

WIND RESILIENCE IN OVERWINTERING MONARCH BUTTERFLIES:
AN EMPIRICAL TEST OF THE MICROCLIMATE HYPOTHESIS

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by
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An empirical test of the microclimate hypothesis

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ABSTRACT

Wind resilience in overwintering monarch butterflies: An empirical test of the microclimate hypothesis

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Keywords: Monarch butterfly, overwintering behavior, wind effects, microclimate, Vandenberg Space Force Base, time-lapse photography, generalized additive mixed models, behavioral ecology, California

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DEDICATION

In memory of Dan Meade, who revealed the fascinating mysteries of monarch butterflies to me and provided the rare freedom to explore them. His patience, generosity, and belief in my ideas helped make this research possible.

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Chapter 1

1.1 Introduction

The distribution and survival of invertebrate species are governed by a complex interplay of biotic and abiotic factors. While biotic interactions influence community assembly in part through predation, competition, and parasitism (Blois-Heulin, Crowley, Arrington, & Johnson, 1990; Lafferty & Shaw, 2013; Miller-ter Kuile, Apigo, Bui, et al., 2022), abiotic conditions often set the fundamental limits determining where invertebrates can persist. Temperature constrains invertebrate physiology across all latitudes, from Antarctic midges (*Belgica antarctica*) that survive freeze-thaw cycles through cryoprotective dehydration (Everatt, Convey, Bale, et al., 2015), to desert land snails (*Sphincterochila boissieri*) that tolerate 55°C through metabolic downregulation (Schweizer, Triebkorn, & Köhler, 2019). Rising temperatures directly increase metabolic rates and respiratory water loss, creating compound stress that limits activity windows (Chown, Sørensen, & Terblanche, 2011). Solar radiation drives both direct physiological impacts and behavioral responses. Army ants demonstrate habitat-specific evolution of thermal maxima tied to insolation exposure (Baudier, D’Amelio, Malhotra, et al., 2018), while terrestrial gastropods climb vertical surfaces to escape ground-level heat and evolve reflective pigmentation in exposed populations (Schweizer, Triebkorn, & Köhler, 2019). Among these abiotic factors, wind emerges as a particularly complex environmental force shaping invertebrate ecology through remarkably diverse mechanisms.

Wind influences invertebrate behavior and ecology through diverse mechanisms that vary across species, exhibiting remarkably specific wind detection thresholds and behavioral responses. Cockroaches perceive air currents as low as 0.015–0.03 m/s, with *Periplaneta americana* demonstrating predictable orientation shifts from upwind movement at low velocities to downwind escape at higher speeds (Bell & Kramer, 1979). Mosquito flight activity shows sensitivity to even light winds, with trap catches declining 75% when wind speeds approach their normal flight velocity of 1.0 m/s, effectively grounding entire populations (Bidle, Day, & Evans, 1995). Some species exploit wind for dispersal through specific behavioral triggers, such as spiders exhibiting stereotypic ‘tiptoe’ behavior to initiate ballooning when wind conditions permit controlled trajectories (Bonte & Lens, 2007). Others respond to wind as an environmental stressor requiring active avoidance. Herbivorous larvae like *Uraba lugens* treat moderate winds of 3 m/s as disturbance cues, triggering increased movement to stable microsites on branches and behavioral shifts to leeward sides and abaxial leaf surfaces for protection (Leonard, McArthur, & Hochuli, 2016).

Beyond direct physical effects, invertebrates detect wind through indirect sensory pathways. The Namib desert beetle *Lepidochora discoidalis* perceives substrate vibrations when winds exceeding 5 m/s lift sand grains, using these cues to time surface foraging when detritus becomes concentrated (Hanrahan & and Kirchner, 1997). The katydid *Copiphora brevirostris* adjusts vibratory communication to avoid wind-induced noise, concentrating signaling between 2:00 and 5:00 AM when winds are calmest and exploiting short-term lulls during gusty periods (Velilla, Muñoz, Quiroga, et al., 2020). This complexity in wind-organism interactions becomes particularly evident when examining species that must navigate multiple life stages with different environmental exposures.

The monarch butterfly (*Danaus plexippus*) offers an exceptional system for studying how abiotic factors, particularly wind, shape invertebrate ecology through its remarkable multi-generational migration. North American monarchs complete an annual cycle that links vast northern breeding ranges with small, highly specific overwintering sites (L. Brower, 1995; S. Jepsen, Schweitzer, Young, et al., 2015; Solensky, 2004). The continent is home to two populations separated by the Rocky Mountains: a larger Eastern population and a Western population (Cockrell, Malcolm, & Brower, 1993; Freedman, de Roode, Forister, et al., 2021; S. Jepsen, Schweitzer, Young, et al., 2015). During the spring and summer, multiple short-lived generations of butterflies (2–5 weeks) breed throughout North America, with females laying eggs exclusively on milkweed (*Asclepias* spp.), the larval host plant (Cockrell, Malcolm, & Brower, 1993; Zalucki, 1982). This breeding phase builds the population as they radiate northward, but as late summer approaches, environmental cues such as shortening day length and cooling temperatures trigger the shift to the migratory generation (Barker & Herman, 1976; Goehring & Oberhauser, 2002; Herman & Tatar, 2001; Reppert & de Roode, 2018). These migratory adults exhibit a unique phenotype: they enter a state of reproductive diapause (suspended reproduction) and possess elongated wings suited for long-distance travel (Barker & Herman, 1976; Tuskes & Brower, 1978; Yang, Ostrovsky, Rogers, & Welker, 2016).

The fall migration begins as these long-lived adults (6–8 months) orient themselves southward, flying up to thousands of kilometers, a journey fueled by energy stored as lipid reserves accumulated from nectaring flowers along their route (Chaplin & Wells, 1982; Herman & Tatar, 2001; Urquhart & Urquhart, 1978). Navigational feats are guided by a sophisticated system that includes a time-compensated sun compass residing in the antennae, allowing them to maintain direction throughout the day (Mouritsen & Frost, 2002; Nguyen, Beetz, Merlin, & el Jundi, 2021). Eastern monarchs travel to the high-altitude oyamel fir (*Abies religiosa*) forests in central

Mexico, while the Western population migrates to overwintering groves located along the Pacific coast of California (L. Brower, 1995; Urquhart & Urquhart, 1978).

The overwintering period, lasting roughly from mid-October through mid-March, represents an important phase of the annual migration where the entire North American population concentrates into remarkably small forested areas (S. J. Jepsen & Black, 2015; Solensky, 2004; Vidal & Rendón-Salinas, 2014). During these months, monarchs must survive exclusively on lipid reserves accumulated during autumn migration while maintaining precise thermoregulatory balance (Chaplin & Wells, 1982; Masters, Malcolm, & Brower, 1988). As ectotherms, monarchs face a fundamental trade-off: they must maintain body temperatures cool enough to conserve energy through metabolic suppression, yet warm enough to permit essential daily movement (Alonso-Mejia & Arellano-Guillermo, 1992; Chaplin & Wells, 1982; Kammer, 1970; Masters, Malcolm, & Brower, 1988). The flight threshold, established at 12.7-16.0°C for Mexican populations, represents the minimum thoracic temperature required for powered flight (Masters, Malcolm, & Brower, 1988). Below this threshold, monarchs employ behavioral thermoregulation through dorsal basking, which can elevate body temperature to flight capability within 30 seconds of sun exposure, or through energetically costly shivering that consumes energy 25 times faster than resting (Masters, Malcolm, & Brower, 1988). Conversely, temperatures above 20°C risk terminating reproductive diapause and triggering premature remigration, while direct sun exposure can rapidly elevate thoracic temperatures to 33.6°C, forcing butterflies to adopt sun-minimizing postures or engage in heat-dissipating flights (Barker & Herman, 1976). This delicate energetic balance means that monarchs selecting overwintering sites must find locations that minimize both freezing risk and elevated metabolic expenditure (Alonso-Mejia & Arellano-Guillermo, 1992; Calvert, Zuchowski, & Brower, 1983; Masters, Malcolm, & Brower, 1988).

Building on early studies from Mexican overwintering sites that identified abiotic factors limiting butterfly survival, Leong proposed the microclimate hypothesis for western monarchs overwintering in California (K. L. H. Leong, 1990). This hypothesis posited that monarchs select clustering locations within groves based on a measurable microenvironmental envelope characterized by four key parameters: wind protection below 2 m/s to prevent cluster disruption, cool temperatures maintaining reproductive diapause while avoiding freezing mortality, dappled sunlight enabling behavioral thermoregulation, and high humidity with accessible moisture to prevent desiccation (K. L. H. Leong, 1990; K. L. Leong, Frey, Brenner, et al., 1991). Wind emerged as particularly critical in this framework, though these conclusions derived from correlational measurements rather than direct behavioral observations. Leong’s initial studies measured wind speeds at trees with and without butterfly clusters, while noting that “during winter storms, the butterflies clustered on those few trees that offered the greatest protection against winds of 2 m/s or greater” (K. L. H. Leong, 1990), though the highest wind speed measured in this study was 1.66 m/s. Based on these correlational patterns, Leong reported that “butterflies cluster in areas of the grove that offer exposure to filtered sunlight and shelter from strong wind movement” (K. L. Leong, Frey, Brenner, et al., 1991). In later publications, Leong described increasingly dramatic wind effects through anecdotal observations, noting that “roosting butterflies were blown from their clusters or dislodged by excessive branch movements (shaking) caused by winds exceeding 2 m/sec” and that “upon dislodgment, the butterflies flew to and resettled on foliage of trees that offered better shelter from strong winds” (K. L. H. Leong, 1999). When storm winds coincided with cold morning temperatures below 15°C, “the dislodged butterflies would be blown to the ground and remain there until temperatures reached flight threshold,” with “butterflies littering the ground at the base of roosting trees” commonly observed after winter storms (K. L. H. Leong, 1999). Despite originating from correlational field measure-

ments and anecdotal observations, this hypothesis gained widespread acceptance and directly informed management guidelines at multiple levels. Leong’s 2016 synthesis for California Department of Fish and Wildlife formally established that “winds ≥ 2 m/s are disruptive to the aggregating butterflies by blowing them from their roosting branches or dislodging them by shaking the branches,” and that when subjected to such winds above flight threshold, butterflies “either flew to a more sheltered area of the grove or, if no refuge area was available, abandoned the grove temporarily or for the remainder of the season” (K. L. H. Leong, 2016). The microclimate hypothesis thus dictated that successful overwintering sites must consistently exhibit this specific suite of conditions, particularly wind protection, implying that these abiotic parameters should guide habitat restoration efforts, a principle now widely adopted in monarch conservation plans (Althouse & Meade, Inc. & Creekside Science, 2023; S. Jepsen, Pelton, Black, et al., 2017; E. Pelton, 2020; Weiss & Rich, 2008; Xerces Society, 2016).

However, empirical testing has gradually dismantled the microclimate hypothesis’s core assumption of a uniform environmental envelope. When researchers tested whether monarchs select for consistent microclimatic attributes across groves, they found that the realized microclimate varied significantly with latitude and local geography (Saniee & Villablanca, 2022). Temperature responses proved more complex than originally proposed, with monarchs avoiding freezing temperatures but selecting the warmest of cold temperatures available at their latitude (Fisher, Saniee, Van der Heide, et al., 2018). Humidity requirements showed geographic variability rather than consistency (Saniee & Villablanca, 2022). Of the four original parameters, only light exposure showed potential support as a unifying factor, with successful overwintering sites exhibiting consistent patterns of canopy openness (Saniee & Villablanca, 2022; Weiss, Rich, Murphy, et al., 1991). This geographic variability in microclimate preferences, where selection occurs hierarchically across multiple spatial scales

rather than for a single environmental envelope, fundamentally contradicts Leong’s original hypothesis (Fisher, Saniee, Van der Heide, et al., 2018; Saniee & Villablanca, 2022). The gradual rejection of the uniform microclimate hypothesis through empirical testing suggests that monarch habitat selection may be driven by physiological and energetic constraints that vary with local environmental conditions rather than by a rigid set of universal requirements.

The wind disruption component of the hypothesis stands apart as the only major parameter that has never undergone direct empirical testing of butterfly behavioral responses to wind exposure. Despite wind protection below 2 m/s being identified as a critical factor in Leong’s framework (K. L. H. Leong, 2016), widely adopted in restoration efforts (Althouse & Meade, Inc. & Creekside Science, 2023; S. Jepsen, Pelton, Black, et al., 2017; U.S. Fish and Wildlife Service, 2024; Weiss, 2018; Xerces Society, 2018), no study has established causal relationships between wind exposure and butterfly behavior. Leong’s methodology of comparing wind measurements between occupied and unoccupied trees provided only correlational evidence, never directly testing butterfly responses to wind exposure or distinguishing whether butterflies actively avoid wind or whether wind simply correlates with other unmeasured variables.

The absence of empirical testing for the wind disruption hypothesis becomes critically important given the catastrophic decline of western monarch populations. Between the 1980s and mid-2010s, populations collapsed by approximately 97% (Schultz, Brown, Pelton, & Crone, 2017), with population viability analyses revealing a 72% quasi-extinction risk within 20 years (Schultz, Brown, Pelton, & Crone, 2017). The winter 2018 to 2019 count recorded fewer than 30,000 monarchs, a single-year drop of 86%, representing over 99% decline from 1980s abundance (E. M. Pelton, Schultz, Jepsen, et al., 2019). The situation reached its most critical state in 2020 when the

Western Monarch Thanksgiving Count documented only 1,901 butterflies, the lowest number ever recorded (Xerces Society, 2025a). While populations showed some recovery in subsequent years, the 2024 to 2025 count of just 9,119 butterflies represents the second-lowest count on record, demonstrating the population’s continued precarity (Xerces Society, 2025a). These dramatic declines result from multiple interacting stressors including breeding habitat loss, pesticide exposure, climate change, and critically, the loss and degradation of overwintering habitat (Crone, Pelton, Brown, et al., 2019; E. M. Pelton, Schultz, Jepsen, et al., 2019). Evidence increasingly suggests that the overwintering stage represents the most limiting phase of the monarch’s annual cycle, with population declines concentrated during winter and early spring periods (Marini & Zalucki, 2017; E. M. Pelton, Schultz, Jepsen, et al., 2019). California’s coastal overwintering groves, where the entire western population concentrates into remarkably small forested areas from October through March, have thus emerged as critical conservation priorities. Yet management of these critical sites continues to rely on the untested wind disruption hypothesis, with restoration efforts investing millions of conservation dollars based on the presumed necessity of maintaining wind speeds below 2 m/s (Althouse & Meade, Inc. & Creekside Science, 2023; The Monarch Press, 2019).

Testing the wind disruption hypothesis requires addressing a fundamental methodological challenge: isolating wind effects from confounding environmental variables that naturally covary in field settings. Solar radiation can trigger butterfly departures through direct heating, enabling flight when ambient temperatures remain below thermal thresholds (Kammer, 1970; Masters, Malcolm, & Brower, 1988). Temperature independently influences activity patterns, with monarchs exhibiting predictable responses as temperatures approach and exceed flight thresholds (Barker & Herman, 1976). Time of day creates inherent activity rhythms related to sun angle and thermal conditions (Mouritsen & Frost, 2002). Furthermore, wind itself is multidimensional,

characterized not only by average speed but also by gustiness and variability (Nathan, Sapir, Trakhtenbrot, et al., 2005) that could differentially affect butterfly behavior. A rigorous test must therefore control for these confounding factors while examining multiple aspects of wind exposure, including both maximum wind speeds and duration above the proposed 2 m/s threshold. With western monarch populations facing potential extinction and limited conservation resources available, the need for empirically validated management strategies has never been more urgent.

This study provides the first direct empirical test of whether wind disrupts overwintering monarch butterflies. Our primary objective was to evaluate the foundational 2 m/s wind disruption threshold that has guided over three decades of conservation practice. We employed continuous monitoring at 30-minute intervals throughout the overwintering season, simultaneously measuring wind speed, temperature, and solar radiation at butterfly clustering locations. This approach enabled direct observation of butterfly responses to changing environmental conditions while controlling for confounding variables. We analyzed the data using an information-theoretic framework that compared multiple competing models to identify the strongest predictors of butterfly movement.

First, we hypothesized that wind, alongside other environmental factors, predicts butterfly abundance at overwintering clusters. If true, we predict that an information-theoretic approach will identify wind as a significant predictor of abundance changes, with monarch abundance decreasing when exposed to higher wind speeds.

Second, we hypothesized that wind becomes disruptive above a specific threshold of 2 m/s. If this threshold represents a meaningful biological boundary, we predict that monarch abundance will decline at roosts experiencing winds exceeding 2 m/s.

Third, we hypothesized that wind’s disruptive effects scale with intensity. If disruption increases with wind speed, we predict proportionally greater decreases in monarch abundance as wind speeds rise above the threshold.

Finally, we hypothesized that experiencing disruptive winds affects monarch site fidelity. If wind disruption influences future roost selection, we predict decreased site fidelity manifested as sustained abundance reductions at wind-disturbed roosts compared to pre-disturbance levels.

1.2 Materials and Methods

1.2.1 Study Site

Site selection followed a systematic filtering process driven by project requirements and practical constraints. The study was supported by a federal grant that mandated research be conducted on federal lands. We selected Vandenberg Space Force Base (VSFB, 34.7398°N, 120.5725°W) in Santa Barbara County, California, based on several key advantages: mild winters with infrequent frost events, extensive historical plantings of blue gum eucalyptus (*Eucalyptus globulus*) that have created suitable overwintering habitat throughout the installation, and restricted access that provided security for long-term equipment deployment. The base contains thirty documented monarch overwintering groves, with several sites consistently ranking within the top 10% of population counts statewide over the past decade (Xerces Society, 2025b).

Working with the base’s monarch conservation coordinator, we initially screened twelve locations from the thirty sites based on their documented capacity to support monarch aggregations and provide year-round access. This collaboration leveraged local expertise from managing Western Monarch Thanksgiving Count activities for

multiple years (Xerces Society, 2025b). During the study period, ten of these sites were actively monitored. However, due to low monarch populations during the 2023-2024 season and no observed overwintering behavior in the 2024-2025 season, only two sites (Spring Canyon and UDMH) produced measurable butterfly clusters suitable for our analysis.

Spring Canyon (34.6315°N, 120.6182°W) represents the most productive and historically reliable overwintering site on VSFB. Located in South Base within 300 meters of Space Launch Complex 4, this approximately 2.0-hectare site consists entirely of mature blue gum eucalyptus trees reaching heights of approximately 40 meters. An unnamed perennial creek runs through the center of the grove, creating a riparian corridor that supports heterogeneous canopy structure with variable tree spacing and diverse understory vegetation. Surf Road, an infrequently used paved access road, bisects both the perennial creek and forest canopy.

The UDMH site (34.6719°N, 120.5950°W), also located in South Base, comprises a 5.1-hectare eucalyptus grove planted in windrows adjacent to a waste treatment facility. The uniformly spaced trees maintain a largely clear understory with scattered low shrubs. Although only recently documented as an overwintering location in 2022, UDMH immediately emerged as a significant site, supporting over 6,000 monarchs during its initial count and ranking among the base’s highest population sites.

1.2.2 Monitoring Strategy

Equipment deployment strategies differed between monitoring seasons to accommodate research objectives and field experience. During the 2023-2024 season, we employed two strategies: targeted deployments at sites with confirmed monarch presence, and anticipatory deployments at locations where monarchs were expected based on

historical data but not currently observed. Targeted deployments concentrated at Spring Canyon and UDMH where active aggregations were documented throughout the season. Anticipatory deployments occurred at four overwintering sites: additional locations within Spring Canyon and UDMH, plus SLC-6 and Tangair. No monarchs were recorded at anticipatory deployment sites; consequently, these data are excluded from analysis.

Building on insights from the initial season, for the 2024-2025 season we modified our approach to establish monitoring stations at ten sites before monarch arrival, based on historical occurrence records compiled by the base conservation coordinator. This expanded spatial coverage aimed to capture greater environmental variation across potential overwintering sites. However, the 2024-2025 season coincided with historically low monarch abundance throughout California (Xerces Society, 2025b), resulting in no observed clustering behavior at any monitored location on base. Consequently, our final dataset comprises two sites (Spring Canyon and UDMH) from the 2023-2024 season only.

1.2.3 Field Equipment

To observe changes in monarch abundance in response to strong wind events, we deployed remote monitoring equipment near butterfly clusters at overwintering sites. Field observations utilized 15-meter telescoping fiberglass poles (Max-Gain Systems, Inc., Marietta, GA) anchored at three points using ground anchors with guy lines securing both the top and base to create stable, freestanding structures.

Poles were positioned 4-17 meters from cluster locations. This range, determined through field testing, balanced image resolution requirements for our grid-based counting method against disturbance minimization. Closer positioning compromised field

of view, while greater distances degraded butterfly visibility below classification thresholds. Pole placement considered ground stability for the 15-meter structures, infrastructure clearance requirements, and clear viewing angles. When deploying near active clusters, we approached from directions that minimized disturbance; no butterfly dispersal was observed during equipment deployment.

We monitored monarch abundance using modified trail cameras (GardePro E7 and E8, Shenzhen, China) configured for near-infrared imaging to enhance contrast between clustering butterflies and surrounding vegetation. Trail cameras were selected for their durability in extended field deployment, native time-lapse functionality, and modification potential. Near-infrared wavelength selection followed previous literature demonstrating effectiveness for butterfly population estimation (Hristov, Nikolaidis, Hubel, & Allen, 2019).

Hardware modifications exploited the camera’s internal filter-switching mechanism by engaging nighttime mode to access the clear glass filter position, then disconnecting power to prevent reversion to the infrared cut filter. Near-infrared pass filters (λ 850 nm) were mounted externally to restrict incoming light to NIR wavelengths. This configuration produced images where clustering butterflies appeared as dark masses against bright eucalyptus foliage reflectance in the near-infrared spectrum. Field validation confirmed sufficient contrast for visual distinction of monarch clusters from background vegetation, supporting our human-labeler analytical approach.

Cameras were mounted atop poles using lightweight tie-down straps and positioned horizontally toward butterfly clusters at roosting height. The wireless live view feature enabled real-time preview and precise camera aiming during deployment. Cameras operated in time-lapse mode with motion detection disabled.

Sampling interval selection balanced temporal resolution, battery life, and data processing feasibility through empirical optimization and rigorous statistical validation. Initial deployments used 10-minute intervals to capture significant changes in butterfly abundance, which preliminary observations indicated occurred on hourly rather than minute scales, while maintaining approximately 6-week continuous operation. Post-deployment statistical analysis using mixed-effects models and information-theoretic approaches systematically compared multiple sampling intervals across deployments. We conducted sequential subsample analyses starting with full temporal resolution and progressively testing reduced frequencies. Information-theoretic model comparison using Akaike Information Criterion (AIC) demonstrated that 30-minute intervals provided optimal balance, losing less than 5% of information compared to full temporal resolution (measured by root mean square error) while reducing image classification workload by 67%. Variance comparison analysis and visual assessment of fitted trend lines confirmed that this interval preserved essential time-series patterns including diurnal activity cycles, weather-response dynamics, and multi-day population trends. Battery life constraints and field deployment logistics further supported this interval choice, enabling extended autonomous operation essential for capturing complete behavioral sequences during variable weather conditions.

To quantify the wind conditions hypothesized to influence butterfly behavior, wind monitoring equipment consisted of Rain Wise WindLog Wind Data Loggers (Rain Wise Inc., Trenton, Maine) installed at pole apices to measure wind at heights approximating butterfly roosting locations. These instruments recorded average wind speed and maximum wind gust at one-minute intervals, the highest frequency supported by the sensors. This recording interval enabled calculation of wind speed variance within each photographic sampling period, capturing gustiness lost with longer averaging periods.

To systematically organize our heterogeneous monitoring efforts, we defined discrete monitoring periods as deployment units. Each deployment represented a unique combination of monitoring location, camera configuration (including camera ID, mounting height, and viewing angle), associated wind measurements, and temporal coverage period. Since equipment was frequently reused across locations and time periods, this deployment-based structure provided standardized sampling units that accounted for variation in environmental conditions and equipment configurations while treating each deployment as independent for statistical analyses. This approach produced time-series images from each deployment for estimating monarch cluster abundance through systematic grid-based counting methods, enabling analysis of abundance patterns in relation to wind speed and other environmental variables.

1.2.4 Image Analysis

1.2.4.1 Grid-based Counting Method

To quantify changes in monarch butterfly abundance from collected imagery, we developed a systematic grid-based counting protocol balancing accuracy with the practical constraints of analyzing tens of thousands of images. This approach addressed the challenge of estimating abundance in large aggregations where individual counts would be prohibitively time-consuming and emulated field researcher methods, including those used in the annual Thanksgiving Count (Xerces Society, 2018). We subdivided each image using a grid overlay system where human labelers assigned order-of-magnitude estimates per cell. Grid dimensions remained fixed throughout each deployment to ensure consistency. Custom software developed using the Electron framework in JavaScript facilitated this labeling effort.

Grid cell size varied by deployment based on camera-to-cluster distance. Cell dimensions were optimized to ensure most occupied cells contained butterflies in the 10–99 count range, balancing classification efficiency with spatial resolution. This standardization minimized cells alternating between widely different order-of-magnitude categories across the time series.

1.2.4.2 Counting Protocol

Human labelers estimated butterfly abundance within each grid cell using four order-of-magnitude categories: 0 (no butterflies), 1–9 (single digits), 10–99 (dozens), and 100–999 (hundreds). Labelers trained using a comprehensive online guide with example images and detailed classification criteria (https://kylenessen.github.io/monarch-trailcam_classifier/). The protocol prioritized efficiency while maintaining consistency across observers.

Because abundance estimates derived exclusively from two-dimensional photographic images, our classification protocol quantified only butterflies visible in the image plane without estimating three-dimensional cluster structure or depth. This approach intentionally excluded hidden individuals behind visible butterflies in overlapping aggregations, providing a conservative but consistent measure reflecting observable surface area rather than total volume. For cells containing partial butterflies at grid boundaries, labelers included these in counts unless double-counting would cause an adjacent cell to move to a higher category. When butterfly counts fluctuated between categories across the time series, we consistently applied the lower estimate to maintain conservative abundance estimates.

In addition to estimating monarch abundance, labelers recorded whether cells received direct sunlight. Direct sunlight classification presented challenges because oversatu-

rated conditions eliminated the contrast enabling butterfly detection in shaded areas. Labelers classified cells as receiving direct sunlight when branches or butterflies exhibited additional illumination clearly from direct rather than indirect light, even when individual butterflies became difficult to distinguish due to pixel oversaturation. This classification required careful attention to subtle shape recognition and contextual awareness about butterfly locations established from previous images in the time series. This measurement was recorded only for occupied cells and stored separately.

Labelers received ongoing feedback throughout the classification process. All classifications underwent review for common errors including mislabeled cells, incorrect category assignments, and inconsistent counting criteria application. Direct communication of corrections to labelers ensured consistent protocol application.

1.2.4.3 Abundance Calculation

We calculated an abundance index for each frame by summing the products of cell counts and their assigned category values across all grid cells, employing conservative estimates using minimum values within each order-of-magnitude category:

$$\text{Abundance index} = \sum_i \rho_i \times C_i \quad (1.1)$$

where ρ_i represents the number of cells in category i , and C_i represents the conservative estimate for that category. We used minimum category values ($C_1 = 1$ for category 1–9, $C_2 = 10$ for category 10–99, and $C_3 = 100$ for category 100–999) rather than midpoint or maximum values to ensure temporal analyses reflected genuine population shifts rather than estimation uncertainty.

1.2.5 Temperature Data Extraction

Temperature represents a critical environmental variable influencing monarch activity patterns and potentially confounding wind effects. Ambient temperature data were extracted from trail camera images using optical character recognition (OCR). Each camera displayed temperature readings on the image overlay, but these values were not accessible through EXIF metadata, necessitating visual extraction methods. We developed an automated Python script utilizing OCR technology to extract temperature values from approximately 56,000 images across all deployments. The extraction process employed multiple preprocessing strategies and pattern matching algorithms to accommodate variations in image quality and display characteristics.

Following initial automated extraction, we manually reviewed and corrected edge cases where OCR failed or produced anomalous values. All temperature data underwent systematic quality control through visualization of deployment-specific time series, enabling identification and correction of erroneous values. This process ensured complete temperature coverage for all analyzed images, providing the ambient temperature covariate required for our statistical models.

1.2.6 Statistical Analysis

1.2.6.1 Data Preparation

Statistical analysis employed a lag-based framework to capture the temporal dynamics of butterfly responses to environmental changes, comparing butterfly counts between consecutive 30-minute intervals. Observation pairs were constructed by matching counts at time t with counts at time $t - 30$ minutes, applying a ± 5 minute tolerance window to accommodate minor temporal variations in image capture. The response

variable (change in butterfly abundance between time points) underwent cube root transformation to achieve approximate normality while preserving directional information: $y = \text{sign}(\Delta) \times |\Delta|^{1/3}$, where Δ represents the difference in butterfly counts. While exploratory data analysis revealed generally well-behaved distributions, we observed bimodality in the raw butterfly abundance data driven primarily by a single anomalous event at deployment SC8. At this deployment, a large butterfly aggregation abruptly declined to near zero without corresponding changes in the measured environmental variables (wind speed, temperature, or solar exposure). This singular event was unlike any other observation in the dataset. We retained this deployment in the final analysis for two reasons: first, to maximize sample size and avoid arbitrary data exclusion, and second, sensitivity analysis showed that the cube root transformation of abundance differences adequately addressed the distributional concerns, with model selection and parameter estimates remaining consistent whether SC8 was included or excluded. The transformation approach made the anomaly’s inclusion or exclusion immaterial to the final results. Observation pairs where both time points recorded zero butterflies were excluded as uninformative, reducing the dataset from approximately 2,500 potential pairs to 1,894 analyzable observations across 115 unique deployment-day combinations.

1.2.6.2 Variable Selection

Predictor variables were selected to test specific hypotheses while avoiding multicollinearity. Maximum wind gust speed during each 30-minute interval served as the primary wind metric, with alternative wind measurements (average sustained speed, modal gust, gust standard deviation) excluded due to high correlation ($r > 0.75$). Environmental predictors included average temperature between observation pairs, number of butterflies in direct sunlight at the previous time point, and minutes

elapsed since the first observation of each day to capture diurnal patterns. Total butterfly count at the previous time point was included as a control variable, enabling distinction between proportional and absolute changes in abundance. When included, this variable tests effects on proportional change; when excluded, models test effects on absolute change.

1.2.6.3 Model Framework

Analysis employed generalized additive mixed models (GAMMs) implemented through the `mgcv` package in R. Model selection followed an information-theoretic approach, comparing 48 candidate models using Akaike Information Criterion (AIC). The candidate set comprised two fundamental frameworks: models including the lag abundance term (24 models) and models excluding it (24 models), with each framework containing null models, single predictor models, additive combinations, two- and three-way interactions, and models incorporating smooth terms for non-linear relationships. Random effects structure accounted for variation at three hierarchical levels: deployment location, observer, and deployment-day. Temporal autocorrelation within days was addressed using a first-order autoregressive (AR1) correlation structure grouped by deployment-day. All models were fitted using restricted maximum likelihood (REML) estimation.

To test specifically for threshold effects at the proposed 2 m/s disruptive wind speed, we conducted a sensitivity analysis using an alternative wind metric. We repeated the entire model selection process, replacing maximum wind gust speed with a threshold-based predictor: the count of minutes within each 30-minute observation period where wind gusts equaled or exceeded 2 m/s. This variable ranged from 0 to 30 minutes and was tested using the same 48 model structures, allowing direct comparison of continuous versus threshold-based wind effects.

1.2.6.4 Model Validation

Model assumptions were verified through standard residual diagnostics including examination of residual distributions, fitted versus residual plots, and quantile-quantile plots. Convergence was confirmed for all candidate models in both the primary and sensitivity analyses. Model performance and predictor significance were evaluated through AIC comparison, with models differing by less than 2 AIC units considered equivalent.

1.2.6.5 Statistical Power Analysis

To evaluate whether our study had adequate statistical power to detect wind effects if present, we conducted a simulation-based power analysis. This approach assessed our ability to detect various effect sizes given our sample size of 1,894 paired observations. We simulated 200 datasets from the best-fitting model (which excluded wind effects) and artificially introduced wind effects of known magnitude ranging from 0.05 to 0.20 standard deviations of the response variable. For each effect size, we refitted models including wind terms to determine the proportion of simulations where the artificial effect was detected as statistically significant ($\alpha = 0.05$). This simulation approach accounts for the complexity of our GAMM framework and hierarchical data structure, providing robust estimates of statistical power for detecting wind effects across a range of biologically plausible magnitudes.

1.2.6.6 Dynamic Window Analysis

To examine whether day-to-day changes in roost size depend on cumulative weather exposure aligned with butterfly roosting biology, we conducted a complementary anal-

ysis using dynamic temporal windows. This approach tested wind effects at a daily scale, capturing overnight and full-day weather exposure that the 30-minute lag analysis could not assess.

We constructed two window definitions to test the robustness of our findings. The sunset window spanned from the previous day’s maximum butterfly count to the current day’s last observation, approximating functional sunset when roosting decisions finalize. This biologically-aligned window varied in duration (mean = 29.6 hours) to capture the complete exposure period from peak aggregation through the subsequent roosting decision point. The 24-hour window provided a standardized comparison, extending exactly 24 hours from the previous day’s maximum count.

Daily aggregates were computed for each deployment-day combination, including maximum butterfly count, 95th percentile count, and mean of the top three counts. We retained only days with 15-25 daytime photographs to ensure adequate temporal coverage, then constructed consecutive day pairs separated by exactly one day. Pairs where both days recorded zero butterflies were excluded as uninformative. The response variable, defined as the change in maximum daily count between consecutive days, underwent signed square root transformation to achieve approximate normality while preserving directional information.

Weather metrics were calculated within each dynamic window. Temperature variables included minimum, maximum, and mean values, plus cumulative metrics such as degree-hours above 15°C. Wind measurements comprised average sustained speed, maximum gust, cumulative gust exposure, and time above the proposed 2 m/s threshold. Direct sun exposure was quantified as the cumulative count of butterflies observed in direct sunlight across all frames within the window, integrating both exposure duration and instantaneous abundance. We required 95% data completeness across

temperature, wind, and daylight observations, calculated as the geometric mean of coverage ratios.

Variable selection for the dynamic window analysis began with 19 candidate predictors spanning baseline abundance metrics, temperature summaries, wind exposure measures, and cumulative sun exposure. We conducted correlation analysis to identify multicollinearity within predictor families, particularly among the highly intercorrelated wind metrics (all pairwise correlations $r > 0.75$) and temperature variables. Based on this analysis, we selected predictors that minimized redundancy while maintaining interpretability and adequate degrees of freedom relative to sample size.

For wind exposure, we selected maximum wind gust as the primary metric because it captured the variance of all wind variables in a single interpretable measure, showed high correlation with sustained speed, gust summation, and threshold exceedance metrics, and maintained consistency with the 30-minute analysis. We excluded wind mode gust despite its biological relevance because it contained only approximately five unique values across the dataset, causing model convergence issues. Temperature representation focused on non-overlapping summaries that captured both the exposure range (minimum and maximum) and the thermal state at the previous day’s peak abundance. We excluded highly correlated metrics such as mean temperature and degree-hours above 15°C to reduce multicollinearity. The cumulative direct sun exposure variable was retained as a biologically relevant measure of thermal conditions that integrated both exposure duration and instantaneous abundance. For the sunset window analysis, we included lag duration (hours) as a control variable to account for varying window lengths.

Model selection followed the same information-theoretic approach as the 30-minute analysis. We evaluated 76 candidate models per window type using generalized additive mixed models with deployment random intercepts and AR(1) temporal cor-

relation structures. The candidate set included null models, single predictors, additive combinations, and models with smooth interaction terms. To address potential overfitting given the reduced sample size ($n = 94\text{--}96$ pairs), we applied conservative thresholds for the ratio of effective degrees of freedom to sample size and conducted leave-one-deployment-out cross-validation on top-performing models. The final predictor set comprised: temperature minimum and maximum, maximum wind gust, cumulative direct sun exposure, and baseline abundance controls.

1.3 Results

1.3.1 Descriptive Statistics

Environmental conditions varied substantially across the 78-day monitoring period at Spring Canyon and UDMH during the 2023-2024 overwintering season. The dataset comprised 1,894 observations collected at 30-minute intervals during daylight hours (07:00–17:00) from November 17, 2023, to February 4, 2024, totaling 947 observation hours across 115 unique deployment-day combinations.

Wind speeds ranged from complete calm to moderately strong conditions, with maximum gusts reaching 12.4 m/s (mean = 2.2 ± 1.4 m/s, median = 2.2 m/s). The interquartile range of 1.3–3.0 m/s indicated that most observations occurred under relatively mild wind conditions. Temperature showed considerable variation throughout the monitoring period, ranging from 3.0 to 30.0°C (mean = 14.6 ± 3.8 °C, median = 14.0°C), with an interquartile range of 12.5–17.0°C typical of California coastal winter conditions. Direct solar exposure occurred in 31.7% of observations ($n = 601$), with butterflies actively basking when present in sunlight, averaging 17.0 individuals in direct sun (range: 1–295).

Monarch abundance exhibited high variability across sites and time periods. Butterfly counts ranged from 0 to 770 individuals per observation, with a mean of 81.4 ± 100.0 butterflies and a median of 37 butterflies. The wide interquartile range (9–119 butterflies) reflected substantial variation in cluster sizes. Zero-count observations, representing either the beginning of cluster formation or cluster dissolution, comprised 2.3% of the dataset ($n = 43$).

Cluster sizes varied markedly among the 10 deployment locations. Site SC10 recorded the largest aggregation with 770 monarchs, while mean abundances ranged from 0 at SC9 to 325.8 at UDMH2. Eight deployments observed maximum cluster sizes exceeding 100 butterflies, with mean maximum cluster size across sites reaching 315.6 individuals. This variation in cluster sizes across deployments reflects the heterogeneous distribution of monarchs across overwintering microhabitats within the study sites.

The comprehensive temporal coverage, with observations at 30-minute intervals capturing 16.5 observations per deployment-day on average, provided fine-scale resolution of monarch behavioral responses to changing environmental conditions. Peak observation activity occurred at 16:00 hours (196 observations), corresponding with afternoon warming periods when monarchs typically exhibit increased movement.

1.3.2 Wind Disruption Analysis

To examine how monarchs respond to immediate environmental conditions, we analyzed 1,894 paired observations collected at 30-minute intervals throughout the overwintering season. This responsive change analysis tested whether short-term fluctuations in cluster size could be explained by concurrent weather variables, particularly wind exposure.

Table 1.1: Top 5 models ranked by AIC (30-minute analysis)

Model	Terms	AIC	Δ AIC	Weight
M50	Previous butterfly count, Temperature, Time since sunrise, Interaction (tensor): Maximum wind speed, Butterflies in direct sun	8074.03	0.00	0.86
M23	Previous butterfly count, Temperature, Butterflies in direct sun, Time since sunrise	8077.86	3.83	0.13
M22	Previous butterfly count, Temperature (linear), Butterflies in direct sun, Time since sunrise	8082.90	8.87	0.01
M24	Previous butterfly count, Maximum wind speed, Temperature, Butterflies in direct sun, Time since sunrise	8084.05	10.02	0.01
M52	Temperature, Time since sunrise, Interaction (tensor): Maximum wind speed, Butterflies in direct sun	8092.72	18.69	0.00

1.3.2.1 Model Selection

We evaluated 52 candidate models using generalized additive mixed models (GAMMs) to identify the environmental predictors of monarch abundance changes. Model selection via Akaike Information Criterion (AIC) identified M50 as the decisively best-fit model, capturing 85.8% of the total model weight (Table ??). The next best model (M23) showed substantially weaker support with Δ AIC = 3.8 and only 12.6% model weight. Model M50 incorporated smooth terms for previous butterfly count, temperature, and time since sunrise, along with a tensor interaction between maximum wind speed and butterflies in direct sun.

1.3.2.2 Analysis of Best Fit Model

The best-fit model (M50) predicted change in butterfly abundance as a function of: (1) the previous observation’s butterfly count, (2) average temperature, (3) time since

sunrise, and (4) an interaction between maximum wind gust speed and the number of butterflies in direct sunlight.

Statistical analysis of the model revealed significant effects for three of the four predictors (Table 1.2). The previous butterfly count ($F = 12.50$, $p < 0.001$), time since sunrise ($F = 9.85$, $p < 0.001$), and the wind-sunlight interaction ($F = 4.67$, $p < 0.001$) all showed strong statistical significance. Temperature effects approached but did not reach conventional significance thresholds ($F = 3.19$, $p = 0.057$). The model explained 6.4% of the variance in butterfly abundance changes (adjusted $R^2 = 0.064$, $n = 1894$).

Table 1.2: Summary of best-fit model (M50) for predicting changes in butterfly abundance. The model uses cube-root transformed butterfly count differences as the response variable.

Smooth Term	edf	Ref.df	F	p-value
Previous butterfly count	2.41	2.41	12.50	$< 0.001^{***}$
Average temperature	3.68	3.68	3.19	0.057
Time since sunrise	4.87	4.87	9.85	$< 0.001^{***}$
Wind gust \times Sunlight exposure	7.35	7.35	4.67	$< 0.001^{***}$
<i>Model performance:</i> Adj. $R^2 = 0.064$, Scale est. = 4.03, $n = 1894$				

Partial effects for the smooth terms are shown in Figure 1.1. The previous butterfly count showed a significant non-linear negative relationship ($p < 0.001$) consistent with proportionally greater departures from larger aggregations. Time since sunrise captured a significant diurnal pattern ($p < 0.001$) with morning departures and afternoon returns. Temperature showed a marginally non-significant trend ($p = 0.057$) suggesting possible effects near the 12.7–16°C flight threshold range.

The tensor interaction between wind speed and butterflies in direct sun ($p < 0.001$) revealed a complex conditional relationship where wind effects depended on solar exposure conditions (Figure 1.2). When butterflies in direct sun were held at zero (all butterflies in indirect light), cluster size changes showed no consistent trend across

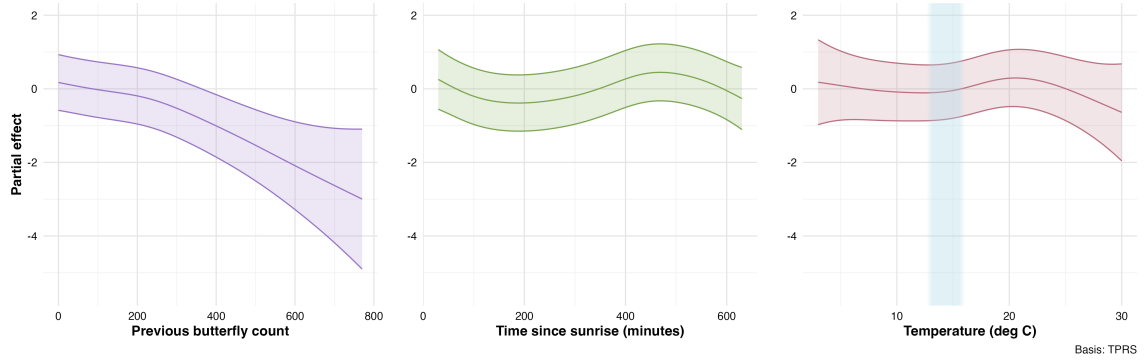


Figure 1.1: *Partial effects of environmental predictors on monarch butterfly abundance changes from the best-fit GAMM model (M50). Shaded regions represent 95% confidence intervals.*

the observed wind speed range (0-12 m/s). Conversely, when wind was held constant, low numbers of butterflies in direct sun were associated with decreasing cluster sizes, while higher counts led to increasing cluster sizes. At low butterfly counts in direct sun, the wind effect showed distinct patterns: clusters decreased in size at very calm winds (<1 m/s), showed no change from 1-3 m/s, and tended to increase from 4-8 m/s. At moderate wind speeds (1-3 m/s) and high butterfly counts (>100), cluster sizes tended to decrease. However, as wind speeds exceeded 3 m/s at these same butterfly counts, the pattern reversed, with cluster sizes increasing. The red dashed line at 2 m/s indicates the behavioral threshold identified in previous analyses. Gray regions mask areas too distant from observed data points for reliable interpretation, and caution is warranted when interpreting the strongest partial effects at the edges of the data distribution, where observations are sparse and interpolation artifacts may occur. Notably, the overwhelming majority of observations occurred at very low butterfly counts in direct sun, emphasizing that most clustering behavior happens when few butterflies are exposed to direct sunlight.

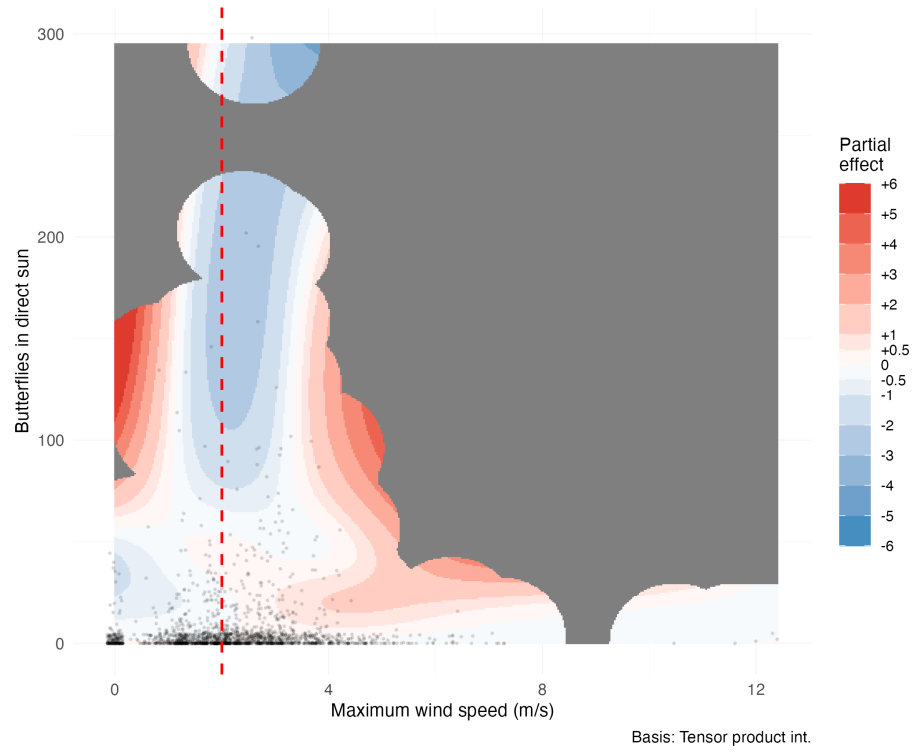


Figure 1.2: Tensor smooth interaction between maximum wind speed (m/s) and butterflies in direct sun on cluster size changes. Color gradient indicates partial effect magnitude (red = positive, blue = negative). Black points show observed data distribution. Red dashed line marks the 2 m/s behavioral threshold. Gray regions indicate areas beyond reliable interpolation range.

1.3.2.3 Model Diagnostics

Model diagnostic plots confirmed the adequacy of the GAMM specification (Figure 1.3). Residual versus fitted value plots showed no systematic patterns or heteroscedasticity, indicating appropriate model structure. The quantile-quantile plot revealed approximately normal residual distribution with minor deviations in the tails, acceptable given the large sample size and complexity of ecological data.

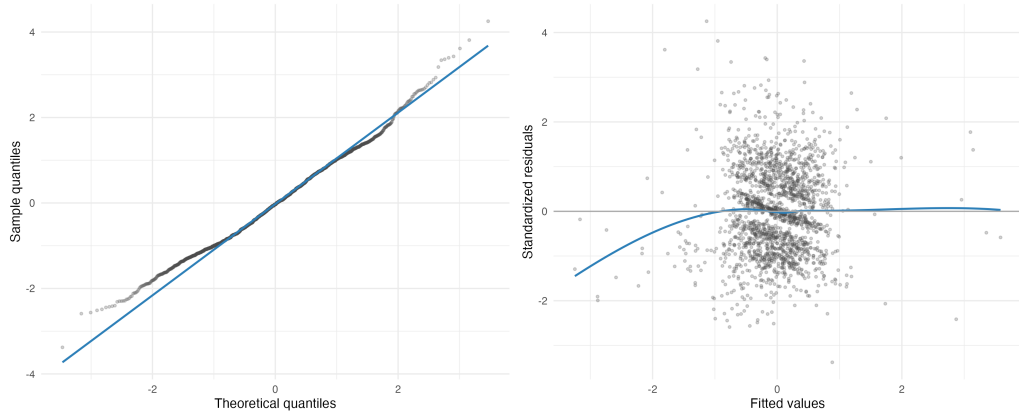


Figure 1.3: Diagnostic plots for the best-fit GAMM model (M50). Left panel shows quantile-quantile plot comparing model residuals to theoretical normal distribution. Right panel displays residuals versus fitted values to assess homoscedasticity and model adequacy.

Basis dimension checks confirmed adequate smoothing parameter selection for all model terms (Table 1.3). All smooth functions showed k-index values near 1.0, indicating sufficient basis dimensions to capture the underlying functional forms. None of the smooth terms showed evidence of undersmoothing (all p-values > 0.05), with the possible exception of time within day which showed marginal evidence (k-index = 0.96, $p = 0.065$). These diagnostics confirm that the chosen basis dimensions adequately represent the complexity of the smooth relationships without overfitting.

Temporal autocorrelation analysis revealed minimal residual correlation structure after accounting for the AR(1) correlation within deployment days (Figure 1.4). The

Table 1.3: Basis dimension adequacy checks for smooth terms in best-fit GAMM model (M50). Low p -values (k -index $\neq 1$) may indicate insufficient basis dimensions, particularly when edf approaches k' .

Smooth Term	k'	edf	k -index	p -value
$s(\text{total butterflies } t_{lag})$	9.00	2.41	1.00	0.735
$s(\text{temperature avg})$	9.00	3.67	1.02	0.895
$s(\text{time within day } t)$	9.00	4.87	0.96	0.065
$ti(\text{max gust, butterflies direct sun } t_{lag})$	16.00	7.35	0.99	0.490

autocorrelation function showed rapid decay with all lags beyond lag 1 falling within the significance bounds, confirming that the model adequately captured temporal dependencies in the data. This indicates that our mixed-effects structure with autoregressive errors appropriately addressed the repeated measures nature of the time-series observations.

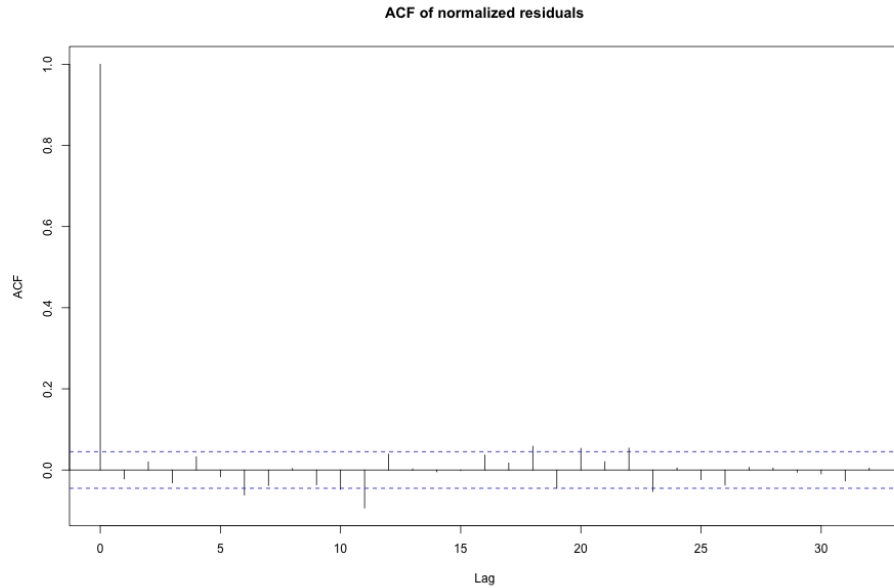


Figure 1.4: Autocorrelation function of model residuals showing minimal temporal correlation after accounting for $AR(1)$ structure within deployment days. Blue dashed lines indicate 95% confidence bounds for white noise.

1.3.2.4 Sensitivity Analysis

To test the hypothesis that wind acts as a binary disruption threshold rather than a continuous variable, we repeated the entire analysis using minutes above 2 m/s as the wind predictor. This threshold-based approach directly tests our second hypothesis that wind becomes disruptive above the 2 m/s threshold, which, if it represents a meaningful biological boundary, should predict declining monarch abundance at roosts experiencing sustained winds exceeding this threshold. The best threshold model (T50) maintained the same structure as our primary analysis but showed notably weaker performance (Table 1.4).

While T50 achieved the lowest AIC among threshold models, it failed to decisively outperform simpler alternatives, capturing only 55.4% of model weight compared to 40.4% for the model without any wind term (T23). The negligible difference in AIC ($\Delta\text{AIC} = 0.63$) between these models indicates substantial uncertainty about whether the threshold wind variable improves predictions. Despite this weaker overall performance (adjusted $R^2 = 0.061$ compared to 0.064 in the primary analysis), the interaction term between minutes above threshold and butterflies in direct sun achieved statistical significance ($p = 0.0001$), and notably, T50 was the only model among the top five candidates to include any wind parameters. This suggests that while the threshold approach may not optimally characterize wind effects, the interaction with solar exposure warrants examination.

The interaction plot from the threshold analysis reveals complex conditional relationships between wind exposure duration and solar conditions (Figure 1.5). When butterflies in direct sun are held at zero (all butterflies in indirect light), cluster size changes show no apparent trend across the entire range of wind exposure duration,

Table 1.4: *Top 5 models ranked by AIC (30-minute threshold analysis)*

Model	Terms	AIC	Δ AIC	Weight
T50	Previous butterfly count, Temperature, Time since sunrise, Interaction (tensor): Minutes above 2 m/s, Butterflies in direct sun	8077.23	0.00	0.55
T23	Previous butterfly count, Temperature, Butterflies in direct sun, Time since sunrise	8077.86	0.63	0.40
T22	Previous butterfly count, Temperature (linear), Butterflies in direct sun, Time since sunrise	8082.90	5.67	0.03
T24	Previous butterfly count, Minutes above 2 m/s, Temperature, Butterflies in direct sun, Time since sunrise	8085.41	8.18	0.01
T47	Temperature, Butterflies in direct sun, Time since sunrise	8097.30	20.07	0.00

from no time above threshold to the full 30-minute observation period. This suggests that wind effects on shaded butterflies are minimal regardless of exposure duration.

As butterfly counts in direct sun increase, distinct patterns emerge. At moderate counts (25-50 butterflies), cluster sizes tend to decrease when wind exposure extends from 15 to 25 minutes above threshold. However, at the extremes of sustained wind exposure (greater than 25 minutes), cluster sizes tend to increase. When wind exposure is minimal (0-5 minutes above threshold), increasing butterfly counts in sun show no effect on cluster size changes. The strongest effects appear at intermediate wind exposure durations (15-25 minutes) combined with moderate solar exposure levels.

The same caveats apply regarding sparse data at the extremes and the limits of interpolation, particularly given that most observations occurred at low butterfly counts in direct sun.

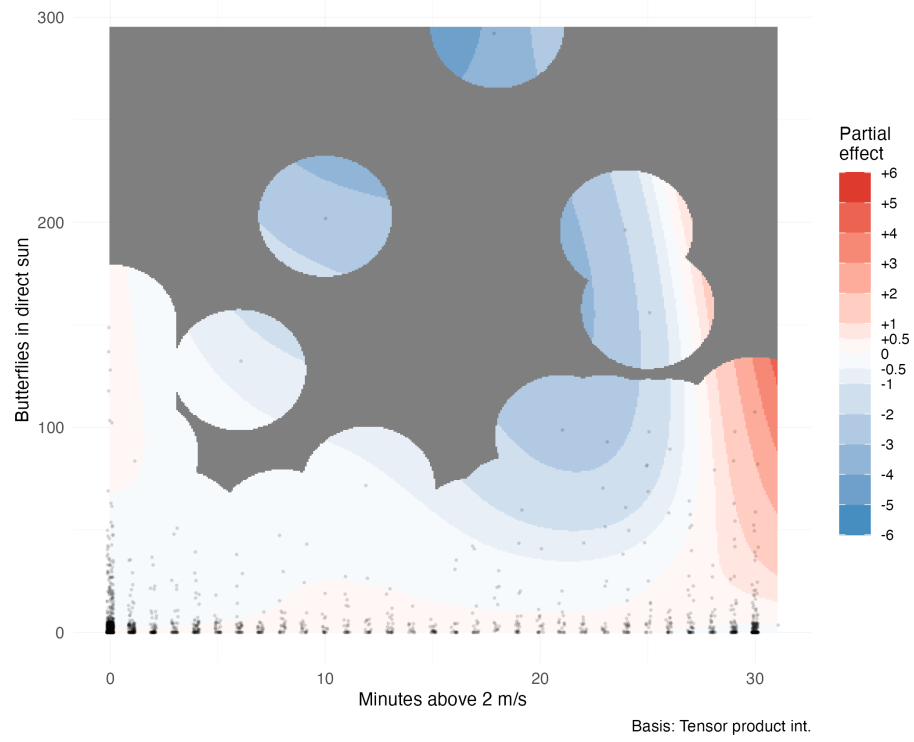


Figure 1.5: Tensor smooth interaction between minutes above 2 m/s wind threshold and butterflies in direct sun on cluster size changes. Color gradient indicates partial effect magnitude (red = positive, blue = negative). Black points show observed data distribution. Gray regions indicate areas beyond reliable interpolation range.

1.3.3 Statistical Power to Detect Wind Effects

Post-hoc power analysis confirmed our study had adequate statistical power to detect biologically meaningful wind effects (Table 1.5). With 1,894 paired observations, we achieved 87.5% power to detect moderate effect sizes (0.15 standard deviations) and 98.5% power to detect larger effects (0.20 standard deviations). Power for small effects (0.10 standard deviations) was 56%, while very small effects (0.05 standard deviations) yielded only 16.5% power. These results indicate that our study has sufficient statistical power for effect sizes of biological relevance.

Table 1.5: *Estimated power to detect wind effects of varying magnitudes. Effect sizes are expressed in standard deviations of the response variable (cube root transformed change in butterfly abundance).*

Effect Size (SD units)		Power (Proportion)	Power (%)
0.05	0.05	0.165	16.5%
0.1	0.10	0.560	56%
0.15	0.15	0.875	87.5%
0.2	0.20	0.985	98.5%

1.3.4 Site Fidelity Analysis

To test whether cumulative weather exposure influenced day-to-day roost dynamics, we analyzed 96 consecutive-day pairs from the same deployment dataset using biologically-aligned temporal windows. The primary analysis employed a sunset window spanning from the previous day’s maximum count to the current day’s last observation (mean duration = 29.6 hours), capturing the full period from peak aggregation through the subsequent roosting decision. A secondary analysis using fixed 24-hour windows ($n = 94$ pairs) provided a sensitivity test of our findings.

Daily maximum cluster sizes ranged from 0 to 770 butterflies (mean = 134.7 ± 138.1), with day-to-day changes in maximum count ranging from losses of 376 butterflies to gains of 464 butterflies (mean change = -10.5 ± 111.6). Within the sunset windows, maximum wind gusts ranged from 2.0 to 12.8 m/s (mean = 4.5 ± 1.8 m/s), with all observation windows exceeding the proposed 2 m/s threshold. Cumulative direct sun exposure varied from 0 to 1,122 butterfly-observations in sunlight per window (mean = 139.8 ± 206.9), reflecting diverse thermal exposure conditions across monitoring days.

1.3.4.1 Model Selection

We evaluated 76 candidate models using generalized additive mixed models (GAMMs) to identify environmental predictors of day-to-day changes in maximum cluster size. The model space included null, single-predictor, interaction-only, additive, main effects with interactions, and complex formulations, all incorporating deployment random intercepts and AR(1) temporal correlation. Model selection via corrected Akaike Information Criterion (AICc) identified M32 as the decisively best-fit model, capturing 84.7% of the total model weight (Table ??). The next best model (M52) showed substantially weaker support with $\Delta\text{AICc} = 5.6$ and only 5.2% model weight. Model M32 incorporated a tensor smooth interaction between maximum wind gust and cumulative direct sun exposure, along with baseline controls for previous day's maximum count and window duration.

1.3.4.2 Analysis of Best Fit Model

The best-fit model (M32) predicted square-root transformed change in butterfly abundance as a function of: (1) the previous day's maximum butterfly count, (2) window

Table 1.6: *Top 5 models ranked by AICc (sunset analysis)*

Model	Terms	AICc	Δ AICc	Weight
M32	Interaction (tensor): Maximum wind gust, Cumulative butterflies in direct sun	648.85	0.00	0.85
M52	Maximum wind gust, Cumulative butterflies in direct sun, Interaction (tensor): Maximum wind gust, Cumulative butterflies in direct sun	654.45	5.60	0.05
M20	Interaction (tensor): Minimum temperature, Cumulative butterflies in direct sun	656.77	7.92	0.02
M46	Maximum temperature, Cumulative butterflies in direct sun, Interaction (tensor): Maximum temperature, Cumulative butterflies in direct sun	657.70	8.85	0.01
M30	Interaction (tensor): Temperature at previous maximum count, Cumulative butterflies in direct sun	657.90	9.06	0.01

duration in hours, and (3) a tensor smooth interaction between maximum wind gust speed and cumulative butterflies in direct sunlight.

Statistical analysis revealed significant effects for the previous day’s maximum count ($t = -4.988$, $p < 0.001$) and the wind-sunlight interaction ($F = 4.097$, $p < 0.001$), while window duration showed no significant effect ($t = -1.067$, $p = 0.289$) (Table 1.7). The model explained 39.7% of the variance in day-to-day cluster size changes (adjusted $R^2 = 0.397$, $n = 96$), representing substantially greater explanatory power than the 30-minute responsive change analysis.

Table 1.7: *Summary of best-fit model (M32) for predicting site fidelity. The model uses square-root transformed day-to-day changes in butterfly count as the response variable.*

Smooth Term	edf	Ref.df	F	p-value
Previous day maximum count	1.00	1.00	24.88	$< 0.001^{***}$
Window duration	1.00	1.00	1.14	0.289
Wind gust \times Sunlight exposure	6.68	6.68	4.10	$< 0.001^{***}$
<i>Model performance: Adj. $R^2 = 0.397$, Scale est. = 41.06, $n = 96$</i>				

The previous day's maximum count showed a significant negative linear relationship (coefficient = -0.030, SE = 0.006), indicating that larger clusters experienced proportionally greater losses between days. This pattern aligns with the wind disruption analysis. Window duration showed no significant relationship with cluster size changes. Partial effects for these linear predictors are shown in Figure 1.6.

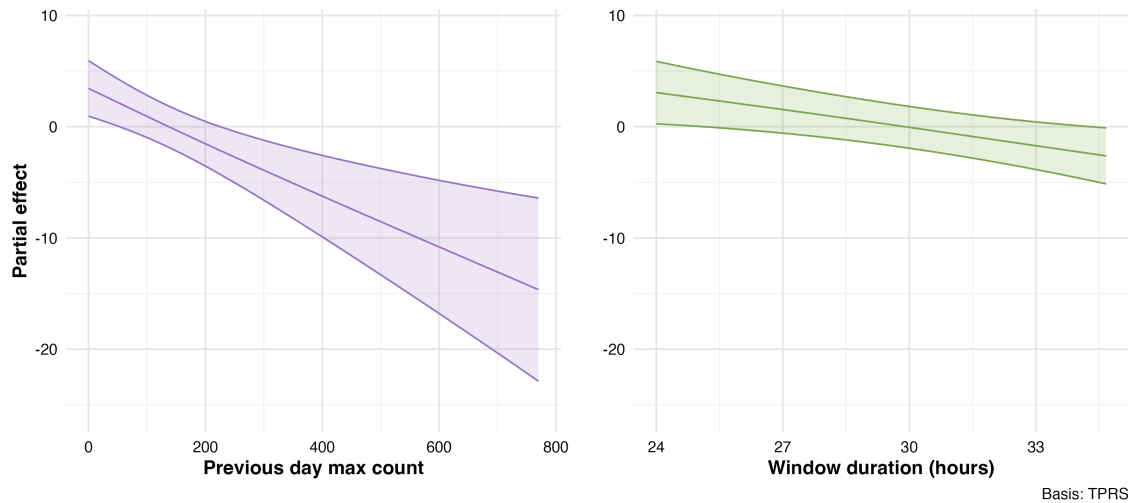


Figure 1.6: *Partial effects of control variables on day-to-day monarch butterfly cluster size changes from the best-fit GAMM model (M32). Left panel shows the strong negative effect of previous day maximum count. Right panel shows window duration had no significant effect on cluster size changes. Shaded regions represent 95% confidence intervals.*

The tensor smooth interaction between maximum wind gust and cumulative direct sun exposure ($p < 0.001$) revealed complex conditional relationships between sustained weather exposure and cumulative butterflies in direct light (Figure 1.7). All observations during the study period experienced wind speeds exceeding 2 m/s. Under low wind speeds around 2 m/s with minimal butterfly counts in direct sun, clusters increased the following day, though this pattern reversed sharply as butterfly counts increased, resulting in decreased cluster sizes. When butterfly counts approached zero, cluster sizes showed minimal change to slight decreases across most wind speeds, with the exception of extreme wind values where sparse data limits interpretation. At in-

termediate to high values of both wind speed and butterfly sun exposure, cluster sizes increased the next day. Interpretation requires caution at interpolation boundaries and regions with single observations.

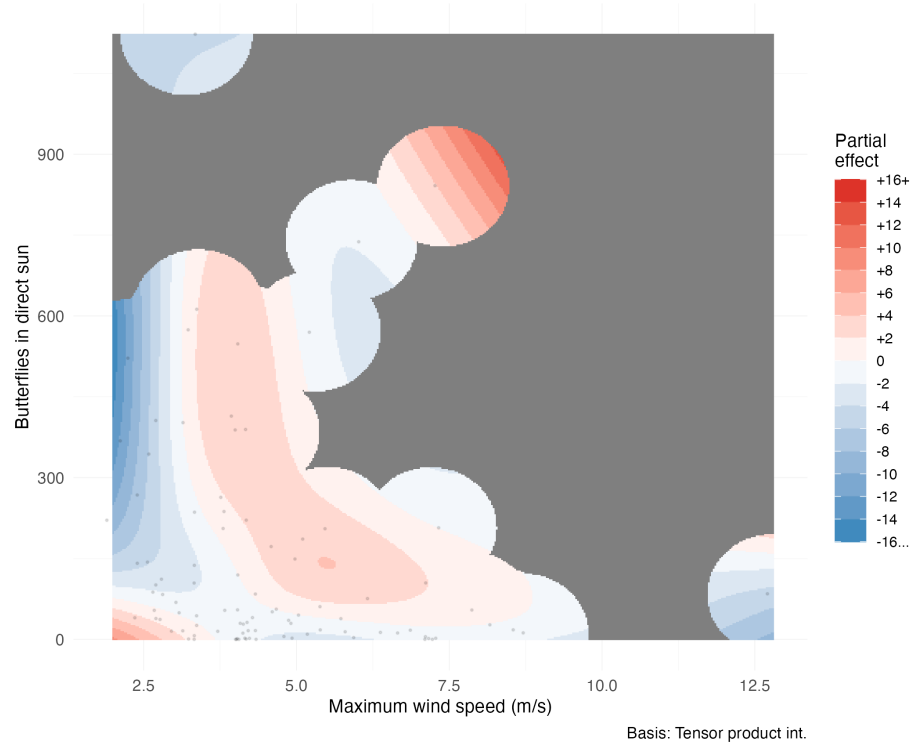


Figure 1.7: *Tensor smooth interaction between maximum wind gust (m/s) and cumulative butterflies in direct sun on day-to-day cluster size changes. Color gradient indicates partial effect magnitude on square-root transformed scale (red = positive, blue = negative). Black points show observed data distribution. Gray regions indicate areas beyond reliable interpolation range.*

1.3.4.3 Model Diagnostics

Model diagnostic plots confirmed the adequacy of the GAMM specification (Figure 1.8). Residual versus fitted value plots showed no systematic patterns or heteroscedasticity, indicating appropriate model structure. The quantile-quantile plot

revealed approximately normal residual distribution with minor deviations in the tails, acceptable given the sample size and complexity of ecological data.

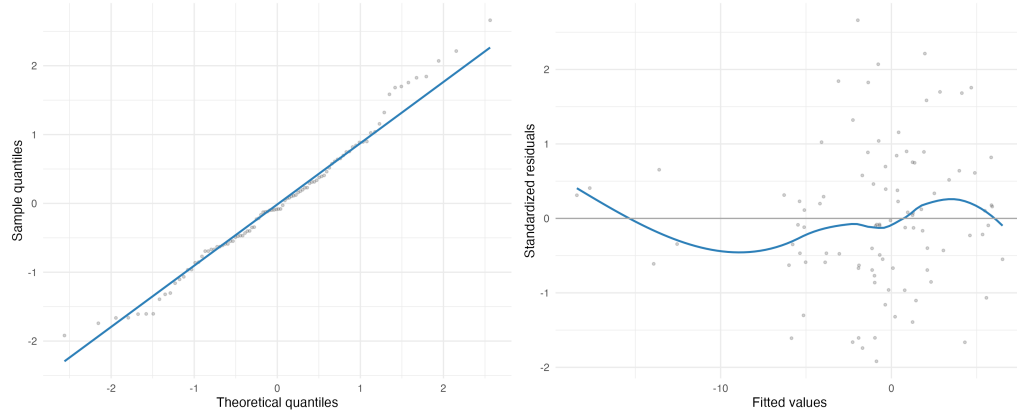


Figure 1.8: *Diagnostic plots for the best-fit GAMM model (M32). Left panel shows quantile-quantile plot comparing model residuals to theoretical normal distribution. Right panel displays residuals versus fitted values to assess homoscedasticity and model adequacy.*

Basis dimension checks confirmed adequate smoothing parameter selection for the tensor smooth interaction term. The wind-sunlight interaction showed a k-index value of 1.06 ($p = 0.72$), indicating sufficient basis dimensions to capture the underlying functional form without evidence of undersmoothing. This confirms that the chosen basis dimensions adequately represent the complexity of the smooth relationship without overfitting.

Temporal autocorrelation analysis revealed minimal residual correlation structure after accounting for the AR(1) correlation within deployment days (Figure 1.9). The autocorrelation function showed rapid decay with all lags beyond lag 1 falling within the significance bounds, confirming that the model adequately captured temporal dependencies in the data.

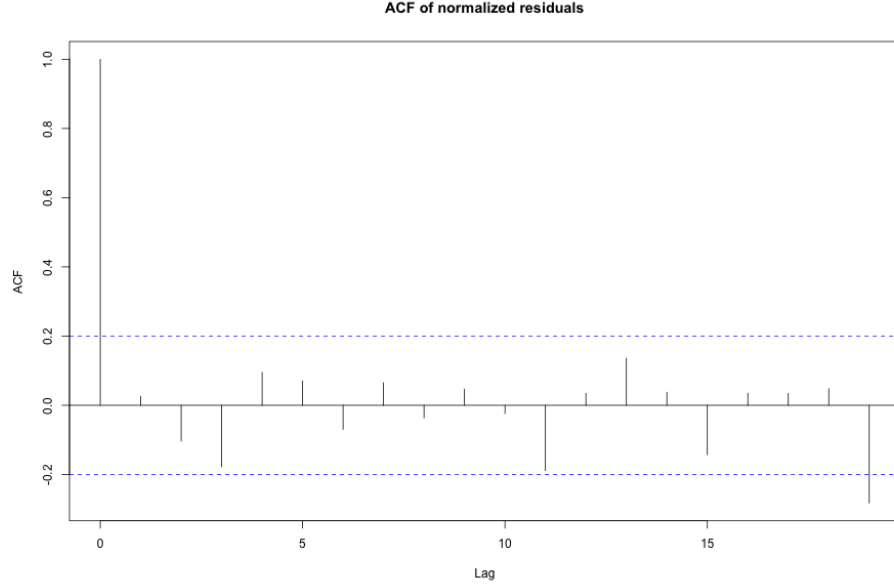


Figure 1.9: Autocorrelation function of model residuals showing minimal temporal correlation after accounting for $AR(1)$ structure within deployment days. Blue dashed lines indicate 95% confidence bounds for white noise.

1.3.5 Sensitivity Analysis: 24-Hour Butterfly Change

To assess the robustness of our findings, we conducted a sensitivity analysis examining butterfly cluster changes over 24-hour periods rather than sunset-specific intervals. This analysis evaluated the same 72 candidate models using identical GAMM specifications with deployment random intercepts and $AR(1)$ temporal correlation. Notably, model selection converged on the same structural form as the primary sunset analysis. Model M31, incorporating a tensor smooth interaction between maximum wind gust and cumulative direct sun exposure, emerged as the decisively best-fit model with 50.7% of the total model weight (Table 1.8). Alternative models showed substantially weaker support, with the next best model achieving only 8.4% weight and $\Delta AIC_c = 3.6$.

The 24-hour analysis revealed qualitatively similar interaction patterns to the sunset-specific model, though with attenuated effect magnitudes reflecting the longer tem-

Table 1.8: *Top five models from 24-hour sensitivity analysis ranked by AICc. The best-fit model (M31) included a tensor smooth interaction between maximum wind gust and cumulative butterflies in direct sun, matching the structure identified in the sunset-specific analysis but applied to 24-hour periods.*

Model	Description	AICc	Δ AICc	Weight	adj. R^2
M31	Wind \times sun exposure (smooth)	636.3	0.0	0.507	0.235
M23	Temperature \times wind (smooth)	639.9	3.6	0.084	–
M29	Temperature \times sun exposure (smooth)	640.8	4.4	0.056	–
M19	Min. temp. \times sun exposure (smooth)	641.1	4.8	0.047	–
M51	Wind + sun + wind \times sun (smooth)	641.7	5.4	0.034	–

poral window (Figure 1.10). Under low wind conditions (approximately 2 m/s) with minimal butterflies in direct sun, clusters increased over the subsequent 24 hours. This effect reversed sharply as butterfly counts increased under low winds, resulting in rapid cluster size decreases. When no butterflies occupied direct sun positions, cluster sizes remained relatively stable across wind speed values. Intermediate values for both wind speed and sun exposure produced cluster size increases. The convergent model selection and consistent interaction patterns across temporal scales strengthen confidence in the identified environmental relationships, while interpretation requires similar caution near data boundaries and regions with sparse observations.

1.4 Discussion

1.4.1 Wind Does Not Disrupt Overwintering Monarch Butterflies

Our study provides the first direct empirical test of the disruptive wind hypothesis and finds no support for wind as a primary factor influencing monarch butterfly clustering behavior. Despite the widespread adoption of the 2 m/s wind threshold in conservation practice, our data reveal no relationship between wind speed and

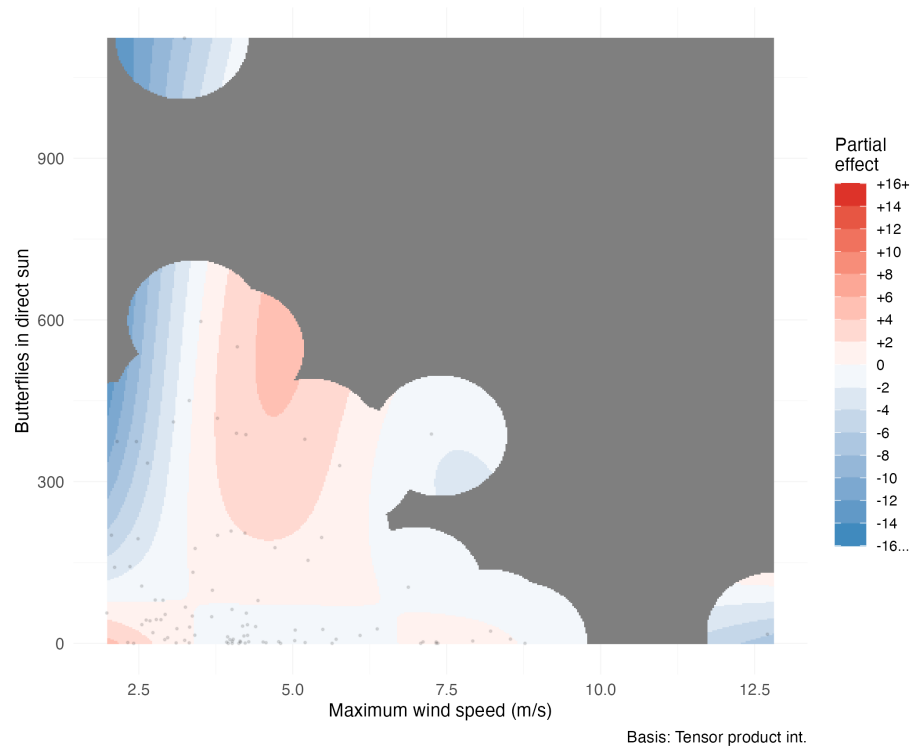


Figure 1.10: Tensor smooth interaction between maximum wind gust (m/s) and cumulative butterflies in direct sun on 24-hour cluster size changes. Color gradient indicates partial effect magnitude on square-root transformed scale (red = positive, blue = negative). Black points show observed data distribution. Gray regions indicate areas beyond reliable interpolation range. The interaction pattern mirrors that observed in the sunset-specific analysis, supporting the robustness of identified environmental relationships.

butterfly departures across the full range of observed conditions (0–12 m/s). While our models explain only 5.7% of variance in butterfly movements, reflecting our focus on testing wind effects rather than comprehensively explaining movement patterns, they had sufficient statistical power to detect environmental signals. This finding challenges assumptions underlying over three decades of management guidance.

The absence of wind effects in our data is particularly striking given that observed mean maximum wind speeds (2.2 m/s, SD = 1.4) frequently exceeded the proposed threshold. If the disruptive wind hypothesis were valid, we should have observed a clear signal: substantial reductions in butterfly abundance, as predicted by the disruptive wind hypothesis. Instead, we observed no change, small changes, or even positive changes in butterfly abundance at wind speeds six times the proposed disruption threshold.

Importantly, our power analysis demonstrated 87.5% power to detect moderate effect sizes (0.15 standard deviations) and 98.5% power for larger effects (0.20 standard deviations), while wind appeared in only one of the top five models (M24). In that model wind showed little evidence of an effect ($p = 0.218$) and resulted in substantially poorer model performance compared to the best model ($\Delta\text{AIC} = 6.2$, capturing only 4% of model weight). This weak wind signal, combined with our high statistical power, allows us to rule out all but very small wind effects. Given that the disruptive wind hypothesis predicts conspicuous reduction in abundance above threshold wind speeds, a substantial effect by any measure, our failure to detect such patterns provides strong evidence against the hypothesis rather than merely absence of evidence.

The methodological validity of our approach is confirmed by the strong signals detected for other environmental variables. Had our counting method or analytical framework been flawed, we would not have captured the pronounced effects of direct

sunlight ($F = 19.36$, $p \leq 0.001$) or the complex diurnal patterns ($F = 8.90$, $p \leq 0.001$) that emerged from the same dataset.

1.4.2 Alternative Drivers of Monarch Movement

While our study was designed specifically to test the wind hypothesis, our results suggest that thermoregulation, light exposure, and diurnal rhythms play more important roles than wind in driving short-term movements at overwintering sites.

1.4.2.1 Direct Sunlight as the Strongest Predictor

Direct sunlight exposure emerged as the strongest environmental predictor of reductions in cluster abundance in our study ($F = 19.36$, $p \leq 0.001$). Butterflies exposed to direct sunlight at the beginning of an observation interval showed the largest decreases in abundance, suggesting that solar radiation rapidly increases butterfly body temperatures well above ambient conditions. This finding aligns with Masters, Malcolm, and Brower’s work showing that monarchs in direct sunlight can elevate their body temperature above ambient conditions within minutes. This rapid warming capability could readily explain why direct sunlight exposure is such a strong predictor of decreased abundance at clusters.

The relationship between sunlight and departure represents a key component of the thermoregulatory equation. Monarchs have evolved to efficiently absorb solar radiation, an adaptation that enables flight at temperatures below what would otherwise be physiologically possible (Masters, Malcolm, & Brower, 1988). Yet this same efficiency becomes a liability when clustering. Butterflies cannot avoid absorbing heat when exposed to direct sun, risking overheating and accelerated depletion of their finite lipid reserves through elevated metabolism (Masters, Malcolm, & Brower, 1988).

This forces them to abandon energetically favorable clustering positions even when ambient temperatures remain cool. This trade-off between the benefits of clustering and the thermal constraints imposed by solar exposure may fundamentally shape daily movement patterns at overwintering sites.

1.4.2.2 Temperature Effects and Their Interpretation

Ambient temperature showed a subtle but significant relationship with monarch abundance changes ($\text{EDF} = 3.93$, $F = 3.23$, $p = 0.028$). The data suggest minimal change below 15°C (within the known flight threshold), a slight positive association around $20\text{--}21^{\circ}\text{C}$, and sharp declines above 25°C , consistent with thermoregulatory constraints. Given that available temperatures vary latitudinally across overwintering sites (Saniee & Villablanca, 2022), our results from Spring Canyon capture only a portion of the temperature continuum experienced across the entire overwintering range. The temperature effects we observed reflect responses within the specific thermal envelope available at our study latitude. Testing these patterns at sites spanning the full latitudinal gradient would reveal whether monarch responses to temperature are consistent or vary with local thermal regimes.

1.4.2.3 Diurnal Activity Patterns

Time since sunrise revealed distinct diurnal patterns ($\text{EDF} = 4.90$, $F = 8.90$, $p < 0.001$), with butterflies departing clusters in the morning and reforming aggregations in the afternoon. This pattern persists even after controlling for temperature and sunlight, aligning with anecdotal observations from overwintering sites throughout California (Chaplin & Wells, 1982; Frey & Leong, 1993; Tuskes & Brower, 1978).

1.4.3 Study Limitations

Several limitations warrant consideration. Our data derive from a single season (2023–2024) with typical monarch abundance at two sites (Xerces Society, 2025a). The following season (2024–2025), virtually no clustering monarchs were observed at Vandenberg Space Force Base (23 individuals total) despite monitoring 10 sites. This coincided with the second-lowest overwintering population on record statewide (Xerces Society, 2025b), preventing temporal replication of our study. Additionally, our counting methodology introduced discretization artifacts that contributed to large confidence intervals for environmental predictors. While we detected strong signals like direct sunlight effects, more subtle relationships require careful interpretation.

Furthermore, our study observed clusters where butterflies maintained direct substrate contact. In historically massive aggregations containing hundreds of thousands of individuals, many butterflies attach only to other butterflies, creating multi-layered formations (L. P. Brower, Williams, Fink, et al., 2008). If substrate attachment confers greater wind resistance than butterfly-to-butterfly attachment, the disruptive wind hypothesis might apply specifically to these larger aggregations. Future work should examine whether wind responses differ between substrate-attached and butterfly-attached individuals, particularly at sites supporting extreme densities.

1.4.4 Management Implications

Our findings suggest that management strategies prioritizing wind protection warrant reconsideration. The absence of wind effects despite frequent threshold exceedances indicates that usable habitat within existing groves may be larger than currently recognized. Areas previously dismissed due to perceived wind exposure may provide suitable conditions because they offer appropriate light and thermal regimes.

While past management efforts aimed at wind protection may have been based on incomplete understanding, they likely produced beneficial outcomes by increasing tree density. The fundamental recommendation to plant and maintain trees remains sound. Management should prioritize maintaining existing mature trees while establishing future roosting habitat at densities that support healthy, long-lived growth. In addition, as suggested by Saniee and Villablanca (2022), it may become relevant to explore ways in which to manage for thermal attributes, specifically sunlight.

1.4.5 Future Research Directions

Our findings open several important avenues for future research. First, explicit testing of light patterns as predictors of clustering locations could establish whether canopy structure guides habitat selection. The strong effect of direct sunlight ($F = 19.36$, $p < 0.001$) combined with the predictability of canopy-created light patterns suggests this may be a primary factor in roost site selection. Monarchs possess well-developed visual systems that enable sophisticated navigation during migration, including specialized neurons tuned to track celestial cues and the ability to detect polarized light patterns (Mouritsen & Frost, 2002; Nguyen, Beetz, Merlin, & el Jundi, 2021). This visual acuity, demonstrated in their use of sun compass orientation during long-distance migration, suggests they are fully capable of detecting and responding to the consistent light patterns created by canopy structure. Previous research also suggests light conditions may play an important role in habitat selection. (Weiss, Rich, Murphy, et al., 1991) examined canopy structure across monarch aggregation sites with different occupancy histories in Santa Barbara County, California. Sites were classified as “permanent sites” that support aggregations throughout the overwintering season (October through March), “transient sites” that support aggregations for only part of the season, or “former sites” that once supported aggregations but no longer

do so. Using hemispherical photography to measure the Indirect Site Factor (ISF), which quantifies percent canopy openness, Weiss found that permanent overwintering sites clustered within a narrow range of canopy openness (approximately 20%) with relatively low variance, while transient and former sites showed progressively greater variability (Figure 1.11). This pattern of consistent light conditions at successful sites provides additional context for understanding how canopy structure might influence clustering behavior.

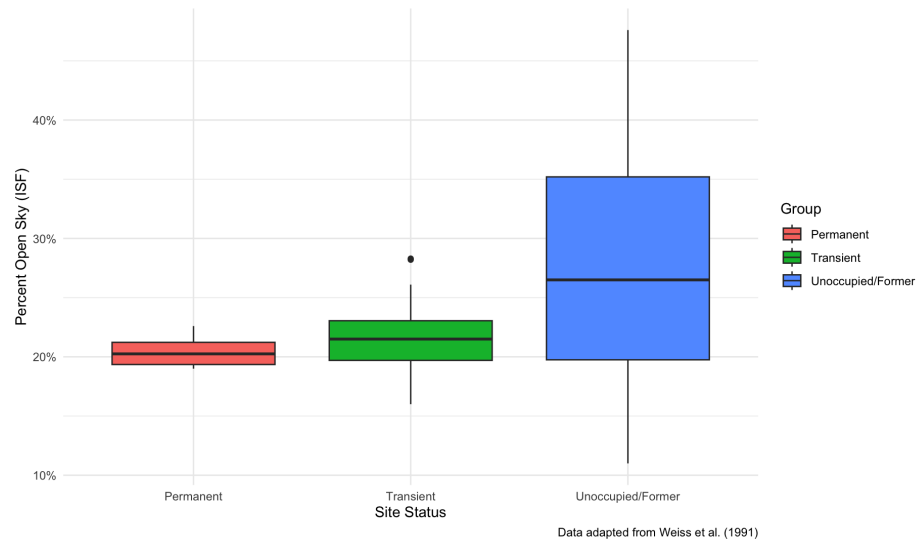


Figure 1.11: *Percent canopy openness (Indirect Site Factor) by occupancy status, adapted from Weiss et al. (1991). Permanent overwintering sites exhibit both a specific range of canopy openness (20%) and lower variance compared to transient and unoccupied/former sites.*

Second, investigation of social dynamics and positive behavioral feedback mechanisms could address unexplained variation in our models. Monarchs may exhibit emergent clustering behaviors where initial settlement increases the probability of others joining, creating self-reinforcing patterns independent of environmental conditions (Berdahl, Torney, Ioannou, et al., 2013).

Research should also examine whether our findings extend across the broader overwintering range. Testing these patterns at sites with different tree species, latitudes, and

in particular population densities would strengthen conclusions about the generality of wind effects, or their absence.

1.4.6 Conclusions

Wind did not disrupt monarch clusters even at speeds far exceeding presumptive thresholds. Instead, butterflies responded primarily to thermal conditions, including light exposure and ambient temperature, and to diurnal rhythms. These findings challenge current assumptions about overwintering habitat requirements and suggest that management priorities should be reevaluated. While our study represents one season at two sites, the absence of wind effects despite adequate statistical power raises important questions regarding decades of conservation guidelines. As monarch populations face continued threats, evidence-based management becomes increasingly critical for conserving the overwintering sites essential for this iconic species.

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Appendix A

FIRST APPENDIX

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Table A.1: *This is the caption for the first table.*

Col1	Col2	Col3	Col4	Col1	Col2	Col3	Col4
1	676	8837	787	544	22	908	229
2	732	78	5415	887	343	1112	870
3	545	778	7507	5554	5432	9867	9
4	545	1874	7560	102	562	223	792
5	88	788	6344	45	998	776	2

Table A.2: *This is the caption for another table.*

Col1	Col2	Col3	Col4	Col1	Col2	Col3	Col4
1	676	8837	787	544	22	908	229
2	732	78	5415	887	343	1112	870
3	545	778	7507	5554	5432	9867	9
4	545	1874	7560	102	562	223	792
5	88	788	6344	45	998	776	2

A.1 A Section

Nulla malesuada porttitor diam. Donec felis erat, congue non, volutpat at, tincidunt tristique, libero. Vivamus viverra fermentum felis. Donec nonummy pellentesque ante. Phasellus adipiscing semper elit. Proin fermentum massa ac quam. Sed diam turpis, molestie vitae, placerat a, molestie nec, leo. Maecenas lacinia. Nam ipsum ligula, eleifend at, accumsan nec, suscipit a, ipsum. Morbi blandit ligula feugiat magna. Nunc eleifend consequat lorem. Sed lacinia nulla vitae enim. Pellentesque tincidunt purus vel magna. Integer non enim. Praesent euismod nunc eu purus. Donec bibendum quam in tellus. Nullam cursus pulvinar lectus. Donec et mi. Nam vulputate metus eu enim. Vestibulum pellentesque felis eu massa. Quisque ullamcorper placerat ipsum. Cras nibh. Morbi vel justo vitae lacus tincidunt ultrices. Lorem ipsum dolor sit amet, consectetur adipiscing elit. In hac habitasse platea dictumst. Integer tempus convallis augue. Etiam facilisis. Nunc elementum fermentum wisi. Aenean placerat. Ut imperdiet, enim sed gravida sollicitudin, felis odio placerat quam, ac pulvinar elit purus eget enim. Nunc vitae tortor. Proin tempus nibh sit amet nisl. Vivamus quis tortor vitae risus porta vehicula.

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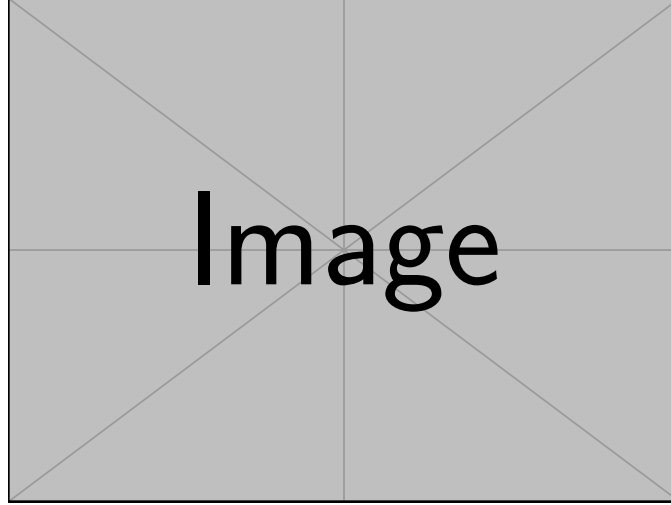


Figure A.1: *This is the caption for first image.*

porttitor. Nulla facilisi. Sed a turpis eu lacus commodo facilisis. Morbi fringilla, wisi in dignissim interdum, justo lectus sagittis dui, et vehicula libero dui cursus dui. Mauris tempor ligula sed lacus. Duis cursus enim ut augue. Cras ac magna. Cras nulla. Nulla egestas. Curabitur a leo. Quisque egestas wisi eget nunc. Nam feugiat lacus vel est. Curabitur consectetur.

A.1.1 A Subsection

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Figure A.2: *This is the caption for another image where the description is rather long and will probably go beyond one line.*

hac habitasse platea dictumst. Pellentesque non elit. Fusce sed justo eu urna porta tincidunt. Mauris felis odio, sollicitudin sed, volutpat a, ornare ac, erat. Morbi quis dolor. Donec pellentesque, erat ac sagittis semper, nunc dui lobortis purus, quis congue purus metus ultricies tellus. Proin et quam. Class aptent taciti sociosqu ad litora torquent per conubia nostra, per inceptos hymenaeos. Praesent sapien turpis, fermentum vel, eleifend faucibus, vehicula eu, lacus.

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Table A.3: *This is the caption for yet another table.*

Col1	Col2	Col3	Col4	Col1	Col2	Col3	Col4
1	676	8837	787	544	22	908	229
2	732	78	5415	887	343	1112	870
3	545	778	7507	5554	5432	9867	9
4	545	1874	7560	102	562	223	792
5	88	788	6344	45	998	776	2

A.2 Another Section

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A.2.1 Another Subsection

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A.2.1.1 A Sub-Subsection

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Appendix B

SECOND APPENDIX

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Table B.1: *This is the caption for the first table.*

Col1	Col2	Col3	Col4	Col1	Col2	Col3	Col4
1	676	8837	787	544	22	908	229
2	732	78	5415	887	343	1112	870
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4	545	1874	7560	102	562	223	792
5	88	788	6344	45	998	776	2

Table B.2: *This is the caption for another table.*

Col1	Col2	Col3	Col4	Col1	Col2	Col3	Col4
1	676	8837	787	544	22	908	229
2	732	78	5415	887	343	1112	870
3	545	778	7507	5554	5432	9867	9
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5	88	788	6344	45	998	776	2

B.1 A Section

Nulla malesuada porttitor diam. Donec felis erat, congue non, volutpat at, tincidunt tristique, libero. Vivamus viverra fermentum felis. Donec nonummy pellentesque ante. Phasellus adipiscing semper elit. Proin fermentum massa ac quam. Sed diam turpis, molestie vitae, placerat a, molestie nec, leo. Maecenas lacinia. Nam ipsum ligula, eleifend at, accumsan nec, suscipit a, ipsum. Morbi blandit ligula feugiat magna. Nunc eleifend consequat lorem. Sed lacinia nulla vitae enim. Pellentesque tincidunt purus vel magna. Integer non enim. Praesent euismod nunc eu purus. Donec bibendum quam in tellus. Nullam cursus pulvinar lectus. Donec et mi. Nam vulputate metus eu enim. Vestibulum pellentesque felis eu massa. Quisque ullamcorper placerat ipsum. Cras nibh. Morbi vel justo vitae lacus tincidunt ultrices. Lorem ipsum dolor sit amet, consectetur adipiscing elit. In hac habitasse platea dictumst. Integer tempus convallis augue. Etiam facilisis. Nunc elementum fermentum wisi. Aenean placerat. Ut imperdiet, enim sed gravida sollicitudin, felis odio placerat quam, ac pulvinar elit purus eget enim. Nunc vitae tortor. Proin tempus nibh sit amet nisl. Vivamus quis tortor vitae risus porta vehicula.

Fusce mauris. Vestibulum luctus nibh at lectus. Sed bibendum, nulla a faucibus semper, leo velit ultricies tellus, ac venenatis arcu wisi vel nisl. Vestibulum diam. Aliquam pellentesque, augue quis sagittis posuere, turpis lacus congue quam, in hendrerit risus eros eget felis. Maecenas eget erat in sapien mattis porttitor. Vestibulum

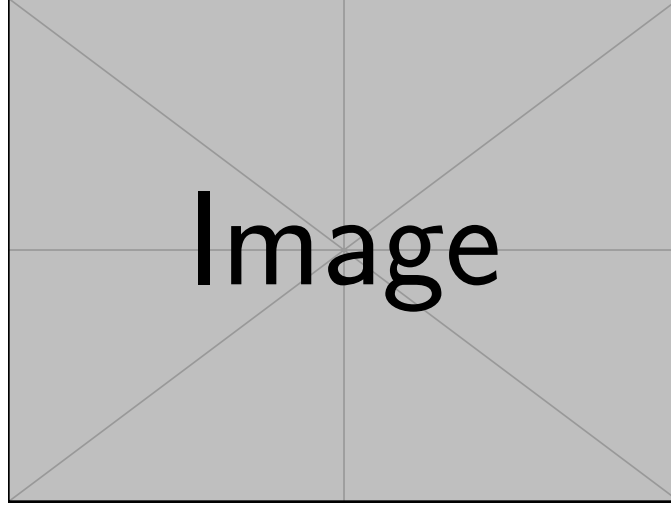


Figure B.1: *This is the caption for first image.*

porttitor. Nulla facilisi. Sed a turpis eu lacus commodo facilisis. Morbi fringilla, wisi in dignissim interdum, justo lectus sagittis dui, et vehicula libero dui cursus dui. Mauris tempor ligula sed lacus. Duis cursus enim ut augue. Cras ac magna. Cras nulla. Nulla egestas. Curabitur a leo. Quisque egestas wisi eget nunc. Nam feugiat lacus vel est. Curabitur consectetur.

B.1.1 A Subsection

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Sed commodo posuere pede. Mauris ut est. Ut quis purus. Sed ac odio. Sed vehicula hendrerit sem. Duis non odio. Morbi ut dui. Sed accumsan risus eget odio. In



Figure B.2: *This is the caption for another image where the description is rather long and will probably go beyond one line.*

hac habitasse platea dictumst. Pellentesque non elit. Fusce sed justo eu urna porta tincidunt. Mauris felis odio, sollicitudin sed, volutpat a, ornare ac, erat. Morbi quis dolor. Donec pellentesque, erat ac sagittis semper, nunc dui lobortis purus, quis congue purus metus ultricies tellus. Proin et quam. Class aptent taciti sociosqu ad litora torquent per conubia nostra, per inceptos hymenaeos. Praesent sapien turpis, fermentum vel, eleifend faucibus, vehicula eu, lacus.

Pellentesque habitant morbi tristique senectus et netus et malesuada fames ac turpis egestas. Donec odio elit, dictum in, hendrerit sit amet, egestas sed, leo. Praesent feugiat sapien aliquet odio. Integer vitae justo. Aliquam vestibulum fringilla lorem. Sed neque lectus, consectetur at, consectetur sed, eleifend ac, lectus. Nulla facilisi. Pellentesque eget lectus. Proin eu metus. Sed porttitor. In hac habitasse platea dictumst. Suspendisse eu lectus. Ut mi mi, lacinia sit amet, placerat et, mollis vitae, dui. Sed ante tellus, tristique ut, iaculis eu, malesuada ac, dui. Mauris nibh leo, facilisis non, adipiscing quis, ultrices a, dui.

Table B.3: *This is the caption for yet another table.*

Col1	Col2	Col3	Col4	Col1	Col2	Col3	Col4
1	676	8837	787	544	22	908	229
2	732	78	5415	887	343	1112	870
3	545	778	7507	5554	5432	9867	9
4	545	1874	7560	102	562	223	792
5	88	788	6344	45	998	776	2

B.2 Another Section

Lorem ipsum dolor sit amet, consectetur adipiscing elit. Ut purus elit, vestibulum ut, placerat ac, adipiscing vitae, felis. Curabitur dictum gravida mauris. Nam arcu libero, nonummy eget, consectetur id, vulputate a, magna. Donec vehicula augue eu neque. Pellentesque habitant morbi tristique senectus et netus et malesuada fames ac turpis egestas. Mauris ut leo. Cras viverra metus rhoncus sem. Nulla et lectus vestibulum urna fringilla ultrices. Phasellus eu tellus sit amet tortor gravida placerat. Integer sapien est, iaculis in, pretium quis, viverra ac, nunc. Praesent eget sem vel leo ultrices bibendum. Aenean faucibus. Morbi dolor nulla, malesuada eu, pulvinar at, mollis ac, nulla. Curabitur auctor semper nulla. Donec varius orci eget risus. Duis nibh mi, congue eu, accumsan eleifend, sagittis quis, diam. Duis eget orci sit amet orci dignissim rutrum.

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B.2.1 Another Subsection

Nulla malesuada porttitor diam. Donec felis erat, congue non, volutpat at, tincidunt tristique, libero. Vivamus viverra fermentum felis. Donec nonummy pellentesque ante. Phasellus adipiscing semper elit. Proin fermentum massa ac quam. Sed diam turpis, molestie vitae, placerat a, molestie nec, leo. Maecenas lacinia. Nam ipsum ligula, eleifend at, accumsan nec, suscipit a, ipsum. Morbi blandit ligula feugiat magna. Nunc eleifend consequat lorem. Sed lacinia nulla vitae enim. Pellentesque tincidunt purus vel magna. Integer non enim. Praesent euismod nunc eu purus. Donec bibendum quam in tellus. Nullam cursus pulvinar lectus. Donec et mi. Nam vulputate metus eu enim. Vestibulum pellentesque felis eu massa.

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Fusce mauris. Vestibulum luctus nibh at lectus. Sed bibendum, nulla a faucibus semper, leo velit ultricies tellus, ac venenatis arcu wisi vel nisl. Vestibulum diam. Aliquam pellentesque, augue quis sagittis posuere, turpis lacus congue quam, in hendrerit risus eros eget felis. Maecenas eget erat in sapien mattis porttitor. Vestibulum porttitor. Nulla facilisi. Sed a turpis eu lacus commodo facilisis. Morbi fringilla, wisi in dignissim interdum, justo lectus sagittis dui, et vehicula libero dui cursus dui. Mauris tempor ligula sed lacus. Duis cursus enim ut augue. Cras ac magna. Cras nulla. Nulla egestas. Curabitur a leo. Quisque egestas wisi eget nunc. Nam feugiat lacus vel est. Curabitur consectetur.

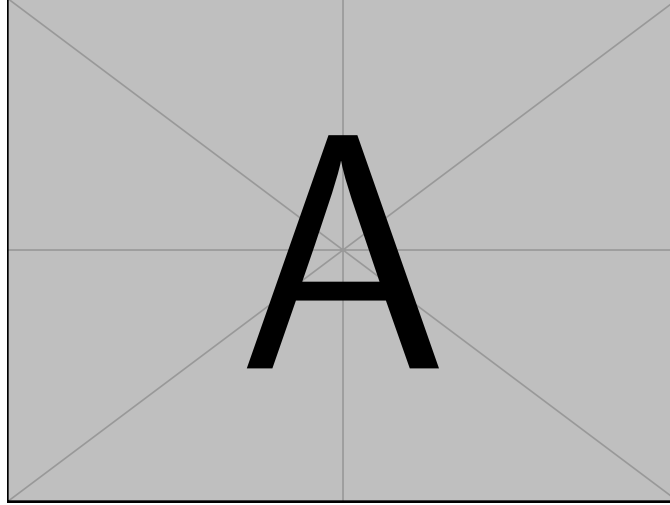


Figure B.3: *This is the caption for an image.*

B.2.1.1 A Sub-Subsection

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Sed commodo posuere pede. Mauris ut est. Ut quis purus. Sed ac odio. Sed vehicula hendrerit sem. Duis non odio. Morbi ut dui. Sed accumsan risus eget odio. In hac habitasse platea dictumst. Pellentesque non elit. Fusce sed justo eu urna porta tincidunt. Mauris felis odio, sollicitudin sed, volutpat a, ornare ac, erat. Morbi quis dolor. Donec pellentesque, erat ac sagittis semper, nunc dui lobortis purus, quis congue purus metus ultricies tellus. Proin et quam. Class aptent taciti sociosqu ad litora torquent per conubia nostra, per inceptos hymenaeos. Praesent sapien turpis, fermentum vel, eleifend faucibus, vehicula eu, lacus.

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Sed neque lectus, consectetur at, consectetur sed, eleifend ac, lectus. Nulla facilisi.
Pellentesque eget lectus. Proin eu metus. Sed porttitor. In hac habitasse platea
dictumst. Suspendisse eu lectus. Ut mi mi, lacinia sit amet, placerat et, mollis vitae,
dui. Sed ante tellus, tristique ut, iaculis eu, malesuada ac, dui. Mauris nibh leo,
facilisis non, adipiscing quis, ultrices a, dui.

Appendix C

CODE EXAMPLES

The following code listings are to demonstrate how code could be included in an appendix.

Code Listing C.1: fibonacci.py

```
def fibonacci(n: int) -> int:
    """This function returns the nth Fibonacci number."""
    if n == 0 or n == 1:
        return n
    else:
        return fibonacci(n-1) + fibonacci(n-2)
```

Code Listing C.2: incmatrix.py

```
import numpy as np

def incmatrix(genl1, genl2):
    m = len(genl1)
    n = len(genl2)
    M = None #to become the incidence matrix
    VT = np.zeros((n*m,1), int) #dummy variable

    #compute the bitwise xor matrix
    M1 = bitxormatrix(genl1)
    M2 = np.triu(bitxormatrix(genl2),1)

    for i in range(m-1):
        for j in range(i+1, m):
            [r,c] = np.where(M2 == M1[i,j])
            for k in range(len(r)):
                VT[(i)*n + r[k]] = 1;
                VT[(i)*n + c[k]] = 1;
                VT[(j)*n + r[k]] = 1;
                VT[(j)*n + c[k]] = 1;

            if M is None:
                M = np.copy(VT)
```



```
    else:
        M = np.concatenate((M, VT), 1)

    VT = np.zeros((n*m,1), int)

    return M
```
