bobwhite population decline: 20 years later. *Wildlife Society Bulletin* **37**, 177–188 (2013).

43. J. R. Allan, J. S. Kirby, C. J. Feare, The biology of canada geese Branta canadensis in relation to the management of feral populations. *Wildlife Biology* **1**, 129–143 (1995).

44. J. L. Tapley, R. K. Abernethy, J. E. Kennamer, N. Carolina, “Status and distribution of the wild turkey in 2004” in *Proceedings of the National Wild Turkey Symposium* (2005)vol. 9, pp. 21–32.

45. I. Benmazouz, J. Jokimäki, S. Lengyel, L. Juhász, M.-L. Kaisanlahti-Jokimäki, G. Kardos, P. Paládi, L. Kövér, Corvids in Urban Environments: A Systematic Global Literature Review. *Animals* **11**, 3226 (2021).

46. K. Princé, B. Zuckerberg, Climate change in our backyards: the reshuffling of North America’s winter bird communities. *Global Change Biology* **21**, 572–585 (2015).

47. G. J. Di Cecco, A. H. Hurlbert, Anthropogenic drivers of avian community turnover from local to regional scales. *Global Change Biology* **28**, 770–781 (2022).

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List of Supplementary Materials

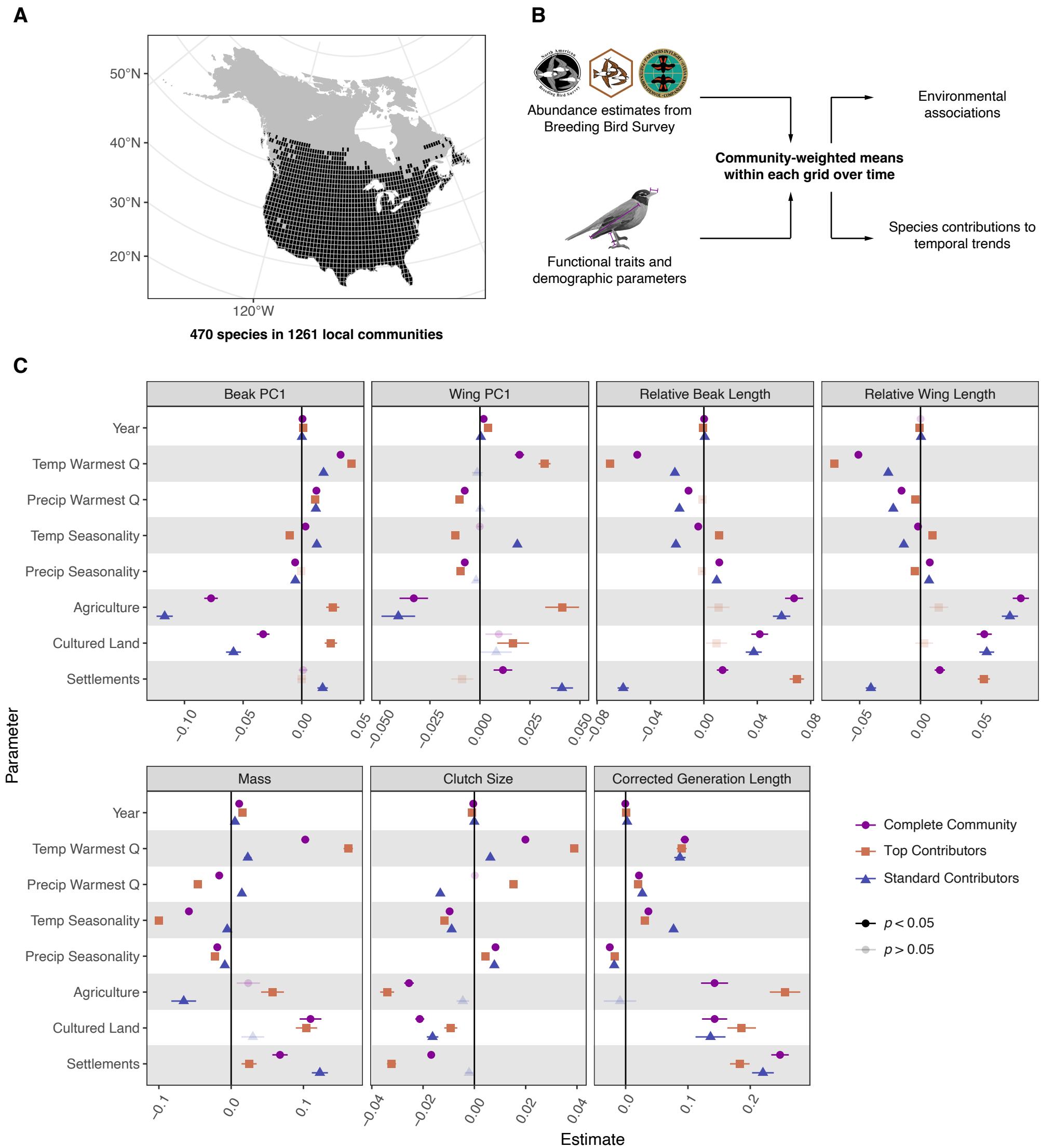
Materials and Methods
Tables S1-S3
Figs. S1 to S18
Supplementary Data S1-S3
References *(48)-(65)*

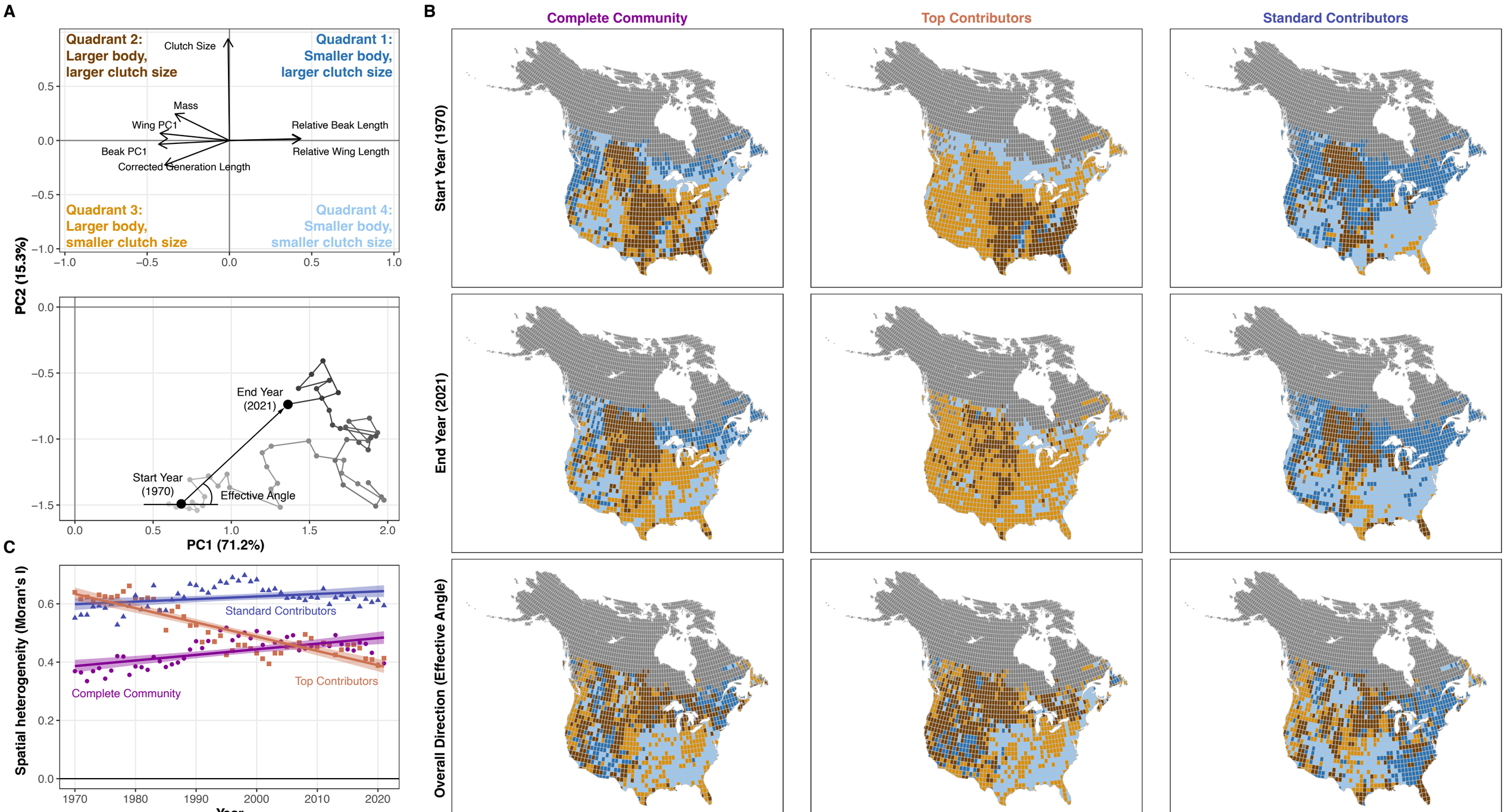
Fig. 1: Overview of the analyses and associations between functional shifts and environmental variables. **A.** Map of the study region, showing the 1261 local communities (one by one degree grids) included in the analyses. **B.** Overview of the analyses. **C.** Associations between community-weighted means (CWMs) of seven key functional traits and main environmental variables, including climate, human-induced land use, and year. CWMs are calculated from either all species in the communities (complete communities), only the top contributors, or only the rest of the species (standard contributors). All statistics are shown in table S1. Illustration by Olivia Stein.

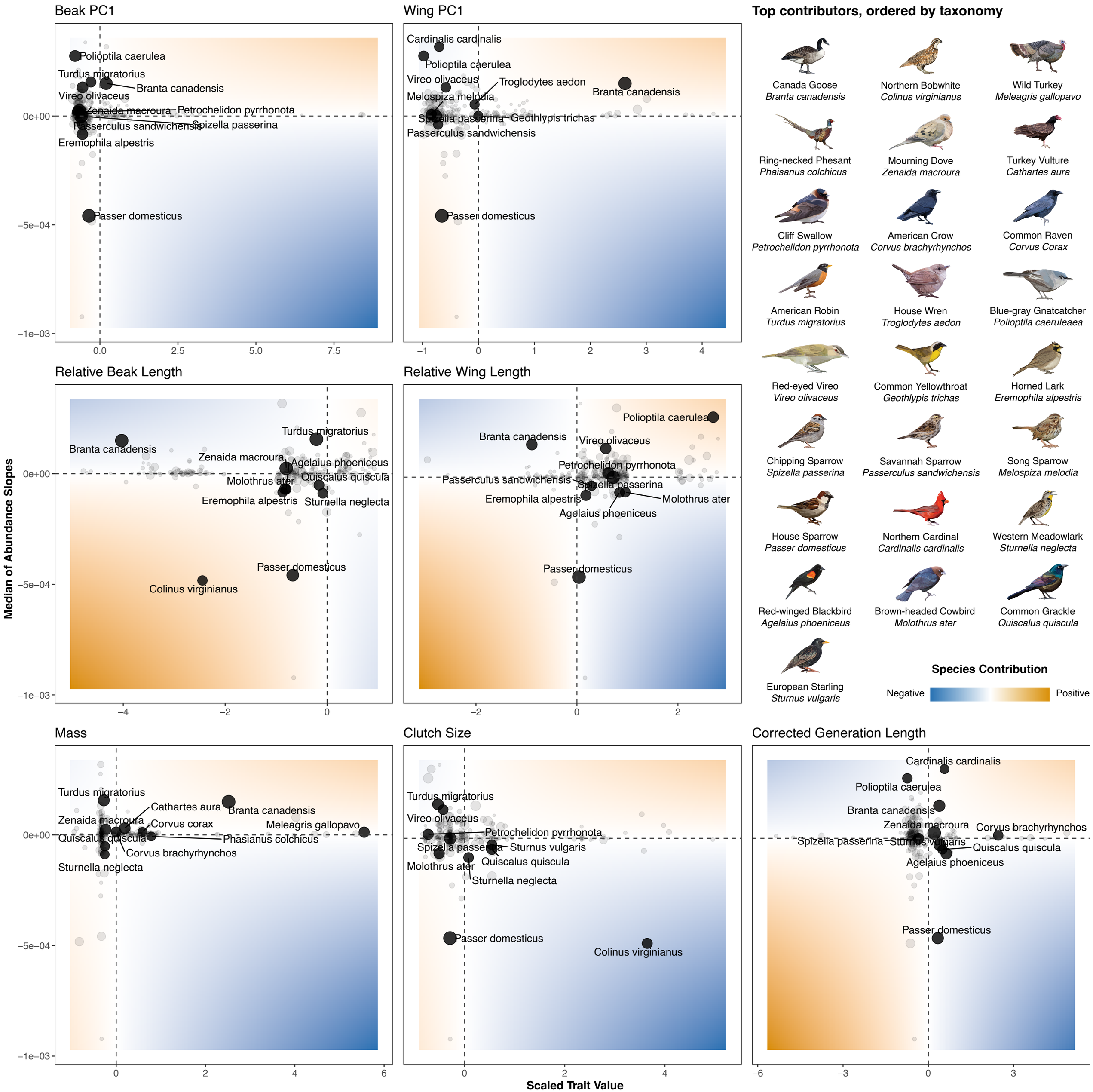
Fig. 2: Analyzing the temporal trajectory of local communities in the functional space. **A.** The functional space constructed by PCA of all communities by their community-weighted mean measurements over time, and a temporal trajectory of one local community (40˚N, 110˚W) moving through the functional space over time, showing the start and end points and the overall direction (effective angle). In the trajectory, lighter shades represent earlier years, and darker shades represent later years. The two panels represent the same functional space, but the scales are adjusted for better visualization. **B.** Maps of each local community's start and end positions in the functional space, measured by the quadrants in **A**, and the overall direction of the functional shifts, measured by the quadrants to which the trajectory travels. Columns show results for complete communities, subcommunities with top contributors, and

subcommunities with the standard contributors. **C.** Spatial heterogeneity of functional positions of the base communities, top contributors, and the rest of the species, calculated as Moran's *I* from the maps. A Moran's *I* closer to 0 means lower spatial heterogeneity.

Fig. 3: Species contributions to the community-weighted means (CWMs) of seven key functional traits. Panels only include species that contribute substantially (ranked top 10% of all species in a local community) in at least one local community; point size denotes the number of grids in which a species contributes greatly. The sign of the contribution depends on the species' temporal trends of relative abundance and its trait value, e.g., if a species with below-average trait value increases in relative abundance, it will contribute negatively by lowering the CWM of the trait. For each trait, the identity of the top 10 species that contribute to the CWMs of the most local communities is labeled; pooling all these species results in 25 top contributors of the observed functional shifts over time, shown on the right. For each panel, the x-axis is the scaled trait values, and the y-axis is the median of the temporal slopes of relative abundances across each species' range. Shades denote the absolute magnitudes of species contributions: colder colors represent negative contributions, and warmer colors represent positive contributions. Axes and scales are different for each panel for better visualization. Illustrations by Olivia Stein.


A
50°N
40°N
30°N
20°N
120°W
470 species in 1261 local communities
B
Abundance estimates from Breeding Bird Survey
Functional traits and demographic parameters
Community-weighted means within each grid over time
Environmental associations
Species contributions to temporal trends
C
Beak PC1
Wing PC1
Relative Beak Length
Relative Wing Length
Mass
Clutch Size
Corrected Generation Length
Year
Temp Warmest Q
Precip Warmest Q
Temp Seasonality
Precip Seasonality
Agriculture
Cultured Land
Settlements
Parameter
Estimate
Complete Community
Top Contributors
Standard Contributors
p < 0.05
p > 0.05


A
Quadrant 2:
Larger body,
larger clutch size
Quadrant 1:
Smaller body,
larger clutch size
Quadrant 3:
Larger body,
smaller clutch size
Quadrant 4:
Smaller body,
smaller clutch size
Clutch Size
Mass
Wing PC1
Beak PC1
Corrected Generation Length
Relative Beak Length
Relative Wing Length
PC2 (15.3%)
End Year
(2021)
Start Year
(1970)
Effective Angle
PC1 (71.2%)
C
Spatial heterogeneity (Moran's I)
Standard Contributors
Top Contributors
Complete Community
Year
B
Complete Community
Top Contributors
Standard Contributors
Start Year (1970)
End Year (2021)
Overall Direction (Effective Angle)


Beak PC1
Polioptila caerulea
Turdus migratorius
Branta canadensis
Vireo olivaceus
Zenaida macroura
Petrochelidon pyrrhonota
Passerculus sandwichensis
Spizella passerina
Eremophila alpestris
Passer domesticus
0e+00
−5e−04
−1e−03
0.0
2.5
5.0
7.5
Wing PC1
Cardinalis cardinalis
Polioptila caerulea
Vireo olivaceus
Troglodytes aedon
Branta canadensis
Melospiza melodia
Spizella passerina
Geothlypis trichas
Passerculus sandwichensis
Passer domesticus
−1
0
1
2
3
4
Top contributors, ordered by taxonomy
Canada Goose
Branta canadensis
Northern Bobwhite
Colinus virginianus
Wild Turkey
Meleagris gallopavo
Ring-necked Phesant
Phaisanus colchicus
Mourning Dove
Zenaida macroura
Turkey Vulture
Cathartes aura
Cliff Swallow
Petrochelidon pyrrhonota
American Crow
Corvus brachyrhynchos
Common Raven
Corvus Corax
American Robin
Turdus migratorius
House Wren
Troglodytes aedon
Blue-gray Gnatcatcher
Polioptila caeruleaea
Red-eyed Vireo
Vireo olivaceus
Common Yellowthroat
Geothlypis trichas
Horned Lark
Eremophila alpestris
Chipping Sparrow
Spizella passerina
Savannah Sparrow
Passerculus sandwichensis
Song Sparrow
Melospiza melodia
House Sparrow
Passer domesticus
Northern Cardinal
Cardinalis cardinalis
Western Meadowlark
Sturnella neglecta
Red-winged Blackbird
Agelaius phoeniceus
Brown-headed Cowbird
Molothrus ater
Common Grackle
Quiscalus quiscula
European Starling
Sturnus vulgaris
Species Contribution
Negative
Positive
Relative Beak Length
Median of Abundance Slopes
Branta canadensis
Turdus migratorius
Zenaida macroura
Agelaius phoeniceus
Molothrus ater
Quiscalus quiscula
Eremophila alpestris
Sturnella neglecta
Passer domesticus
Colinus virginianus
−4
−2
0
Relative Wing Length
Polioptila caerulea
Branta canadensis
Vireo olivaceus
Petrochelidon pyrrhonota
Passerculus sandwichensis
Spizella passerina
Eremophila alpestris
Molothrus ater
Agelaius phoeniceus
Passer domesticus
−2
0
2
Mass
Turdus migratorius
Cathartes aura
Branta canadensis
Zenaida macroura
Corvus corax
Meleagris gallopavo
Quiscalus quiscula
Phasianus colchicus
Corvus brachyrhynchos
Sturnella neglecta
0
2
4
6
Clutch Size
Turdus migratorius
Vireo olivaceus
Petrochelidon pyrrhonota
Spizella passerina
Sturnus vulgaris
Quiscalus quiscula
Molothrus ater
Sturnella neglecta
Passer domesticus
Colinus virginianus
Corrected Generation Length
Cardinalis cardinalis
Polioptila caerulea
Branta canadensis
Zenaida macroura
Corvus brachyrhynchos
Spizella passerina
Sturnus vulgaris
Quiscalus quiscula
Agelaius phoeniceus
Passer domesticus
−6
−3
0
3
Scaled Trait Value