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Migration of the Butterfly *Panacea prola* (Nymphalidae: Biblidinae) in the Southeastern Peruvian Amazon

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Received: 12 September 2025 | **Revised:** 11 June 2026 | **Accepted:** 17 August 2026

Associate Editor: Francis Brearley | **Handling Editor:** Irene Gélvez-Zúñiga

Keywords: Amazonia | dry season | insect | Lepidoptera | Neotropics | Peru | seasonality

ABSTRACT

Insect migrations rival those of vertebrates in terms of numbers of migrating individuals and even biomass, although instances of the former are poorly documented relative to their share of global biodiversity. This is especially true in the world's tropics, which harbor most of Earth's insect species. Understanding these mass movements is of critical and increasing importance as global climate and land use change accelerate and interact to alter the environmental factors that underly migration, particularly in the tropics. In this study we tested whether *Panacea prola*, a butterfly species found throughout the western Amazon and adjacent Andean foothills, was migratory at a site in lowland southeastern Peru. We show, through direct observation of flight behavior, that *P. prola* migrated annually between 2021 and 2025 during the dry season at the study site. We further show that the flight path of migrating *P. prola* butterflies is nonrandom and roughly northeast, leading toward the central Amazon basin. The discovery of a previously undocumented migration in a widespread and conspicuous butterfly is an important contribution to our currently poor knowledge of insect migration in the Amazon, the world's largest and most biodiverse tropical forest.

RESUMEN

Las migraciones de insectos se pueden equiparar con las de los vertebrados en términos de número de individuos migratorios e incluso de biomasa, aunque en el caso de los insectos, la migración está poco documentada comparada con su proporción de la biodiversidad global. Esto ocurre especialmente en los trópicos, los cuales albergan la mayor parte de las especies de insectos del planeta. Comprender estos movimientos masivos es de importancia crítica a medida que el cambio climático y el cambio en el uso del suelo incrementan e interactúan para alterar los factores ambientales subyacentes a las migraciones, particularmente en los trópicos. En este estudio, evaluamos si *Panacea prola*, una especie de mariposa presente en la Amazonía occidental y las estribaciones andinas adyacentes, era migratoria en un sitio de tierras bajas del sureste de Perú. Se demostró, mediante la observación directa del comportamiento de vuelo, que *P. prola* migró anualmente entre 2021 y 2025 durante la estación seca en el sitio de estudio. Además, se observó que la ruta de vuelo de las mariposas migratorias no es aleatoria y se dirige aproximadamente hacia el noreste, en dirección al centro de la cuenca amazónica. El descubrimiento de una migración previamente no documentada de una mariposa amazónica ampliamente distribuida y conspicua es una contribución importante a nuestro conocimiento sobre la migración de insectos en la Amazonía, el bosque tropical más grande y con mayor biodiversidad del mundo.

1 | Introduction

Migration has been documented across a wide variety of species in most of the world's major biogeographic regions (Dingle 2014). Many insects have been shown to be migratory to date; however, migration in these organisms remains poorly documented relative to their proportion of global biodiversity (Chapman et al. 2015). This is particularly true in the tropics, which harbor the majority of the world's insect species (Stork 2018). A review of butterfly migration by Chowdhury et al. (2021), for instance, showed that no more than 8% of described butterfly species in any of the world's tropical regions have been documented to be migratory; in the Neotropics, which is the world's most species-rich region, the number was only about 2%. By comparison, roughly 12% of butterfly species in the Holarctic region were reported as migratory. Given the overall scarcity of biological research in the tropics (e.g., Barlow et al. 2018; Martin et al. 2012), as well as the extreme diversity of tropical insects, it is likely that many tropical migratory insect species await discovery.

Improving our understanding of migration in tropical insects is important for multiple reasons. First, although individual insects are relatively small, they migrate in such large numbers that the total biomass displaced during a migration can far exceed that of birds or even large mammals (Holland et al. 2006). Massive movements of individual organisms and biomass have important implications for food webs and other ecological processes such as decomposition, herbivory and control of herbivore pests, and pollination (Satterfield et al. 2020), as well as biogeochemical cycles (Green 2011; Landry and Parrott 2016), of which we generally know very little in the tropics. Second, the accelerating and interacting impacts of land use and climate change are altering tropical climates (Franco et al. 2025) and possibly also the environmental variables that serve as underlying drivers and cues for migration, such as temperature and other meteorological factors (Chapman et al. 2015; Shaw 2016). Thus, without even knowledge of whether most tropical insects migrate, we cannot evaluate the ecological importance of their mass movements or how human disturbance might alter them.

The Amazon is the world's largest and most biodiverse tropical forest (ter Steege et al. 2013), yet only a relative handful of migratory Amazonian insect species have been documented. To date and to our knowledge, these include only butterflies (e.g., *Catospila* spp. [Pieridae], Williams 1930; multiple species in the families Nymphalidae, Pieridae, and Hesperiidae, as well as one species each of Riodinidae and Papilionidae, Oliveira 1990). To help fill this major knowledge gap, in this study we explored whether the butterfly *Panacea prola* (Doubleday [1848]) was migratory at a lowland Amazonian site in southeastern Peru. Specifically, we conducted counts of *P. prola* butterflies displaying migratory flight behavior across a 5-year period at the site to test whether migration occurred annually and to evaluate when annual peaks in migratory individuals occurred. We also tested whether the mean flight direction of migratory *P. prola* butterflies was nonrandom during each year of the study period.

2 | Methods

2.1 | Study Site

This study was conducted at Finca Las Piedras (FLP), a 74-ha field station located in Peru's Madre de Dios department, in the country's southeastern Amazonian lowlands (12°13′33″ S, 69°06′57″ W; 240 m a.s.l.; Figure S1). This region lies in the extreme southwestern portion of the Amazon basin and is marked by a strong dry season from approximately May through September, during which < 100 mm of rain falls per month (based on daily measurements at FLP, see Fortier et al. 2025 for details; Figure S2). Finca Las Piedras is located near the recently completed Interoceanic Highway, in an area of extensive upland or "terra firme" forest dominated by Brazil nut (*Bertholletia excelsa*: Lecythidaceae) and other hardwood species (Fortier et al. 2025). Deforestation has occurred immediately adjacent to the highway since its completion ca. 15 years ago, but forest cover remains otherwise mostly intact in the study area (Sánchez-Cuervo et al. 2020).

2.2 | Study Species

Panacea prola is distributed widely throughout the western Amazon and adjacent Andean foothills, from Venezuela south to Bolivia (GBIF.org 2025). It is strikingly colored both dorsally and ventrally, with bright red coloration on the ventral hindwings that easily distinguishes it in flight from its otherwise superficially similar congeners and other butterfly species (Figure S3). Although no detailed, long-term published records exist for *P. prola* in the study region, its abundance appears to peak at FLP during the annual dry season and the species is nearly absent during the wet season based on an ongoing, multiyear butterfly trapping study conducted at the site (G. Gallice, unpublished data). Panacea species feed on trees in the genus *Caryodendron* (Euphorbiaceae) throughout Central and South America (DeVries et al. 1999; Montoya Gaviria 1991), and *P. prola* is known in northern Peru to feed on *Caryodendron orinocense* (Vásquez et al. 2012). *Caryodendron orinocense* is known from forest inventory plots in southeastern Peru but appears to be more common and widespread in Amazonian forests of northern Peru, Ecuador, and Colombia (e.g., Benítez et al. 2023), where it is also cultivated for its fruits' high essential fatty acid content (Alfaro and de Padilla 1994). The host plant of *P. prola*, whether *C. orinocense* or another species, remains undocumented in the study region.

2.3 | Flight Behavior

Counts of migratory *P. prola* butterflies and the estimation of individual butterfly flight directions were conducted annually during the dry seasons of 2021–2025. Counts were performed by an observer positioned in the NW corner of a ca. 0.5-ha clearing within a larger area of regenerating secondary forest at FLP (subsequently, the "flight arena") and facing approximately southeast. This position was chosen to orient the observer's field of vision perpendicular to the overall flight path so that butterflies were clearly visible crossing the flight arena. Butterflies

were considered migratory and thus counted if they displayed sustained, directional flight across the entire arena. To estimate individual butterflies' flight directions, a second observer positioned in the flight arena used a magnetic compass to take vanishing bearings of migratory butterflies as they flew overhead into the distance, away from the observer. Flight bearings for individual butterflies were corrected for magnetic declination based on the World Magnetic Model (Chulliat et al. 2020).

To capture the start of the migration each year, an observer watched for migratory *P. prola* in the flight arena daily from 1200 to 1230 h, starting in approximately June (the exact date depended each year on the availability of field assistants). When the first migratory butterfly was observed, count sessions were immediately extended to 1200–1300 h, and any migratory butterflies observed in this initial session were counted. The period 1200–1300 h was chosen for logistical reasons and because it appeared to roughly coincide with migrating butterflies' peak daily activity based on previous observations (G. Gallice, unpublished data).

Daily counts continued after the observation of the first migratory butterfly each year and were halted after counting no individuals for 10 consecutive days, with the exception of 2023, during which counts were reinitiated after a second "wave" of migrating butterflies was observed.

Rayleigh tests were used to test for nonuniformity of *P. prola* flight directions. All data analysis was conducted using the RStudio software (R Core Team 2025).

3 | Results

P. prola butterflies displayed migratory flight behavior, as well as migratory peaks, during all 5 years of the study (Figure 1). The migratory peak, or the maximum number of migratory butterflies observed during a daily 1-h count session for a year, occurred between 20 July (2023) and 16 September (2022) (mean calendar date = 10 August), and varied from 7 (2021) to 116 (2022) butterflies per hour (mean = 56.6, SD = 51.7). The year 2023 was unique in that two migratory peaks of similar magnitude occurred (Figure 1). See Table S1 for detailed information on migrating butterflies across the study period, including dates and magnitudes of migratory peaks for all years.

Rayleigh tests for mean circular direction for migrating *P. prola* butterflies were significant for all 5 years (2021: $N = 48$, $Z = 29.2$, $p < 0.0001$; 2022: $N = 313$, $Z = 214$, $p < 0.0001$; 2023: $N = 153$, $Z = 53.2$, $p < 0.0001$; 2024: $N = 478$, $Z = 232$, $p < 0.0001$; 2025: $N = 91$, $Z = 64.2$, $p < 0.0001$), indicating that mean flight directions each year were nonrandom. The mean magnetic declination-corrected flight directions for 2021–2025 were 62.1° ($N = 48$, SD = 40.3), 64.8° ($N = 313$, SD = 35.4), 45.0° ($N = 153$, SD = 58.9), 37.2° ($N = 478$, SD = 48.7), and 31.9° ($N = 91$, SD = 33.8), respectively (Figure 2).

4 | Discussion

In this study, we present empirical evidence of an annual migration for the Amazonian butterfly *P. prola* across a 5-year study period at a single site in southeastern Peru. This is an important contribution to our knowledge of insect migration in this ecosystem, where very few migratory species have been documented to date.

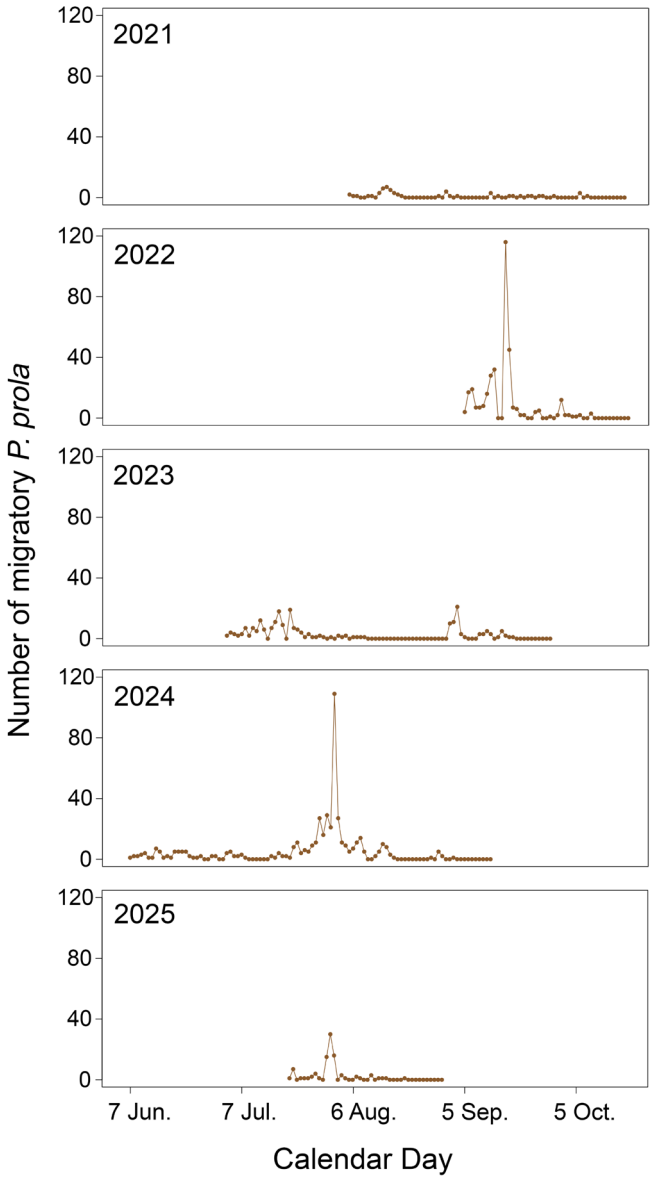

FIGURE 1 | Daily counts of migratory *Panacea prola* butterflies at the study site Finca Las Piedras in southeastern Peru during the dry seasons of 2021–2025.

An obvious question that stems from our findings relates to the geographic extent of the *P. prola* migratory behavior observed in this study. This has important implications for estimating the total number of individuals involved in the annual mass movement, and thus the total biomass displaced and its broader ecological implications. We have anecdotal evidence of similar migratory behavior in *P. prola* as far as ca. 200 km northwest of the study site in southeastern Peru (G. Gallice, Z. Escalante-Arteaga, and J. See, personal observation); however, much more work is needed to answer this question considering the species' large geographic range.

Clarifying the spatial extent of the observed migration would also open the door to exploring potential drivers of the observed

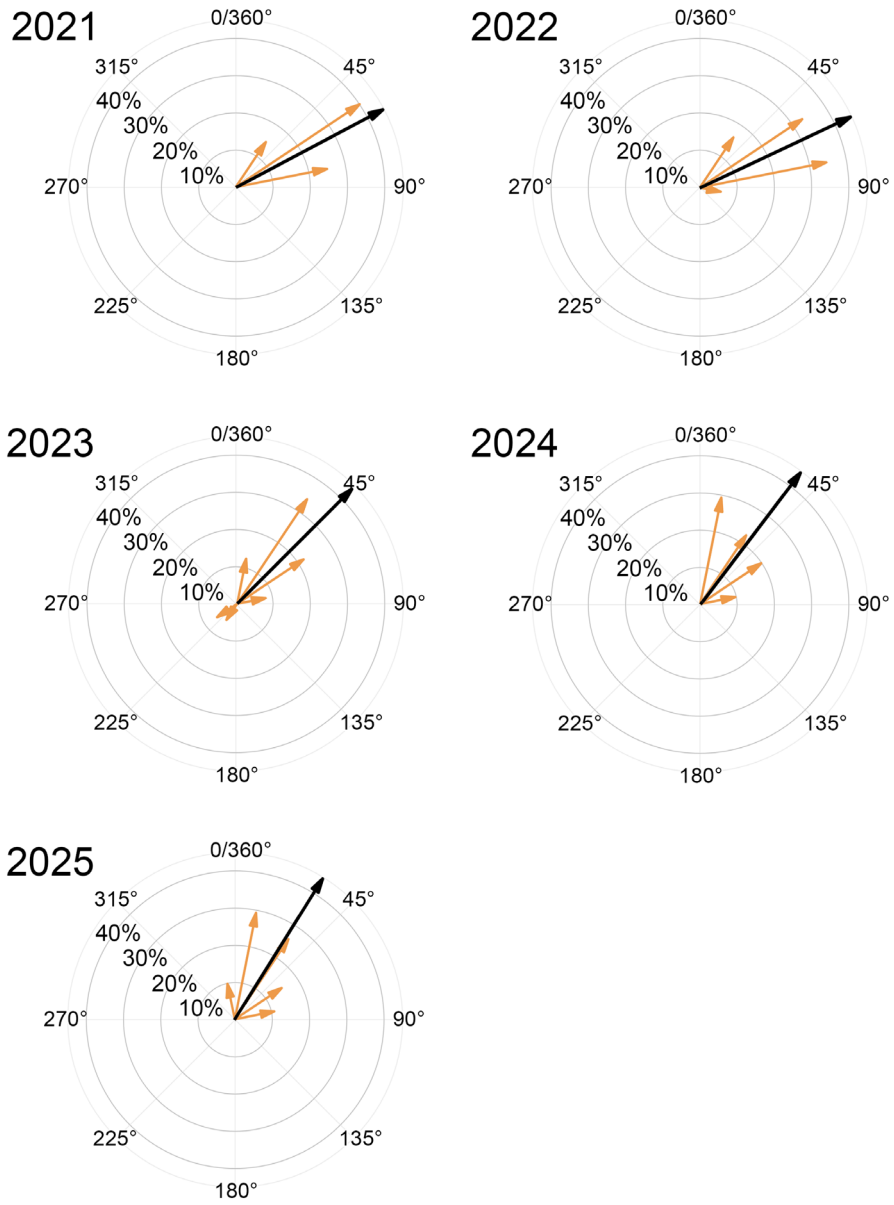

FIGURE 2 | Flight directions for migratory *Panacea prola* butterflies at Finca Las Piedras during the dry seasons of 2021–2025. The percentage of total observations of *P. prola* flight directions in 22.5 degree-wide bins for a year are represented by light brown arrows; bins containing < 5% of total observations for a year are left blank. Mean flight directions of migratory butterflies for all years are represented by thick black arrows.

migration such as seasonality and gradients in key climatic variables, which are pronounced in the study region and across the Amazon basin and adjacent Andean foothills (Sombroek 2001; Michot et al. 2024). Knowledge of the host plant of *P. prola* in the study region, including its distribution and phenology, would allow for the further refinement and testing of hypotheses explaining the observed migration. For example, in a study of the Neotropical migratory butterfly *Aphrissa statira* (Cramer, 1777) in Panama, Srygley et al. (2010) showed that peak migratory behavior was related to dry season leaf flushing of the species' host plant across the Panamanian isthmus. Our results showing an annual peak in migrating individuals and similar mean flight directions across years are consistent with that study, suggesting that *P. prola* might similarly migrate due to spatial or temporal variation in the availability of its presumed host plant *C. orinocense*. However, very little is known about the ecology of *C. orinocense* in southeastern Peru, or even whether it is used by *P. prola* as a host here. Therefore, a detailed hypothesis explaining the migration observed in this study would be highly speculative at present.

The Amazon is experiencing unprecedented deforestation and forest degradation driven largely by expanding road networks and other large-scale infrastructure development (Gallice et al. 2019; Laurance et al. 2001, 2009). These impacts are compounded by global climate change which, according to some projections, may prolong the Amazonian dry season and increase forest loss through dieback and other proximate causes such as intensifying anthropogenic fire (Malhi et al. 2009; Ritchie et al. 2022). Migratory insects may be impacted by these changes, for instance if important host plant resources are lost or if the environmental cues that trigger migration are altered (Shaw 2016). To evaluate future threats, information regarding the spatial extent of the migration of *P. prola* and the species'

host plant use throughout its range could be employed with predictive modeling under future climate and land use scenarios.

The discovery of a previously unrecognized migration in a common, widespread, and highly conspicuous Amazonian butterfly raises the additional question of whether there are other migratory species in this ecosystem that remain to be documented. Given the Amazon's size and high species richness, the current paucity of confirmed migratory insects here likely reflects the fact that most Amazonian species have simply not been evaluated. Given this, as well as the potential threats outlined above, we close in urging that further work be done to identify other migratory Amazonian insect species, as well as the factors underlying their migrations, to inform the conservation of these organisms in the rapidly changing Amazon.

Author Contributions

G.G. conceptualized the study, performed the data analysis, and wrote the paper. J.S. assisted with conceptualization and in data collection. Z.E.-A., Y.V., and T.C.-E. collected data and supervised data collection by field assistants. All authors contributed to the review and editing of the final paper.

Acknowledgments

The authors would like to thank Vicencio Oostra and several anonymous reviewers for providing useful feedback on the manuscript, Shawan Chowdhury for helpful feedback and for providing references, and the numerous research assistants who helped with data collection at Finca Las Piedras. We also thank Wild Green Future for partial financial support of the Alliance for a Sustainable Amazon's Lepidoptera Diversity and Biology Project, CONCYTEC through the PROCIENCIA program under the call "Proyectos de Investigación Básica 2023-1" (contract no. PE501082173-2023), and Peru's Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) for granting permission to conduct the field research (permit no. D000443-2021-MIDAGRI-SERFOR-DGGSPFFS).

Funding

This work was supported by Wild Green Future and by CONCYTEC through the PROCIENCIA program under the call "Proyectos de Investigación Básica 2023-1" (contract no. PE501082173-2023).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.17109335.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Map of the study region and overall flight path of observed migratory *Panacea prola* butterflies between 2021 and 2025 at the study site Finca Las Piedras in southeastern Peru. **Figure S2:** Precipitation at the study site Finca Las Piedras in southeastern Peru. (a) Daily precipitation (mm) from 1 January 2021 to 31 August 2025. *X*-axis labels at first day of each listed month. (b) Average monthly precipitation (mm), 2021–2024. **Figure S3:** The study species, *Panacea prola*. (A) Dorsal view. (B) Ventral view. Black scale bar at bottom right = 1 cm. **Table S1:** Key dates and numbers of migrating *Panacea prola* butterflies counted during daily 1-h observation sessions during the dry seasons of 2021–2025 at the study site Finca Las Piedras in southeastern Peru. Migration start date is the date on which the first migratory *P. prola* was counted; migration end date is the date after which no individuals were counted for 10 consecutive days. Peak number of migratory butterflies is the maximum number of migratory individuals counted during daily sessions for a given year.