SYMPOSIUM

The Wind Niche: The Thermal and Hydric Effects of Wind Speed on Terrestrial Organisms

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Synopsis   Wind can significantly influence heat and water exchange between organisms and their environment, yet microclimatic variation in wind is often overlooked in models forecasting the effects of environmental change on organismal performance. Accounting for the effects of wind may become even more critical given the anticipated changes in wind speed across the planet as climates continue to warm. In this study, we first assessed how wind speed varies across the planet and how wind speed may change under climate warming at macroclimatic scales. We also used microclimatic data to assess how wind speed changes temporally throughout the day and year as well as the relationship between wind speed, temperature, and standard deviation in each environmental variable using data from weather stations in North America. Finally, we used a suite of biophysical simulations to understand how wind speed (and its interactions with other environmental variables and organismal traits) affects the temperatures and rates of water loss that plants and animals experience at a microclimatic scale. We found substantial latitudinal variation in wind speed and the change in wind speed under climate change, demonstrating that temperate regions are predicted to experience simultaneous warming and reductions in wind speed. From the microclimatic data, we also found that wind speed is positively associated with temperature and temperature variability, indicating that the effects of wind speed may become more challenging to predict under future warming scenarios. The biophysical simulations demonstrated that convective and evaporative cooling from wind interacts strongly with organismal traits (such as body size, solar absorptance, and conductance) and the heating effects of solar radiation to shape heat and water fluxes in terrestrial plants and animals. In many cases, the effect of wind (or its interaction with other variables) was comparable to the effects of air temperature or solar radiation. Understanding these effects will be important for predicting the ecological impacts of climate change and for explaining clinal variation in traits that have evolved across a range of thermal environments.

Introduction

Life on Earth is expected to experience unprecedented rates of warming over the next century, potentially leading to a global reshuffling of species' distributions and the next global extinction event (Burrows et al. 2011; Bates et al. 2014; Urban 2024). Given the potential for these dramatic effects, most studies predicting the ecological and evolutionary effects of climate change have justly focused on changes in air temperature (Spence and Tingley 2020). However, changes in temperature also interact with other environmental variables, such as humidity and precipitation, which have prompted im-portant insight into the physiological and ecological effects of these climatic variables (Helmuth et al. 2005; Boyle et al. 2020; Riddell et al. 2023a). Wind speeds are also expected to change over the next century due to uneven patterns of warming across the planet, in a phenomenon termed "the global stilling" (Zeng et al. 2019; Zha et al. 2021). Due to the more rapid rates of warming at the poles (particularly in the Northern Hemisphere), near-surface wind speeds are expected to fall by approximately 10% (IPCC 2023) as warming leads to greater homogenization of global temperatures (and thus the air pressure gradients that drive wind). Wind

speed has already begun to slow down in many regions of the planet, although some regions have experienced an increase in wind speed (Zeng et al. 2019; Zhang and Wang 2020; Ma et al. 2025). Because wind plays important roles in the ecology and evolution of plants and animals, changes in wind speed may become a key factor in accurately predicting organismal responses to climate change.

Wind can have dramatic effects on organismal performance in both terrestrial plants and animals. Wind speed and direction influence flight performance and the energetic cost of flight in volant animals, such as birds, insects, and mammals (Spear and Ainley 1997; Verboom and Spoelstra 1999; Weimerskirch et al. 2000; Combes and Dudley 2009; Chapman et al. 2016; Nourani et al. 2023). Recent evidence indicates that pelagic seabirds have distinct wind niches—specific ranges of wind speeds and directions they preferentially use—likely to minimize the costs and risks associated with flight (Nourani et al. 2023). Wind also has dramatic influences on more sessile organisms, such as plants, which adapt to wind speeds by developing smaller leaves and shorter heights to minimize the potential for damage (Langre 2008; Louf et al. 2018). Wind also plays a fundamental role in seed dispersal and ultimately species richness of wind-dispersed plants in terrestrial ecosystems (Damschen et al. 2014). The direction and speed of wind also shape predator–prey interactions, as both predators and their prey rely on olfaction to detect each other's scent in the wind (Togunov et al. 2017). Together, these examples suggest that many organisms exhibit preferences or tolerances for particular wind regimes—behaviorally, morphologically, or physiologically—indicating a bounded range of wind conditions that support survival and reproduction, consistent with the Hutchinsonian definition of a niche. Wind speed also plays a critical role in shaping related niche axes, such as temperature and humidity.

Wind can have dramatic effects on heat and mass balance in terrestrial animals and plants, which have shaped the evolution of physiological, morphological, and behavioral phenotypes. Wind primarily influences heat and mass flux by affecting the boundary layer, which is defined as a transition zone between the organism and the environment characterized by a gradient of temperature, humidity, and/or wind speed that mostly occurs perpendicular to the surface of the object (Gates 1980). By wicking away the boundary layer, high wind speeds reduce the transition zone, thereby increasing rates of heat flux and water loss with the environment (Foley and Spotila 1978). Conversely, the depth of the boundary layer increases at low wind speeds and becomes shaped less by the friction of air against the surface and more by the thermal and hydric proper-

ties of the organism-environment interface (Gates 1980; Campbell and Norman 1998). In response to these effects on heat and mass exchange, some mammals, for instance, have evolved lower fur conductivity that simultaneously provides insulation in cool conditions while promoting heat loss in hot conditions (Riddell et al. 2022). Also, arboreal frogs that live in high wind environments exhibit greater physiological resistance to water loss compared to non-arboreal frogs (Wygoda 1984; Buttemer 1990) and also behaviorally avoid high water loss by jumping from tree canopies during periods of high wind (Stewart 1985). Similarly, leaves at the tops of canopies exhibit thicker cuticles and higher concentrations of phenolic substances compared to leaves near the ground to cope with higher solar radiation and wind speeds (Van Wittenberghe et al. 2012). Therefore, plants and animals have demonstrated clear evidence for a wind (or "eolian") niche (Kocurek 1991), particularly in relation to the thermal and hydric environments they experience. These studies support further exploring the potential effects of reductions in wind speed on organismal performance under climate change.

As climates warm, biologists are forecasting changes in key organismal phenotypes, such as body size, body shape, coloration, and physiological tolerance, as organisms adapt to changing thermal environments (Gardner et al. 2011; Sheridan and Bickford 2011; Roulin 2014; Diamond 2017; Delhey et al. 2020). These predictions are bolstered by the observed relationship between these phenotypes and clines of temperature across elevation and latitude (Clusella Trullas et al. 2007; Sunday et al. 2019; He et al. 2023). Like temperature, wind speeds also likely vary with latitude and elevation in predictable ways that may influence our understanding of the physical processes shaping phenotypic variation. In this study, we explore the spatial patterns of wind at macro- and microclimatic scales to understand how they may interact with temperature and influence our predictions of phenotypic responses to climate change. We also use biophysical models to predict the effects of reductions in wind speed on body temperature of ectotherms, leaf temperature, heat balance in endotherms, and water loss in ectotherms. Each of these simulations focuses on unique phenotypes that interact with wind (such as stomatal conductance, insulation, body size, etc.) to demonstrate their importance and potential for adaptive changes that could mitigate the effects of changing wind speeds. These simulations provide a framework for developing hypotheses on the potential impacts of changes in wind speed on plant and animal performance under future warming scenarios. In an attempt to be consistent with the Hutchinsonian fundamental niche, we define the niche here as the range of environmental conditions (i.e., the *n*-dimensional hy-

pervolume) that promote survival, reproduction, and thus positive population growth (Hutchinson 1957). We focus on the wind axis of the fundamental niche, with an emphasis on the interactive effects of wind on the thermal and hydric niche axes. By demonstrating the effects of wind on organismal performance, our study underscores the need to more explicitly consider wind as an ecologically important factor in global change biology.

Methods

Macroclimate data

To assess the clinal variation in wind, we downloaded climatic data on mean temperature and wind speed under contemporary conditions and a future warming scenario (SSP5–8.5) using the IPCC WGI Interactive Atlas developed by the Intergovernmental Panel on Climate Change (https://interactive-atlas.ipcc.ch/regional-information, accessed January 15, 2025). This represents the most severe warming scenario with a significant rise in greenhouse gas emissions by the end of the century (IPCC 2023). We then used QGIS (v 3.34) to clip the layers to only consist of climate data over land and convert the GeoTIFF files to ASCI text files. We then imported these files into Python to convert the maps into datasets consisting of the values of interest (temperature or wind speed) and latitude. We summarized the climatic data based on 5° intervals of latitude to calculate means, standard deviations, and ranges of values within each bin. We then used DataGraph (v. 5.4) to plot the relationship between the variable of interest and latitude under both current and future scenarios to illustrate current and future values associated with each latitudinal bin. These were then used to draw inferences on the changes in temperature and wind that organisms might experience in the future.

Microclimate data

We also used microclimatic data from weather stations distributed across North America to understand the relationship between temperature, wind speed, solar radiation, and time of day. We downloaded hourly weather station data from 17 weather stations distributed across North America from the USGS Soil Climate Analysis Network (SCAN), encompassing approximately 16.5 years on average (ranging from 1999 to 2022) across 2088,173 hourly observations of local weather conditions. On average, each weather station had 68,651 observations (ranging from 48,552 to 203,468 observations). We imported these data into Python to combine them into a single dataset and summarized wind speeds with respect to temperature, solar radiation, time of day, and the daily standard deviation in temperature to un-

derstand how wind speed changes with respect to each variable. We expected wind speeds to increase with temperature and solar radiation due to their role in creating pressure gradients that drive airflow. Thus, wind speeds should peak at midday. We then plotted the means and standard deviations using DataGraph (v. 5.4) to illustrate these relationships and make inferences about the environmental conditions that terrestrial organisms experience.

To analyze the relationship between temperature variability and wind speed, we used mixed effects linear models in R (v. 4.3.1) (R Core Team 2017). We specifically determined whether wind speed was related to temperature variability, treating monthly wind speed as the response variable and the monthly standard deviation in air temperature as a covariate. We also included month of year (as a factor) and its interaction with temperature variability. We then included site as a random effect to account for the repeated measures at each site for each month. We also determined whether variability in wind speed was related to the variability in air temperature using the same modeling framework as above using the monthly standard deviation in wind speed as the response variable. We then used a Type II Analysis of Covariance for both models to assess significance of predictors.

Biophysical simulations

We used a suite of biophysical models to understand the effects of wind on heat and water flux in plants and animals. These models couple environmental variables with organismal traits to predict heat and mass balance in organisms (Briscoe et al. 2022). They typically rely on downscaling macroscale climatic data to the microclimatic conditions that organisms experience in their environment to predict body temperatures, water balance, or other metrics related to performance, survival, and reproduction (Riddell et al. 2023a). These models have been used in a wide variety of contexts, including but not limited to the effects of plant physiology on ectotherm body temperature (Riddell et al. 2023a,b), heat flux in desert mammals and birds (Riddell et al. 2019; Riddell et al. 2021, 2022), thermoregulatory behavior and performance of ectotherms (Gunderson et al. 2022), and water balance of wet-skinned ectotherms (Riddell et al. 2018a,b; Newman et al. 2022). Here, we used previously published simulations from these studies to explore the effects of wind on various organisms. Although our simulations span a full 24-h period to characterize microclimatic variability, we recognize that organisms occupy discrete activity periods and may use sheltered microhabitats outside those times. Thus, users can interpret model outputs in the context

of taxon-specific activity windows (e.g., nocturnal versus diurnal). Moreover, these biophysical simulations are not spatially explicit with respect to vegetation or habitat structure; they provide a general characterization of wind–temperature–humidity interactions. Applying the models to specific landscapes or vegetation types would require additional habitat-scale parameterization.

In each of the simulations below, we used estimates of hourly air temperature, relative humidity, and wind speed from the weather stations described above. For the simulations on endotherms, we arbitrarily increased the air temperature such that daytime operative temperatures exceeded body temperature to illustrate the effect of wind speed on net sensible heat flux when the animal was too cold (at night) and too warm (during the day). For each simulation, we ran the models assuming the average hourly wind speed as well as nine additional simulations in which we slowed the wind speed down by 10% intervals. Thus, we ran simulations ranging from 100% of the average wind speed down to 10% of the average wind speed. This approach illustrates the effect of slowing wind speeds across a broad range of wind speeds, ranging from moderate ($\sim$5 m s^{-1}) to essentially still air ($\sim$0.5 m s^{-1}) during the warmest (and windiest) hours of the day. For each simulation, we assumed coordinates that were centrally located relative to the weather stations to calculate solar irradiance [latitude (32.0$'$), longitude (-98.0$'$), elevation (0 m)]. We also assume that the organisms experience full sun and therefore were not in shade to more completely understand the interactions between solar radiation and wind speed.

To understand the effects of wind speed on body temperatures of diurnal ectotherms (such as a lizard), we used a biophysical model to estimate ground surface temperatures for soils with high and low reflectivity (that is, albedo). These simulations are relevant for any organism that lives near or on the ground surface, but particularly diurnal ectotherms, due to the ground playing a major role in determining body temperatures (Buckley et al. 2010; Sears and Angilletta 2015). We calculated ground surface temperatures using an iterative analytic model that incorporates properties of the underlying soil, heat exchange between deep soil and surface, convective heat loss, and evaporative heat loss (Leaf and Erell 2018). These simulations have been previously validated with weather station data and were found to be highly similar to observed soil temperatures (Porter et al. 2023). We simulated ground temperature under light and dark colored soils to explore the interaction between soil albedo and wind speed. We specifically simulated ground surface temperature for soil with an albedo of 0.4 for the light soil and 0.1 for the dark soil,

which approximates white sand and dark soil, respectively (Campbell and Norman 1998). The goal of this analysis was to understand how wind interacted with solar absorptance to influence the temperature of the ground surface (and thus body temperatures that ectotherms experience near the ground).

To simulate the effect of wind speed on leaf temperature, we used an analytical model for predicting humid operative temperature (Campbell and Norman 1998). The model incorporates the typical variables associated with operative temperatures (such as air temperature, solar radiation, reflected radiation, etc.), as well as estimates of convective cooling based on the evaporative water loss rate (Riddell et al. 2023ab). To estimate evaporative water loss, we arbitrarily selected a high and low value for stomatal leaf conductance (0.4 and 0.01 mol m^{-2} s^{-1}, respectively) to understand how wind speed and evaporative cooling interact to influence leaf temperature. These values of stomatal leaf conductance correspond to leaves with open and nearly closed stomata, respectively (Campbell and Norman 1998). We also adjusted the angle of the leaf relative to the sun to increase solar absorption (and thus photosynthesis) when the sun was lower in the sky (morning and evening) and reduce solar absorption during the hottest part of the day (midday), which is commonly observed in plants (Nilsen and Forseth 2018). For solar absorptance, we used a value of 0.5, which approximates the solar absorptance for a typical leaf (Campbell and Norman 1998).

To understand the effects of slowing wind on endotherm heat balance, we used biophysical models that estimate heat flux from the environment and the required metabolic heat production or evaporative cooling that would be necessary to maintain a stable body temperature (normothermic homeothermy). For these simulations, we parameterized the model using the attributes of a bird approximately the size, shape, and thermal properties of a tree swallow (*Tachycineta bicolor*) sitting 2 m from the ground surface. The routines for estimating heat flux and thermal properties of tree swallows have been described in more detail in recent studies (Riddell et al. 2019; Porter et al. 2024). In brief, the simulations estimate net sensible heat flux (Q) based on the physiological and morphological traits of an endotherm and microclimatic conditions. Positive values represent heating costs that an endotherm would need to generate via metabolic heat production, and negative values indicate cooling costs that an endotherm would need to lose via evaporative cooling to achieve heat balance (Bakken 1981). To explore interactions with organismal phenotypes, we ran these simulations in which we adjusted the typical conductivity of plumage (0.075 W m^{-1} C^{-1}) (Wolf and Walsberg 2000)

by increasing or decreasing conductivity by 50%. For these simulations, we assumed ground surface temperature was equivalent to air temperature, which would underestimate the amount of longwave radiation from the ground. These results then inform how insulation may interact with wind speed to influence the energetic cost of homeothermy.

We finally simulated the effects of wind speed on evaporative water loss of wet skinned ectotherms (such as an amphibian) to understand how reductions in wind speed may influence the risk of dehydration. These simulations rely on using skin resistance to water loss (s cm^{-1}) to estimate water loss rates based on the evaporative demand of the air. Skin resistance is a physiological metric of water loss that controls for the surface area of the animal and evaporative gradient driving water loss, thereby quantifying the capacity of the skin to limit water loss (Riddell et al. 2017). The metric therefore reflects the physiological basis of water loss compared to other metrics that do not account for the environmental effects, such as total evaporative water loss rate (e.g., g H$_2$O h^{-1}) or cutaneous water loss rate (e.g., g H$_2$O h^{-1} cm^{-2}). For these simulations, we predicted water loss rates for a small (3 g) and large salamander (15 g) with the same skin resistance (1 s cm^{-1}), which corresponds to an amphibian with very little (but ecologically realistic) skin resistance to water loss (Spotila and Berman 1976; Riddell et al. 2017). The body sizes also correspond to realistic ranges of size for salamanders, such as woodland salamanders (Riddell et al. 2018) or a tiger salamander (Burger et al. 2024). The simulations also incorporated boundary layer resistance to water loss, which we estimated using the characteristic dimension of a cylinder and accounting for both free and forced convection (Newman et al. 2022). These simulations were designed to understand how body size may interact with wind speed to influence water loss rates and the potential risk of desiccation.

For the biophysical simulations, we conducted all statistical analyses in *R* (v. 4.3.1.). We used linear models to analyze the output from each simulation (e.g., soil, plant, bird, salamander) separately. Prior to running analyses, we assessed assumptions of normality using residual plots. For dependent variables, we analyzed soil surface temperature (°C), plant leaf temperature (°C), net sensible heat flux (W) for the tree swallow, or water loss rate (g h^{-1}) for the salamander. For independent variables, we included the proportional reduction in wind speed (0.1 increments from 0.1 to 1.0), air temperature (°C), and the relevant trait of interest (i.e., albedo, stomatal conductance, insulation conductivity, body mass). We also included the interaction between wind speed and trait of interest. For biophysical simulations conducted during daytime conditions (i.e.,

soil, leaf, bird), we also included solar radiation and its interaction with reduction in wind speed. For simulations on water loss in salamanders, we did not include solar radiation but instead included humidity and its interaction with reduction in wind speed. For humidity, we used the vapor pressure deficit (VPD, kPa), which is defined as the difference between the pressure of ambient humidity and saturation vapor pressure and quantifies the evaporative demand of the air (Anderson 1936; Stull 2000). We did not include temperature in these simulations because VPD drives evaporative water loss rates, not temperature, and both variables are highly correlated in the simulation (as observed in nature) (Riddell et al. 2017; Riddell et al. 2019). We opted to include the proportional reduction in wind speed, rather than wind speed itself, to meet the assumptions of normality in the raw data and avoid the issue of wind speed being highly colinear with air temperature (as observed in nature). We also calculated effect size using ω^2 (Olejnik and Algina 2003) from the *effectsize* package in *R*. Effect sizes are used to determine whether the effect of an independent variable is large (>0.14), moderate (0.14–0.06), or small (<0.05). We do not report *P*-values because these statistics are highly sensitive to sample size and thus not as useful for analyzing data from large simulations.

Results

Macroclimate data

We observed latitudinal clines in temperature and wind speed from macroclimatic data. The highest average air temperatures are located in the tropics (Fig. 1A), and the greatest increase in air temperature from climate change is forecasted to occur at high latitudes in the Northern Hemisphere (Fig. 1B, C). For wind speed, we found the slowest wind speed occur in the tropics, and wind speed generally increases into more temperate latitudes, especially in the Southern Hemisphere (Fig. 1D). The forecasted change in wind speed from climate change is highly variable across the planet, with wind speed generally expected to slow in the Northern Hemisphere and increase in the tropics. Collectively, the Northern Hemisphere in particular is expected to experience both warming and reductions in wind speed.

Microclimate data

Wind speed fluctuated with the hour of day, with the highest wind speeds typically occurring at midday (Fig. 2A). Wind speed varied little with month of the year ($F_{11,164} = 0.83$, $P = 0.61$), with wind speeds generally falling between 3 and 4 m s^{-1} (Fig. 2B). We also noted that wind speed generally increased with air tempera-
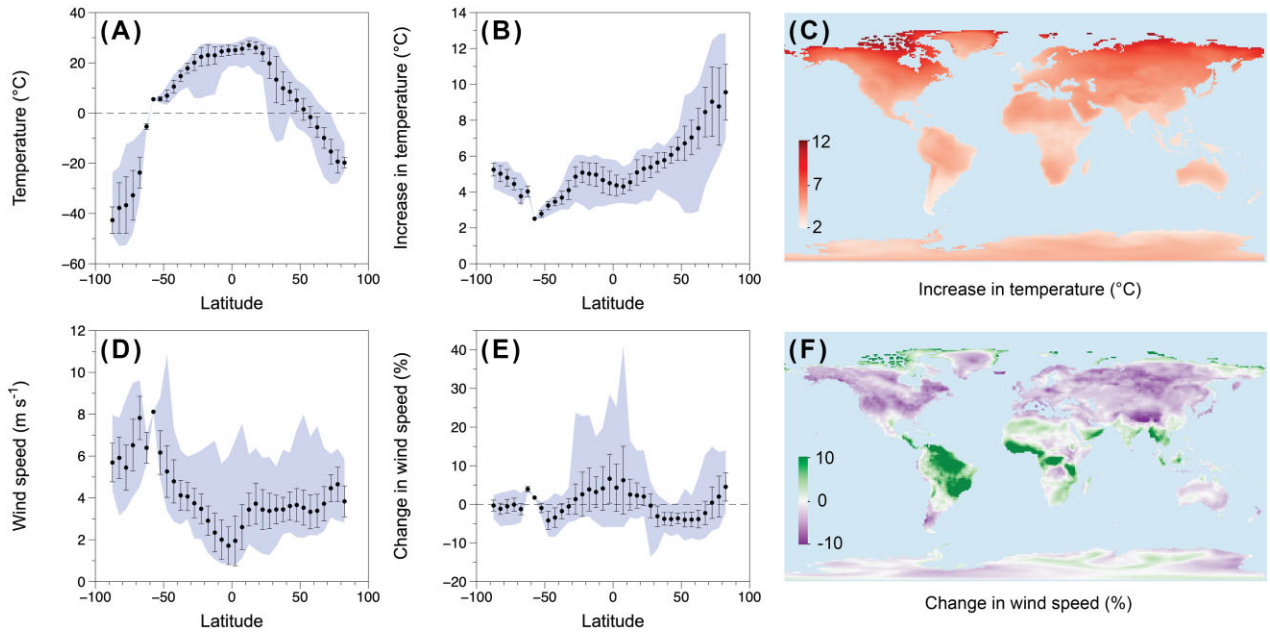
Fig. 1 Latitudinal variation in temperature and wind speed under a warming scenario. (A) Mean temperature (solid points) across latitude with standard deviation (error bars) and the range of values (indigo shading). (B) The mean increase in temperature (solid points) across latitude with standard deviation (error bars) and the range of values (indigo shading). (C) A global map of the mean increase in temperature under warming scenario SSP5–8.5. (D) Mean wind speed (solid points) across latitude with standard deviation (error bars) and the range of values (indigo shading). (E) The mean change in wind speed (solid points) across latitude with standard deviation (error bars) and the range of values (indigo shading). (F) A global map of the mean change in wind speed under warming scenario SSP5–8.5. Data from maps were downloaded from IPCC WGI Interactive Atlas under the Creative Commons Attribution 4.0 International License.

ture and solar radiation (Fig. 2C, D). We found significant effects of temperature variability on wind speed (Fig. 2E, $F_{1,164} = 109.98$, $P < 0.0001$), but not the interaction between month and temperature variability ($F_{11,164} = 1.03$, $P = 0.42$). We also found significant effects of temperature variability on the variability of wind speed (Fig. 2F, $F_{1,165} = 37.27$, $P < 0.0001$), as well as significant effects of month ($F_{11,164} = 2.51$, $P = 0.006$) and the interaction between month and temperature variability ($F_{11,164} = 1.92$, $P = 0.04$).

Biophysical simulations

In the soil surface temperature simulations, solar radiation had the largest effect on soil surface temperature ($\omega^2 = 0.95$). Air temperature also had a large effect on soil temperature ($\omega^2 = 0.62$) as did wind speed ($\omega^2 = 0.50$). The interaction between solar radiation and wind speed also had a large effect on soil surface temperature ($\omega^2 = 0.52$). Soil albedo ($\omega^2 = 0.10$) had a moderate effect on soil temperature, and the interaction between albedo and wind speed had a small effect on soil surface temperature ($\omega^2 = 0.03$). At high wind speeds, soil temperatures were similar and diverged as wind speed declined and temperature increased (Fig. 3A). Soil surface temperatures reached 52.0°C in dark soils and 46.6°C in light soils at the low-

est wind speed (Fig. 3A). Moreover, dark soil experienced a much greater range of temperature (15.21°C) relative to light soils (10.8°C).

In the leaf temperature simulations, solar radiation ($\omega^2 = 0.96$), air temperature ($\omega^2 = 0.86$), and stomatal conductance ($\omega^2 = 0.19$) had large effects on leaf temperature. Wind speed had a moderate effect on leaf temperature ($\omega^2 = 0.14$). The interaction between solar radiation and wind speed also had a moderate effect on leaf temperature ($\omega^2 = 0.11$), and the interaction between stomatal conductance and wind speed had a small effect ($\omega^2 = 0.01$). At the lowest wind speed and warmest time of day, the leaf with the lower stomatal conductance exhibited a leaf temperature 2.6°C warmer than the leaf with high stomatal conductance (Fig. 3B).

In the tree swallow simulations, solar radiation had the largest effect on net sensible heat flux ($\omega^2 = 0.93$), followed by air temperature ($\omega^2 = 0.85$). Wind speed ($\omega^2 = 0.13$) and insulation conductivity ($\omega^2 = 0.06$) had moderate effects on heat flux. The interaction between insulation conductivity and wind speed ($\omega^2 < 0.01$) and the interaction between solar radiation and wind speed ($\omega^2 = 0.02$) had small effects on heat flux. We also note that reductions in wind reduced net sensible heat flux when values were positive (indicating less required metabolic heat production to maintain homeothermy with lower wind), but increased net sensible heat flux
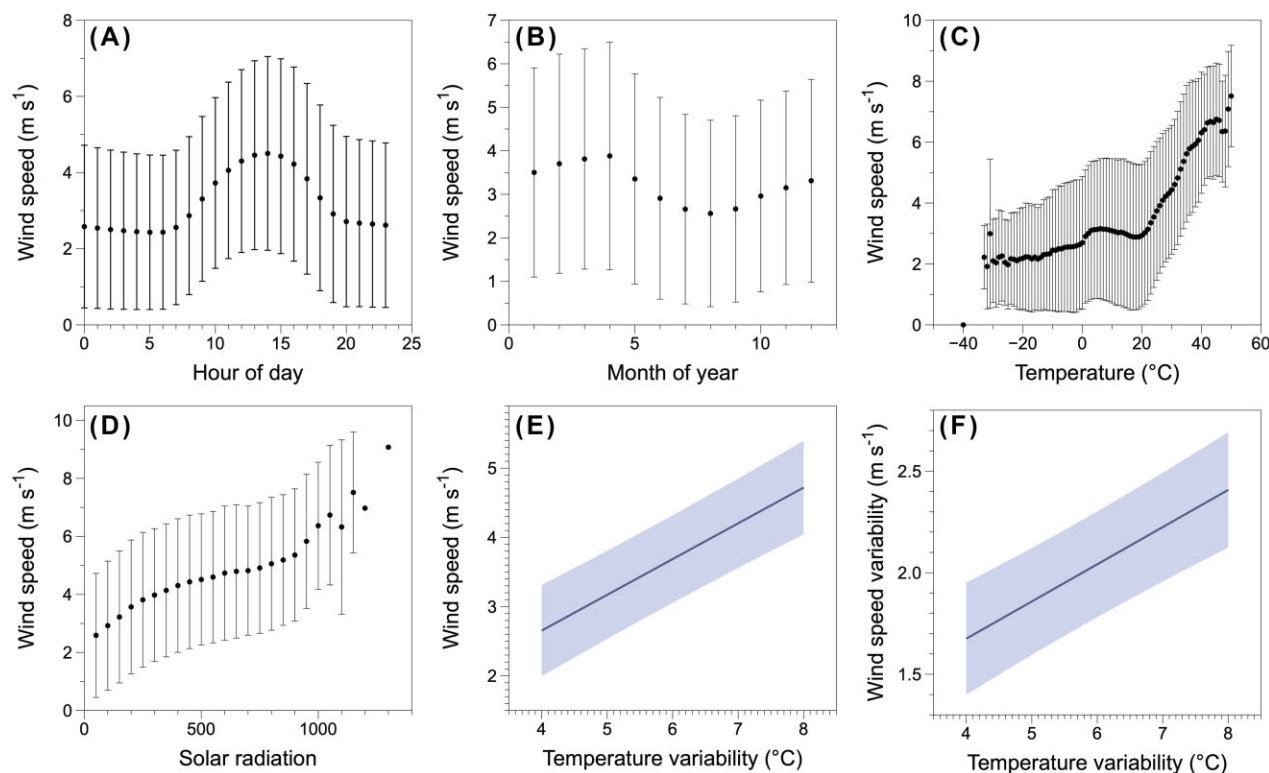
Fig. 2 Microclimate variation in wind speed and relations with temperature. (A) Mean wind speed (solid points) across the hour of day with standard deviation (error bars) from weather stations in North America. (B) Mean wind speed across the month of year with standard deviation. (C) Mean wind speed with standard deviation across 1°C intervals of air temperature. (D) Mean wind speed with standard deviation across 500 W m^{-2} intervals of solar radiation. (E) The positive effect of temperature variability (the standard deviation in monthly temperature) on monthly wind speed from weather station data. (F) The positive effect of temperature variability (the standard deviation in monthly temperature) on monthly variability in wind speed from weather station data.

when negative (indicating greater evaporative cooling required with lower wind speed; Fig. 3C). Simply put, slowing winds reduce the amount of metabolic heat production required when air temperatures are cool and also reduce the amount of evaporative cooling necessary when conditions are hot. Both processes occur because of the slowing of convective heat loss or heat gain, respectively.

In the salamander simulations, we found that body mass had the largest effect on water loss rates ($\omega^2 = 0.94$), then followed by the vapor pressure deficit ($\omega^2 = 0.78$). Wind speed also had a large effect on evaporative water loss ($\omega^2 = 0.20$). The interaction between mass and wind speed had a moderate effect on evaporative water loss ($\omega^2 = 0.06$), and the interaction between the vapor pressure deficit and wind speed had a small effect on evaporative water loss ($\omega^2 < 0.01$). Also, the large-bodied salamander was relatively more affected by the change in wind speed compared to small-bodied individuals (Fig. 3D). Specifically, water loss rate in the small-bodied individual decreased by 26.7% between the highest and lowest wind speed,

where water loss decreased by 32.5% in the large-bodied individual.

Discussion

Our study highlights the importance of wind on organismal performance at both macro- and microclimatic scales. Like air temperature, wind varies in ways that could systemically influence organismal performance across broad spatial scales. For instance, wind speeds are lowest in the tropics and highest in the temperate regions (Fig. 1). Thus, in the tropics, organisms experience some of the highest ambient temperatures and lowest wind speeds, suggesting greater risk of overheating in the tropics (Fig. 1). Overheating risk may be particularly relevant for tropical organisms that also experience solar radiation or rely on evaporative cooling to offload excess heat due to the high solar radiation and high humidity in the tropics. That said, the tropics are generally heavily vegetated and therefore provide ample microhabitats to buffer animals from overheating (Neel et al. 2021). Moreover, wind speeds are generally
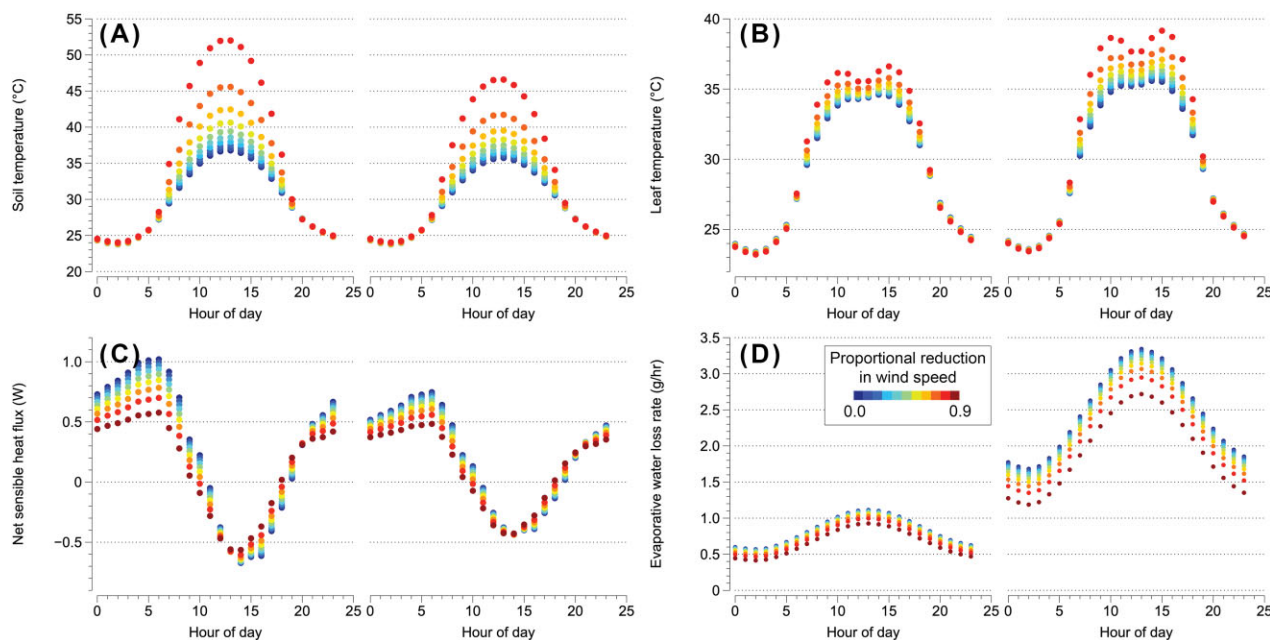
Fig. 3 Biophysical simulations demonstrate the impact of wind speed on soil temperature, plant leaf temperature, heat flux in a bird, and water loss in an amphibian. (A) The effect of wind speed on soil temperature for soil with low albedo (left) and soil with high albedo (right). (B) The effect of wind on leaf temperature for a leaf with high stomatal conductance (left) and low stomatal conductance (right). (C) The effect of wind on net sensible heat flux on a bird (tree swallow) with low insulation conductivity (left) and high insulation conductivity (right). (D) The effect of wind on water loss rate for an amphibian (salamander) with small body mass (left) and large body mass (right). The color codes correspond to the reduction in wind speed across the simulation, ranging from no reduction (0) to a 90% reduction in wind speed.

predicted to increase in the tropics (Fig. 1), potentially alleviating some overheating risk from solar radiation in terrestrial animals. Conversely, the greatest reductions in wind speed are forecasted to occur at higher latitudes, especially in the Northern Hemisphere (Fig. 1). Combined with the greater warming, animals in the Northern Hemisphere might experience the greatest increase in overheating risk, especially when considering the reduced convective cooling that offsets the effects of solar radiation. The homogenization of temperature across latitude and reduction in convective cooling might also reduce the intensity of selection hypothesized to drive clinal variation in certain phenotypes, such as critical thermal minima, body size (that is, Bergmann's rule), body shape (that is, Allen's rule), and melanism (Alho et al. 2010; Symonds and Tattersall 2010; Sunday et al. 2019; Mattison and Witt 2021; He et al. 2023). For these traits, studies that quantify changes in the magnitude of clinal variation over the next century might reveal some of the effects of climate change on phenotypic variation. However, microclimate variation may be more relevant as a selective pressure than broad macroclimatic variation.

Like temperature, wind speed varies predictably throughout the day, offering plants and animals the op-

portunity to exploit or avoid specific wind speeds. Being positively associated with air temperature, convective cooling becomes more effective at midday, when organisms are the most vulnerable to overheating (Stiegler et al. 2023). Despite this correlation, many animals cease activity during midday to avoid overheating (Huey and Pianka 1977; Kearney et al. 2009; Sears et al. 2011; Stiegler et al. 2023). Even in environments in which organisms can remain active under these conditions, wind can have negative effects on thermoregulation, with lizards from windy environments exhibiting lower thermoregulatory accuracy than lizards from sheltered, less windy environments (Ortega et al. 2017). More controlled studies in the laboratory have found that lizards select different body temperatures when exposed to high winds possibly to avoid dehydration (Virens and Cree 2022) or in anticipation of evaporative cooling (Spears et al. 2024). These effects may become increasingly difficult to predict under climate change, as greater variability in air temperature (expected under climate change) appears to drive greater variability and higher mean wind speeds (Fig. 2). Changes in wind speed are not typically incorporated into models that forecast the effects of climate warming on animal performance. Yet these examples (and this study) indicate that accurately

predicting the effects of climate change on animal performance likely requires incorporating wind speed, particularly at the microclimatic scale. These simulations might reveal how wind contributes to shaping the environmental conditions that define an organism's ability to survive and reproduce, thereby defining the species' niche.

Our biophysical models also underscored the important interactions between solar radiation and wind speed on temperatures experienced by plants and animals. High wind speeds increase convective cooling thereby offsetting the effect of solar radiation, which was observed in the biophysical simulations (Fig. 3). This interaction is particularly relevant to the thermal consequences of melanism in plants and animals. Several studies have found that organisms from higher latitudes or altitudes exhibit darker coloration than organisms from lower latitudes or altitudes, presumably as a compensatory response to cooler air temperatures (Alho et al. 2010; Castella et al. 2013; Günter et al. 2019; Mattison and Witt 2021). Even bird species separated only by a few kilometers on cooler islands exhibit darker coloration than conspecifics on the warmer mainland (Porter et al. 2023). However, wind speed has strong interactions with solar radiation and thus may also be involved in shaping clinal variation in melanism. For instance, higher latitudes are generally windier and may increase selection to be darker to offset the higher rates of convective cooling compared to low latitudes. From another perspective, however, very windy environments might eliminate the thermal benefits of melanism altogether, as illustrated by dark- and light-colored objects achieving the same temperature in high wind speeds (Fig. 3). Therefore, our study suggests that wind may modify selective pressure for coloration (that is, solar absorptance). Incorporating wind into these broad spatial or temporal analyses on the change in coloration may improve our ability to predict future responses to selection.

Most endotherms in the Northern Hemisphere maintain body temperatures that are greater than the surrounding air temperature (Prinzinger et al. 1991). Under these conditions, high wind speeds reduce the thermoregulatory demands associated with heat stress but increase the demands associated with cold stress by increasing convective cooling (Fig. 3C). Therefore, future reductions in wind speed and increases in air temperature in the Northern Hemisphere might relax selection on phenotypes that minimize heat loss in cold conditions (e.g., thick insulation layers [Speakman and Król 2010]) while increasing the strength of selection for phenotypes that increase heat loss in warm conditions (e.g., greater reflectance of the integument [Medina et al. 2018], larger appendages to increase radiative heat

loss [Tilkens et al. 2007]). Conversely, when air temperatures exceed body temperatures, high wind speeds promote convective heating, exacerbating heat stress (Mitchell et al. 2018). An increased incidence of extreme heatwaves, when air temperatures exceed the normothermic body temperatures of some endotherms, is predicted under future climate models in the Northern Hemisphere (Horton et al. 2016). Reductions in wind speed may lessen the severity of extreme temperatures, when the strength of natural selection can be intense (Bumpus 1899; Rodríguez-Trelles et al. 2013). However, these dynamics will be highly complex, especially given the association between higher air temperature and higher wind speed that we documented in the microclimate data (Fig. 2C). Regardless of the scenario, wind speed will likely influence both the direction and intensity of selective pressure exerted by air temperature, especially for endotherms.

Similar to heat flux, wind speed also has complex effects on evaporative water loss that may ultimately be shaped by microclimatic processes. From a physical perspective, the rate at which an organism loses water to the environment is a combination of its physiological resistance to water loss (typically determined by the skin, integument, or cuticle) and the ambient convective, thermal, and hydric environment (Tracy 1976; Riddell et al. 2017). Wind speed is slowest for organisms near the ground due to living in the boundary layer of the ground surface (Geiger et al. 2009). Moreover, organisms that live in complex topographic landscapes or vegetation might also buffer themselves from high water loss rates by taking advantage of lower wind speeds (Campbell and Norman 1998). Similarly, many amphibians restrict themselves to very moist environments, in which water loss does not occur due to saturation of the air (Schwarzkopf and Alford 1996; Lertzman-Lepofsky et al. 2020). Amphibians are also generally active at night when the air is often saturated and wind speeds are generally at their lowest (Eccel 2012). Thus, amphibians actively avoid conditions that lead to high water loss and, in many microclimates, have the behavioral repertoire to minimize or completely prevent water loss (Seebacher and Alford 2002). These factors are exceedingly challenging to quantify at global scales, but models that do not consider these variables may greatly overestimate water loss rates (Wu et al. 2024).

Our study highlights the critical role of wind in shaping organismal performance across macro- and microclimatic scales. Wind speed interacts with temperature, solar radiation, and boundary layers in complex ways, potentially altering patterns of overheating risk, clinal variation in morphology, and the effectiveness of convective cooling. As climate change drives shifts in wind patterns—such as increasing wind speeds in the tropics

and declining speeds at higher latitudes—these changes may reshape selection on traits like body size, coloration, and heat dissipation mechanisms. Despite its significance, wind speed is often overlooked in models predicting species' responses to climate change, underscoring the need to incorporate it into future biophysical and ecological studies (Potter et al. 2013; Woods et al. 2015; Briscoe et al. 2022). This study elevates wind from a peripheral to a core environmental axis, suggesting it is essential for fully defining an organism's niche, and pushes the Hutchinsonian niche concept beyond independent axes toward a more integrated view—where interactions among environmental factors jointly shape organismal performance and fitness. Ultimately, a deeper understanding of the eolian niche and its interactions with the thermal and hydric niche will improve predictions of species' vulnerabilities and adaptive responses in a rapidly changing world.

Author contributions

Conceptualization, E.A.R.; Methodology & Materials, E.A.R.; Investigation, E.A.R.; Formal Analysis, E.A.R.; Writing E.A.R. and C.K.P.; Supervision, E.A.R.; Funding Acquisition, E.A.R.

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Data availability

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