Zoological Studies **64:**19 (2025)

First Description of Female and Larva of *Phyllocycla basidenta* Dunkle, 1987 (Anisoptera: Gomphidae), and Ecological Niche Modeling of *Phyllocycla* species in Northwestern Argentina

Carlos Molineri[1],*, José S. Rodríguez[1], and Carolina Nieto[1]

*[1]Instituto de Biodiversidad Neotropical (IBN), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán, Yerba Buena, Tucumán, Argentina. *Correspondence: E-mail: carlosmolineri@gmail.com (Molineri)*
E-mail: josephum@hotmail.com (Rodriguez); carolinanieto@gmail.com (Nieto)

(Received 8 November 2024 / Accepted 6 April 2025 / Published -- 2025)
Communicated byJen-Pan Huang

ORCiD
Carlos Molineri https://orcid.org/0000-0003-2662-624X
José S. Rodríguez https://orcid.org/0000-0002-8917-2882
Carolina Nieto https://orcid.org/0000-0003-1909-1750

We present the first description of female adult and larva of *Phyllocycla basidenta* Dunkle 1987 (Anisoptera: Gomphidae), collected in northwestern Argentina. The female and larva are described in detail, with diagnostic features that differentiate *P. basidenta* from other species like *P. argentina* and *P. viridipleuris*. Larvae of *P. basidenta* inhabit sandy-bottomed rivers alongside *P. argentina*. Additionally, we predict the potential distribution of both species using Ecological Niche Models under current and future climate scenarios. The models suggest that suitable habitats may shift to higher altitudes under moderate climate change, but significant losses are expected under severe warming scenarios. Climate change may threaten *Phyllocycla basidenta* and *P. argentina* as its suitable habitats could shift to higher elevations. Conservation strategies should prioritize areas projected to become suitable under future conditions.

Keywords: Odonata, club tail dragonfly, *Phyllocycla argentina*, *P. viridipleuris*, Potential distribution, Ecological niche models

Citation: Molineri C, Rodríguez JS, Nieto C. 2025. First description of female and larva of *Phyllocycla basidenta* Dunkle, 1987 (Anisoptera: Gomphidae), and ecological niche modeling of *Phyllocycla* species in northwestern Argentina. Zool Stud **64:**19.

BACKGROUND

Gomphids, or clubtail dragonflies, are powerful fliers often seen patrolling rivers. As adults, they are challenging to capture with aerial nets, leading to the development of alternative techniques, such as modified Malaise traps, to address this limitation (Almeida et al. 2013). The distribution range is a crucial aspect in assessing the conservation status of a species. However, for dragonflies known only from their adult stage, this range is sometimes limited to the type locality and a few scattered locations (Collins and McIntyre 2015). In contrast, their larval stage is much easier to collect, highlighting the need for increased field and laboratory efforts to associate both life stages.

Phyllocycla Calvert, 1948 exemplify this situation: while the large adults are difficult to collect, larvae are commonly encountered in ecological and biodiversity studies (Araújo et al. 2020). Six species of *Phyllocycla* are known to occur in Argentina (Lozano et al. 2020): *Phyllocycla argentina* (Hagen in Selys, 1878), which is widely distributed in the Central, NE, and NW regions; *P. basidenta* Dunkle, 1987, found in Salta and Jujuy in the NW; *P. foliata* Belle, 1988, from Misiones province in the NE; *P. propinqua* Belle, 1972, from Entre Ríos and Misiones in the NE; *P. vesta* Belle, 1972, from Buenos Aires; and *P. viridipleuris* (Calvert, 1909), which is widely distributed in the Central and NE regions, with an unconfirmed record from Salta in the NW.

The larvae of only two of these species have been described: *P. argentina* by Rodrigues Capítulo (1983), and *P. viridipleuris* by Belle (1992). The larval stage of *P. propinqua* is reported in the literature (e.g., Belle 1992; Lozano et al. 2020), but these reports reference Needham's (1940) description under the name *P. viridipleuris* (a misidentification of *P. propinqua* sensu Belle 1992). Needham's description is limited to size and a few brief, uninformative sentences, which are insufficient for species characterization. Additionally, the two exuviae reported were not reared, and their association with adults was based solely on the collection site. Thus, there is no justification for considering this species' larval stage as known.

To aid in evaluating the conservation status of *Phyllocycla* species and knowing the variables important in their spatial occupancy, we aimed to identify all larvae collected in our study region (NW Argentina) to the species level. With this information, combined with known adult ranges, we assessed potential and future changes in species distribution. Ecological niche models (ENMs) have emerged as vital tools for understanding and predicting species distributions (Hassall 2012). By correlating environmental variables with species occurrence data, ENMs can identify areas of suitable habitat under present and future climatic conditions. This approach is particularly important for appreciating potential distribution shifts due to climate change, aiding in the conservation and management of species likely to be impacted by environmental changes (Nava-Bolaños et al. 2021).

Phyllocycla basidenta was originally described from a male adult from Bolivia, with von Ellenrieder and Garrison (2007) later reporting its presence in neighboring areas of NW Argentina. Until now, the female adults and larvae of this species were unknown. We have reared numerous specimens, including both males and females, of *P. argentina* and *P. basidenta* in various localities of NW Argentina. Based on these reared specimens, we were able to associate the female adult and larva of *P. basidenta* with the male adult. Here, we present a comparative description of the previously unknown female adult and larva of this species, along with additional observations and measurements of *P. argentina*. We additionally provide a key to the larvae of the three species known from Argentina, as well as the potential distribution and possible future scenarios for both species.

MATERIALS AND METHODS

Studied material

Adults, larvae and larval exuvia of reared specimen of *Phyllocycla argentina*, *Phyllocycla basidenta*, and *Phyllocycla viridipleuris* were studied (see details in Supplementary Information). Taxonomic work. Larvae were collected using kick nets (1 m width, 0.5 m height, 1 mm pore size) on submerged sand/mud patches in streams and rivers. The larvae of the last instars were transported on wet pieces of filter paper in plastic petri dishes. In the lab, we prepared an aquarium (0.5 m length, 0.4 m width, 0.2 m height) with a sandy substrate and water from the stream. A small aquarium pump ensured water movement and oxygenation. Larvae from the same locality were released into the aquarium until emergence. If necessary, the larvae were fed with benthic macroinvertebrates, mainly Chironomidae and small Ephemeroptera. We placed twigs and macrophytes to facilitate larval emergence. The aquarium was covered with a thin mesh. Each day, we checked for teneral adults and molts. Emerged adults were kept alive for 1–2 days and then preserved in 80% alcohol along with the corresponding exuviae. All material is housed in the Odonatological collection of the Instituto de Biodiversidad Neotropical (IBN, CONICET-UNT, Tucumán, Argentina). For each species, the coordinates are given in decimal format, and dates are recorded as day/month/year. The mandibular formula follows the proposal of Watson (1956).

Photographs were taken with a Zeiss Axiocam ICc5 mounted on a Stemi 508 stereomicroscope. Drawings were made using an Olympus BX51 microscope with a camera lucida.

Potential and future distribution

To minimize the spatial autocorrelation between occurrences, all records in a 5 km radius were filtered and reduced to one (Cobos et al. 2019). 15 occurrence records for *Phyllocycla argentina* and 20 for *Phyllocycla basidenta* were compiled. The databases were split into 50% for training and 50% for testing the analyses. The geographical distributions of both species were estimated through correlative ecological niche modeling (ENM), ENMs establish a connection between species presence records and the environmental variables of specific locations, thereby providing an estimation of environmental suitability (Soberón and Peterson 2005). For each species, the same calibration area was designed along the Southern Yungas, extending from 150 m a.s.l. to 4810 m.a.s.l. The nineteen bioclimatic variables from WorldClim database (Hijmans et al. 2005) were utilized, with a spatial resolution of 30 seconds. The environmental data layers were clipped to the calibration area defined. A selection of variables was performed with correlation analysis to eliminate highly correlated variables ($r \geq 0.80$) using the "ntbox" R package (Osorio-Olvera et al., 2018). For *P. argentina*, eight variables were selected: BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)), BIO3 = Isothermality (BIO2/BIO7), BIO4 = Temperature Seasonality (standard deviation ×100), BIO9 = Mean Temperature of Driest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12= Annual Precipitation, BIO13 = Precipitation of Wettest Month. For *P. basidenta*, twelve variables were selected: the same eight ones mentioned above and BIO7 = Temperature Annual Range (BIO5-BIO6), BIO14 = Precipitation of Driest Month, BIO17 = Precipitation of Driest Quarter, and BIO18 = Precipitation of Warmest Quarter.

The calibration and selection of the best ENMs were made using a maximum entropy method with Maxent v3.4.4. K (Phillips et al. 2006) through the R package "kuenm" (Cobos et al. 2019). Candidate models were obtained by combining four values of regularization multiplier (0.1, 0.5, 1, 2), and all possible combinations of four feature classes (linear = l, quadratic = q, product = p, hinge = h). The candidate model selection and performance were evaluated based on significance (partial ROC, with 100 iterations and 50 percent of data for bootstrapping), omission rates (E = 5%), and model complexity (AICc). The best models were selected according to the following criteria: (1) significant models with (2) omission rates ≤ 5%. Then, from among this model set, models with delta AICc values of ≤ 2 were chosen as final models. The final models were generated by performing five bootstrap replicates with logistic outputs, using the full set of occurrences and the selected parameterizations. To determine the relative contribution of each environmental variable to the final model, we used three methods: percentage contribution, permutation importance and jackknife of regularized training gain.

The final models were applied to the calibration area under future climate scenarios: RCP 2.6 and RCP 8.5 for 2021–2040 and 2081-2100. We employed an ensemble approach with two separate climate models: CMCC-ESM2 and EC-Earth3-Veg. The niche distribution was projected independently for each model. We then averaged the raster outputs from both CMCC-ESM2 and EC-Earth3-Veg for each climate scenario. We used the climatic layers from the Community Climate System Model (CCSM6). Also, we performed a MESS analysis (Multivariate Environmental Similarity Surface, Elith et al. 2010) to identify extrapolation risk areas in model transfers. The MESS can identify areas with large environmental differences, which may be at risk of extrapolation. We used this information to prevent over interpretation of the model outcomes by removing the suitability found in areas of strict extrapolation (Cobos et al. 2019). To obtain binary presence-absence maps for present and future scenarios, 10th percentile threshold was applied, using the "ntbox" package (Osorio-Olvera et al. 2018).

To spatially characterize the distribution of *P. argentina* and *P. basidenta*, the proportion of its distribution along different altitudes in present and future scenarios was quantified. For this, an intersection layer of altitudes was obtained from a global 1-km resolution land surface digital elevation model (DEM) derived from U.S. Geological Survey (USGS) 30 arc-second SRTM30 gridded DEM data created from the NASA Shuttle Radar Topography Mission (SRTM). To assess the extent of protection by the existing protected areas, we overlaid the potential distribution areas predicted by our models onto the protected area maps of Argentina and Bolivia (SERNAP 2023; APN 2024; SIGA 2024).

RESULTS

Phyllocycla basidenta **Dunkle, 1987**

(Figs. 1a–d, 2a–f, 3a, 4a–f, 5a–e)

Male adult (Fig. 1a–d): Total length 45.0–48.0 mm; abdomen 34.0–37.0 mm (incl. app.); hind wing 27.0–28.5 mm; costal edge of pterostigma in fore wing 3.1–3.4 mm. Our material matches original description. Wings with 1 basal subcostal cross-vein. Second primary antenodal cross-vein the 5th to 7th in FW and the 4th to 6th in HW. Pterostigma brownish.

Female adult: Total length 45.5–48.0 mm; abdomen 34.0–34.5 mm (including appendages); hind wing 28.5–30.0 mm; costal edge of pterostigma in fore wing 3.5–3.8 mm. Head mostly brown dorsally, except lateral green spots in postclypeus, and posfrons almost completely green except for a blackish median band (Fig. 2a, b). Labrum, mandibles and labium green. Occipital plate brown with straight hind margin fringed with dark brown setae somewhat shorter than plate length. Occipital plate (Fig. 2a, b) stout not so elongated transversally (the anterior margin is less than 2x the length of the plate at medial line). Thorax. Pronotum brown with green areas laterally. Pterothorax: inner pale stripes on dorsum extending medially but not reaching medial carina at anterior ends (Fig. 2a, c). Coloration of rest of pterothorax and legs as in male description except that for a darker metepimeron (dark green to brownish). Wings, legs and abdomen similar to male. Wings with 1 basal subcostal cross-vein. Second primary antenodal cross-vein the 5th in FW and the 4th to 5th in HW. Pterostigma brownish covering 3 to 6 cells of adjacent wing sector. Inferior lateral margins of abdominal segments 8 and 9 not expanded (Fig. 2d, e). Apical rim not distinctly marked. Length (mean of 3 specimens) of abdominal segments 7 (4.4 mm), 8 (2.7 mm), 9 (1.8 mm), 10 (1.0 mm) and cerci (1.1 mm). Vulvar lamina 0.3 of total length of ninth sternum, hind margin with a deep but broad V-shaped notch about 0.6 the length of vulvar lamina, each distal lobe brownish, rounded and covered with stiff setae (Fig. 2e).

Larval exuviae (last instar, n = 4, Fig 3a): Measurements (in mm, mean of 4 specimens unless indicated): Total length 26.5-29.5 (range); head length 3.1; head width 3.9; abdomen length 18.3; abdominal maximum width 4.1; abdominal segment X length 4.6. Antennomers 1-4 length (mm): 0.3, 0.2, 1.2, 0.3. Prementum length 1.3x maximum width, with convex semicircular ligula, palp robust with relatively slender movable hook (Fig 4c); hook 1.1 mm in length. Mandibular formula (Fig. 4e, f): L1234 0 a(m^{1234})b, R1234 y a(m^{12})b. Maxilla with 6 apical hooks (distal one bifid, Fig 4d). Legs. Burrowing hooks small and blunt on fore and middle tibiae. Length of segments (femur/tibia/tarsus/claw) in mm: fore leg 2.1/2.7/1.2/0.4; middle leg 2.2/2.8/1.2/0.4; hind leg 3.0/3.0/2.1/0.7. Wing sheaths (4.9 mm) reaching anterior 1/3 of abdominal tergum 4. Abdomen 0.7x the length of body, maximum width of abdomen (0.2 x total abdominal length) on segments 3 to 5. Tube-like segment 10, 4.6 mm in length (incl. appendages of 0.6 mm), width at middle of segment 10, 0.9 mm.

Coloration of larva (similar in different stages, n = 3): Head, prothorax and legs paler than the rest of body, mesothorax and abdoment yellowish light brown. Stiff setae on body and legs yellowish translucent. Thorax with a pair of submedian triangular blackish marks on fore margin of mesonotum (Fig. 3a). Abdomen yellowish without dark pigments but a paler median band is present along terga 4–9 (Fig. 3a); abdominal segment 10 slightly darker than previous segments (Fig. 3a).

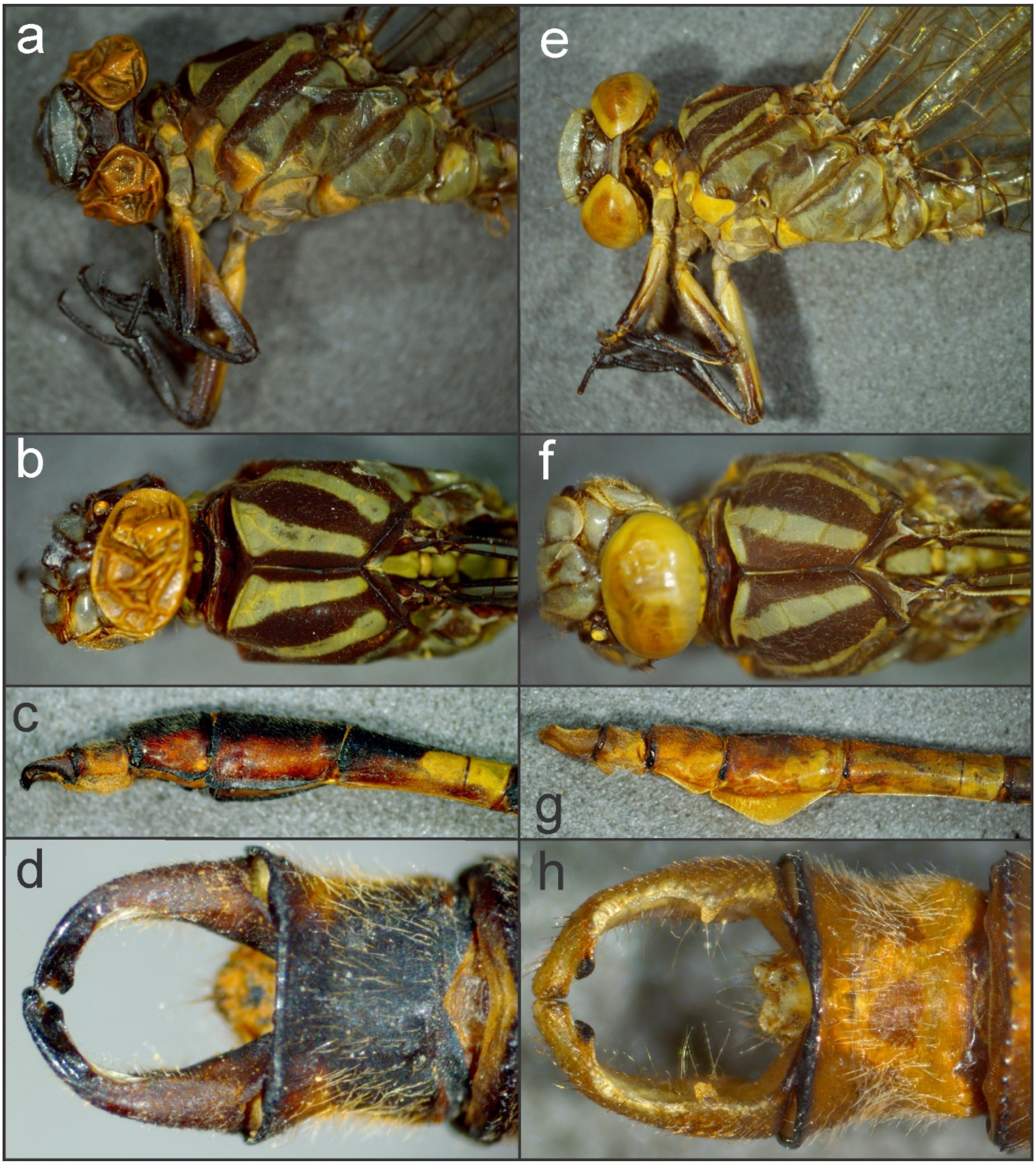

Fig. 1. Male adult, *Phyllocycla basidenta* (male IBN-O-7). a, Head and thorax, l.v.; b, same, thorax in d.v.; c, abdominal segments 7–10, l.v.; d, abdominal segment 10 and cerci, d.v. e–h, *Phyllocycla argentina* (male IBN-O-2). e, Head and thorax, l.v.; f, same, thorax in d.v.; g, abdominal segments 7–10, l.v.; h, abdominal segment 10 and cerci, d.v.

Fig. 2. Female adult. A–F, *Phyllocycla basidenta*. A, Head and thorax, l.v. with detail of FW pterostigma; B, detail of head in d.v.; C, thorax, d.v.; D, abdominal segments 7–10, l.v.; E, abdominal sterna 8-9 and vulvar lamina; F, cerci, v.v. G-L, *Phyllocycla argentina*. G, Head and thorax, l.v. and detail of FW pterostigma; H, detail of head in d.v.; I, Head and thorax in d.v.; J, abdominal segments 7–10, l.v.; K, abdominal sterna 8-9 and vulvar lamina; L, cerci, v.v. Specimens: G, J (IBN-O-25), H–II and K–L (IBN-O-22). Abbrev.: me = metepimeron; op = occipital plate.

Observations: The larva of *P. basidenta* were collected in the same patch of sand with other gomphid larvae, including *Progomphus kimminsis* Belle, 1973, *P. phyllochromus* Ris, 1918 and *Phyllocycla argentina*. Larvae of *Phyllocycla basidenta* and *P. argentina* were found superficially burrowing on fine sediments, including mud and very fine sand, but also on medium to coarse sand. This fine granulometry is more frequent and abundant in streams and rivers from submontane areas, and in NW Argentina both species are present in Chaco and Yungas ecoregions. Female adults are more rarely seen than males, they have been caught with aerial net while ovipositing along the shore. Males patrol along the streams and marginal areas, sometimes perching on stones or marginal vegetation.

Distribution: Bolivia, Argentina (Salta, Jujuy, Tucumán new record).

Diagnosis: Female adult of *P. basidenta* can be distinguished from others in the genus by the combination of the following characters: 1) thoracic color pattern (Fig. 2a, c), 2) absence of lateral dilatation on abdominal segments (Fig. 2d, e), 3) pterostigma brownish covering 3 to 6 cells (Fig. 2a); 4) hind margin of vulvar lamina with a V-shaped notch (Fig. 2e) 0.3 times the length of ninth sternum, and 5) apical rim of segment 10 not differentiated from the remaining of the segment (Fig. 2f). Larva can be distinguished from other known larva in the genus by the following combination: 1) prementum length 1.3 times its width, labial palp and movable hook relatively slender and not pronouncedly curved (Fig. 4c), 2) abdomen with dorsal hooks on terga 3-9 (very small, except on 3–4, Fig. 5e), 3) posterolateral spines on abdominal segments 7-9 (Fig. 5e), 4) abdominal segment 10 relatively stout, ratio length segment 10/total length abdomen = 0.25 (Fig. 3a), 5) small submedian blackish triangular marks anteriorly to wing sheaths (Fig. 3a), abdomen without dark pigments but with paler mediolongitudinal band on segments 4–9 (Fig. 3a).

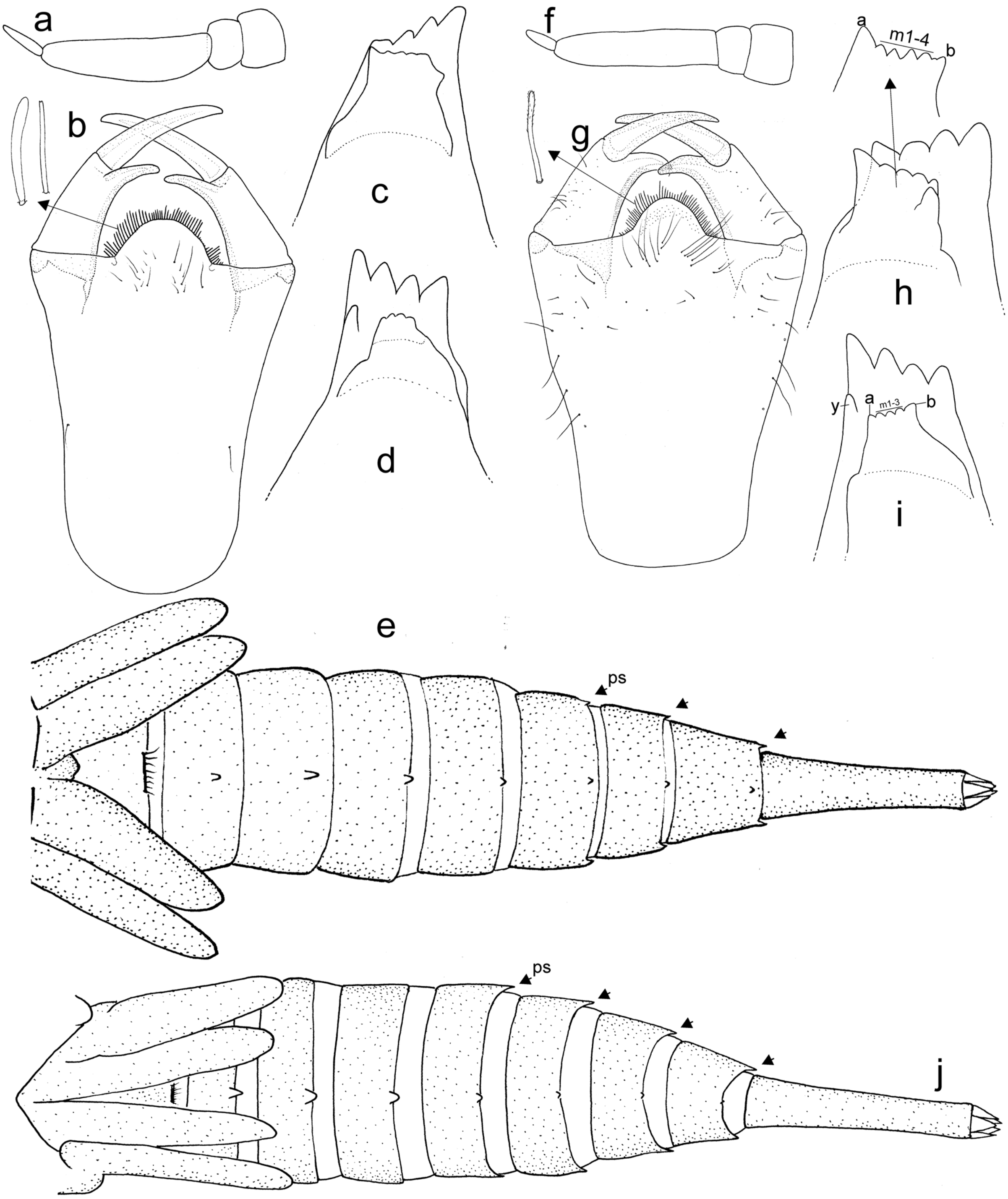

Fig. 3. Larval habitus, dorsal. A, *Phyllocycla basidenta*; B, *P. argentina*.

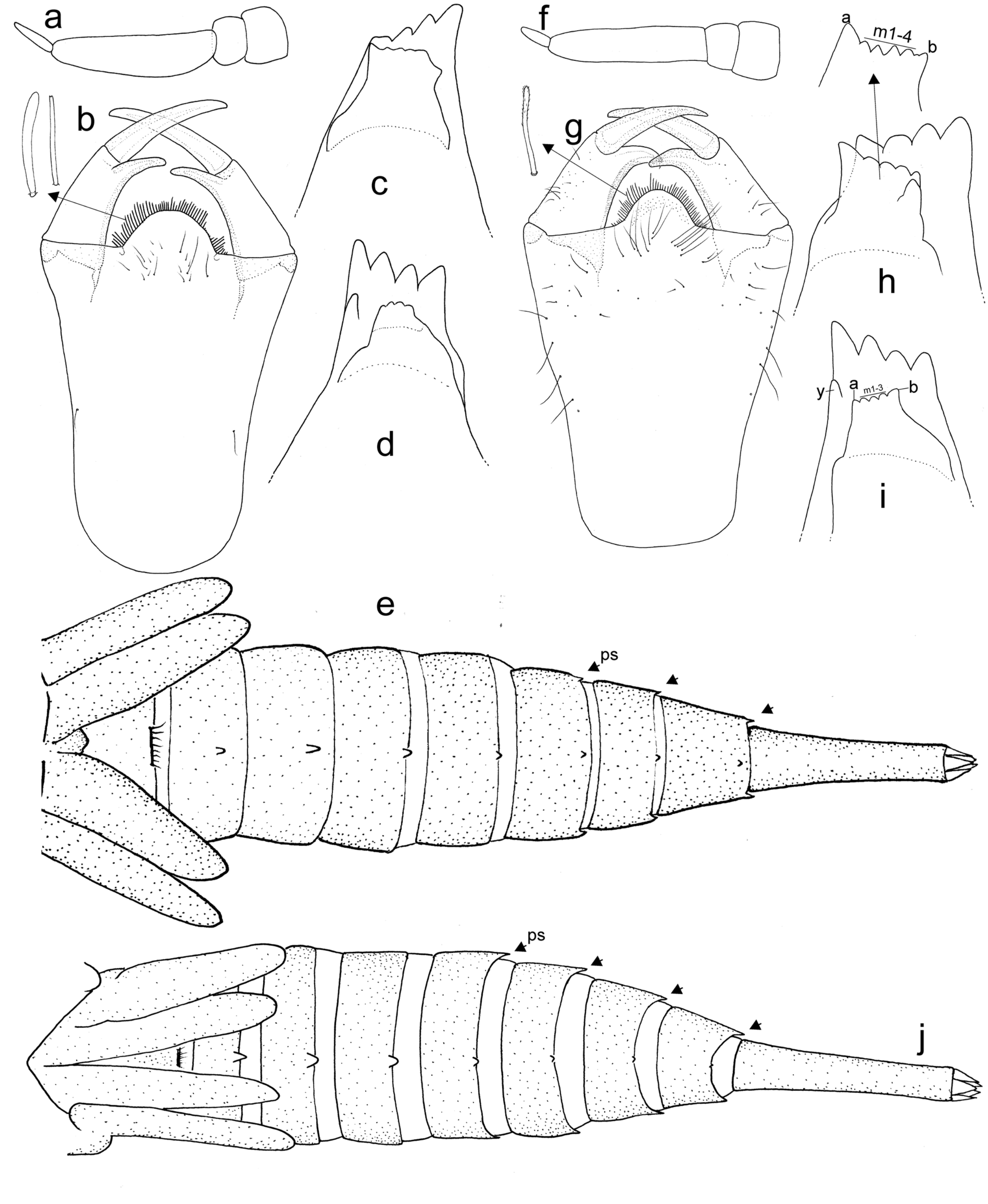

Fig. 4. A–F, *Phyllocycla basidenta*, male exuvia. A, habitus, d.v.; B, antennae, l.v.; C, prementum, v.v.; D, maxilla, v.v.; E, left mandible v.v.; F, right mandible, v.v. Abbreviations: ps = posterolateral spine.

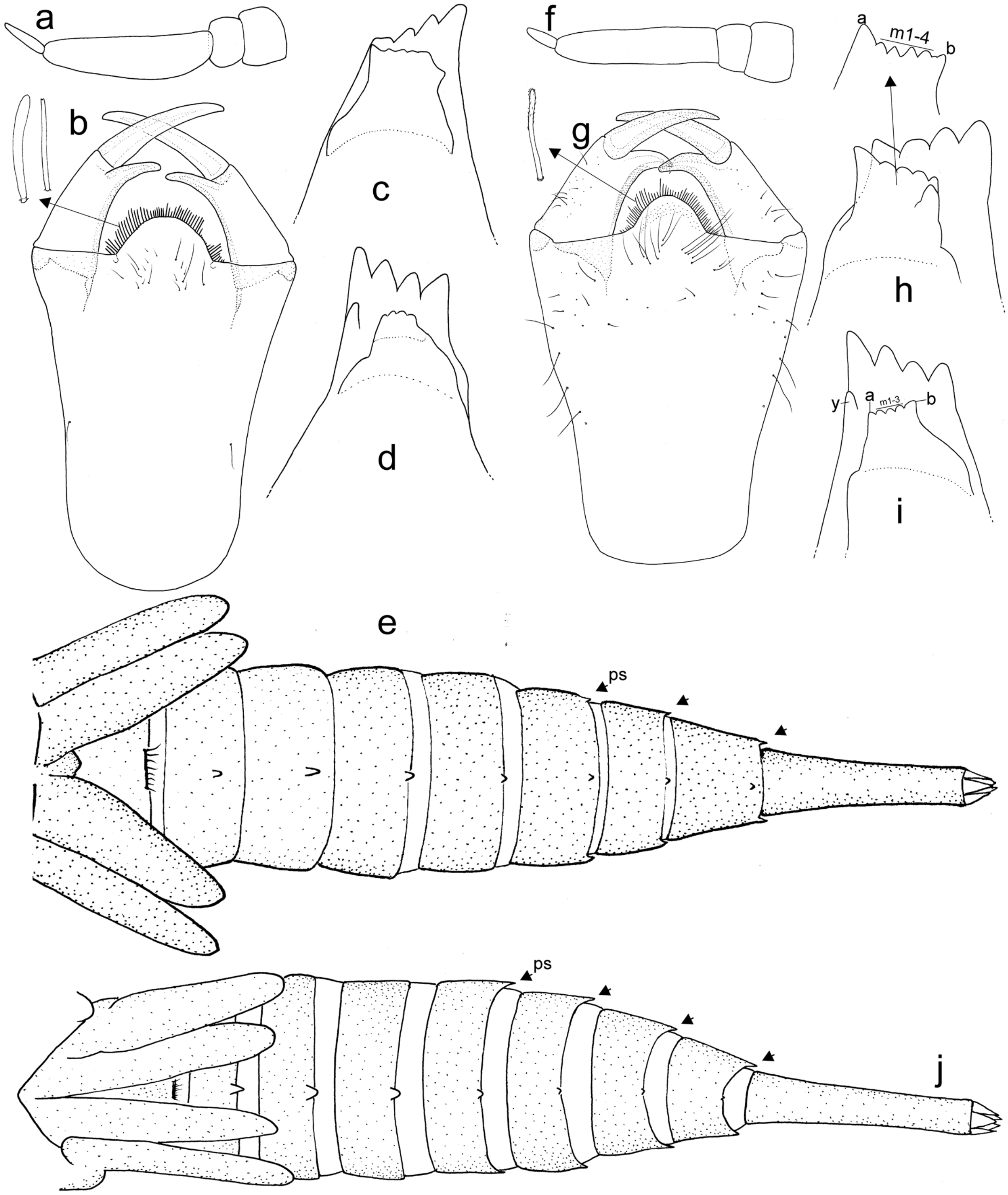

Fig. 5. A–E, *Phyllocycla basidenta*. A, antennae l.v.; B, prementum with detail of rigid setae on ligula; C, left mandible with detail of molar (occlusal view); D, right mandible (occlusal view); E, abdomen, d.v. Figs. F–J, *P. argentina*. F, antennae l.v.; G, prementum with detail of rigid setae on ligula; H, left mandible with detail of molar (occlusal view); I, right mandible (occlusal view); J, abdomen, d.v. Abbreviations: ps = posterolateral spine.

Phyllocycla argentina (Hagen in Selys, 1878)

(Figs. 1e–h, 2g–l, 3b, 5f–j)

Male adult (Figs 1e–h): Total length 50.0-55.0 mm; abdomen 38.0–42.0 mm (incl. app.); hind wing 30.0–32.0 mm; costal edge of pterostigma in fore wing 4.5–4.6 mm. Wings with 1 basal subcostal cross-vein. Second primary antenodal cross-vein the 4th to 6th in both wings.

Female adult: Total length 46.2–52.0 mm; abdomen 35.0–40.0 mm (incl. app.); hind wing 29.2-33.0 mm; costal edge of pterostigma in fore wing 4.3–4.6 mm. Length (mean of 3 specimens) of abdominal segments 7 (4.3 mm), 8 (2.7 mm), 9 (1.8 mm), 10 (1.05 mm) and cerci (1.3 mm). Occipital plate (Fig. 2g–i) elongated transversally (the anterior margin is about 3x the length of the plate at medial line). Pterothorax laterally pale (Fig. 2g), metepimeron pale (yellowish to light brown). Pterostigma yellowish covering 5 to 7 cells of adjacent wing sector (Fig. 2g). Wings with 1 basal subcostal cross-vein. Second primary antenodal cross-vein the 6th or 7th in FW and the 5th to 6th in HW. Vulvar lamina 0.2 of total length of ninth sternum, hind margin with a broad U-shaped (some specimens with a V-shaped) notch about 0.5 the length of vulvar lamina, each distal lobe yellowish to light brown, rounded and covered with stiff setae (Fig. 2k).

Larval exuviae (last instar, Figs 5f–j): Measurements (mm, n = 3): Total length 31.3–33.5; head length 3.3; head width 4.1; abdomen length 22.7; abdominal maximum width 4.5 (located on segments 3-4); abdominal segment X length 6.1. Mandibular formula (Fig. 5h, i): L1234 0 a(m^{1234})b, R1234 y a(m^{123})b.

Coloration of larva (similar in different stages): yellowish to yellowish light brown with blackish to dark brownish submedian marks (Fig. 3b) on abdominal terga 5–9 (some specimens with marks also on 3–4). Abdominal segment 10 with brownish pigments on basal 1/3.

Observations: Figures presented by Belle (1970) from a male adult from Buenos Aires province (Argentina) previously studied by Ris (1913) show a subdistal dorsal spine basally to the subdistal protuberance on cercus. In all the material we have studied except one cercus of a male from Jujuy (Rio Zora), this spine is absent, as was also reported by Rodrigues Capítulo (1983). Another difference observed on our material is that lateral flap on segment 10 is absent in our males (present and pointed in Belle, 1970).

The larvae of *P. argentina* described by Rodrigues-Capitulo (1983) from Córdoba are similar to our larvae relating dorsal median tubercles of abdomen (in both they are relatively thin and better visible on terga 3–5). Nevertheless, our material shows that median dorsal hooks are present through segments 3 to 9 (on segment 2 it takes the form of a short transverse ridge covered by long setae), on segments 6–9 it is small and spine-like (so small that frequently is covered by mud adhered on surrounding setae). Also, our larvae present an additional m denticle on right mandible in relation to what this author reported.

Distribution: Argentina (Salta, Jujuy, Tucumán, Santiago, Córdoba, Misiones, Corrientes, Entre Rios, Santa Fe, Buenos Aires), Brazil (Rio Grande do Sul, Parana), Uruguay.

Key to larva of Phyllocycla known from Argentina

(*P. propinqua* Belle, 1972, *P. vesta* Belle, 1972 and *P. foliata* Belle, 1988 are not known in the nymphal stage).

1. Abdomen with small lateral spines on segments 6-9 (Fig. 5j) ……………………… *P. argentina*
- Abdomen with small lateral spines on segments 7-9 (Fig. 5e) …………………………………… 2
2(1). Tubular abdominal segment 10 relatively stout, 0.25 x total length of abdomen (Fig. 3a) ……………………………………………………………………………… *P. basidenta*
- Tubular abdominal segment 10 long and slender, 0.37 x total length of abdomen (Fig. 40 in Belle 1992) ……………………………………………………………………… *P. viridipleuris*

Estimations of ecological niche modeling

Phyllocycla basidenta. We fitted 124 candidate models for this species (Table S1). Seven models met AICc criteria but none met the criteria for omission rate (with an omission rate less than or equal to 5%). We selected the model linear, product and threshold feature classes and regularization multiplier of 2.0. The model´s performance was better than random (AUC = 0.964). The most significant variables were mean diurnal temperature range, and isothermallity (Table S2). The response curve indicated a negative relationship between suitability for both variables (Fig. S1). The variables precipitation of warmest quarter, mean temperature of coldest quarter, precipitation of driest quarter, mean temperature of driest quarter and temperature annual range had less contribution, while temperature seasonality, precipitation of wettest month, annual mean temperature, precipitation of driest month and annual precipitation had minimal contribution (Table S2).

The suitable area for *P. basidenta* spans along Southern Andean Yungas and Dry Chaco (7968365 km^2) as an almost continuous patch, from 200 to 2360 m a.s.l (Fig. S2). Based on binary maps (Fig. 6), all scenarios (except the 2081–2100 scenario under RCP 8.5) show a net gain in suitability compared to the present time (Table S3). For both RCP scenarios from 2041-2060, an approximate of 10% increase in suitability is expected. From 2081–2100 under the RCP 2.6 scenario, a gain of 5% is expected. However, under the RCP 8.5 scenario from 2081–2100, a 60% loss of suitability is projected. This loss primarily occurs in low-altitude regions, specifically around 200 and 400 m a.s.l., while there are some gains in suitability at higher altitudes between 2300 and 2800 m a.s.l.

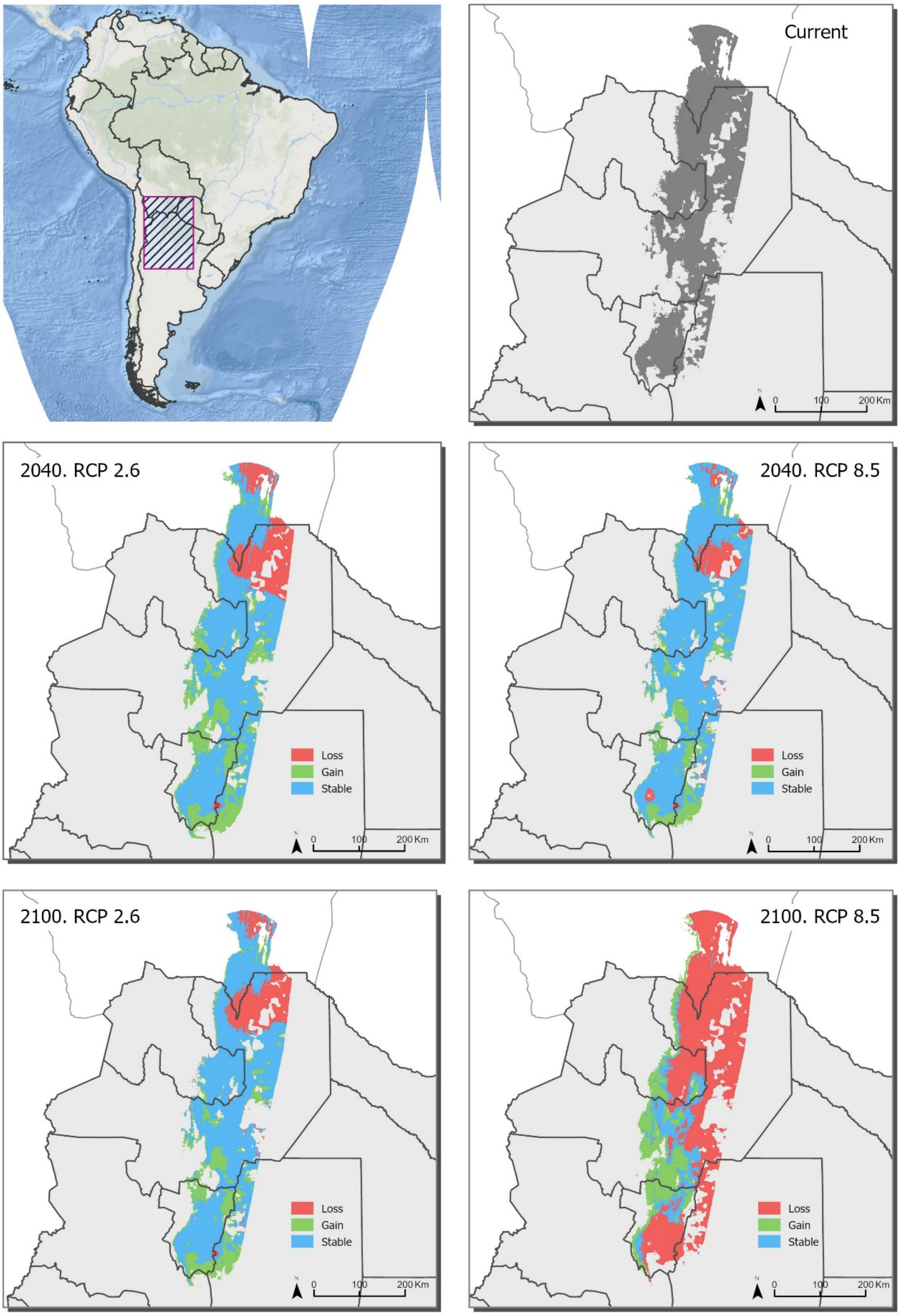

Fig. 6. Changes in climatically suitable areas comparing present conditions with four future climate scenarios for *P. basidenta*. Red indicates a loss in suitability compared to the present, green indicates a gain in suitability and sky blue indicates stable suitability.

Phyllocycla argentina. We fitted 124 candidate models for this species (Table S1). Seven models met AICs criteria and the criteria for omission rate. We selected the model quadratic, product and threshold feature classes and regularization multiplier of 1.0. The model's performance was better than random (AUC = 0.974). The most significant variables (Table S2) were temperature seasonality (BIO4), mean temperature of coldest quarter (BIO11) and mean temperature of driest quarter (BIO9). The response curve indicated a positive relationship between suitability and BIO4 and BIO11 but a negative relationship with BIO9 (Supplementary Information Fig S3). The variables precipitation of wettest month, mean diurnal range and annual precipitation had less contribution, while isothermallity and annual mean temperature had minimal contribution.

The almost continuous suitable area (6846981 km^2) extends through Southern Andean Yungas and Dry Chaco, from 200 to 2660 m a.s.l.) (Fig. S4). Based on binary maps (Fig 7), all scenarios, except for the 2081–2100 scenario under RCP 8.5, show a stable net suitable area compared to the present (Table S4). Under the RCP 8.5 scenario from 2081–2100, a 90% loss of suitability is projected. In this last model and in the previous ones where the net area is conserved, losses primarily occur in low altitude regions, around 200 and 400 m a.s.l. At the same time, there are some gains in suitability at higher altitudes between 2600 and 3200 m a.s.l.

Regarding protected areas, both species face a similar situation. In the present scenario, almost 10% of the suitable habitat for *P. argentina* and 13% for *P. basidenta* is located within regions under some form of conservation status (Tables S3 and S4). This trend remains consistent across all scenarios. However, it is important to highlight that, although the percentage of suitable habitat remains stable, the total area is drastically reduced in the worst-case scenarios for 2081–2100.

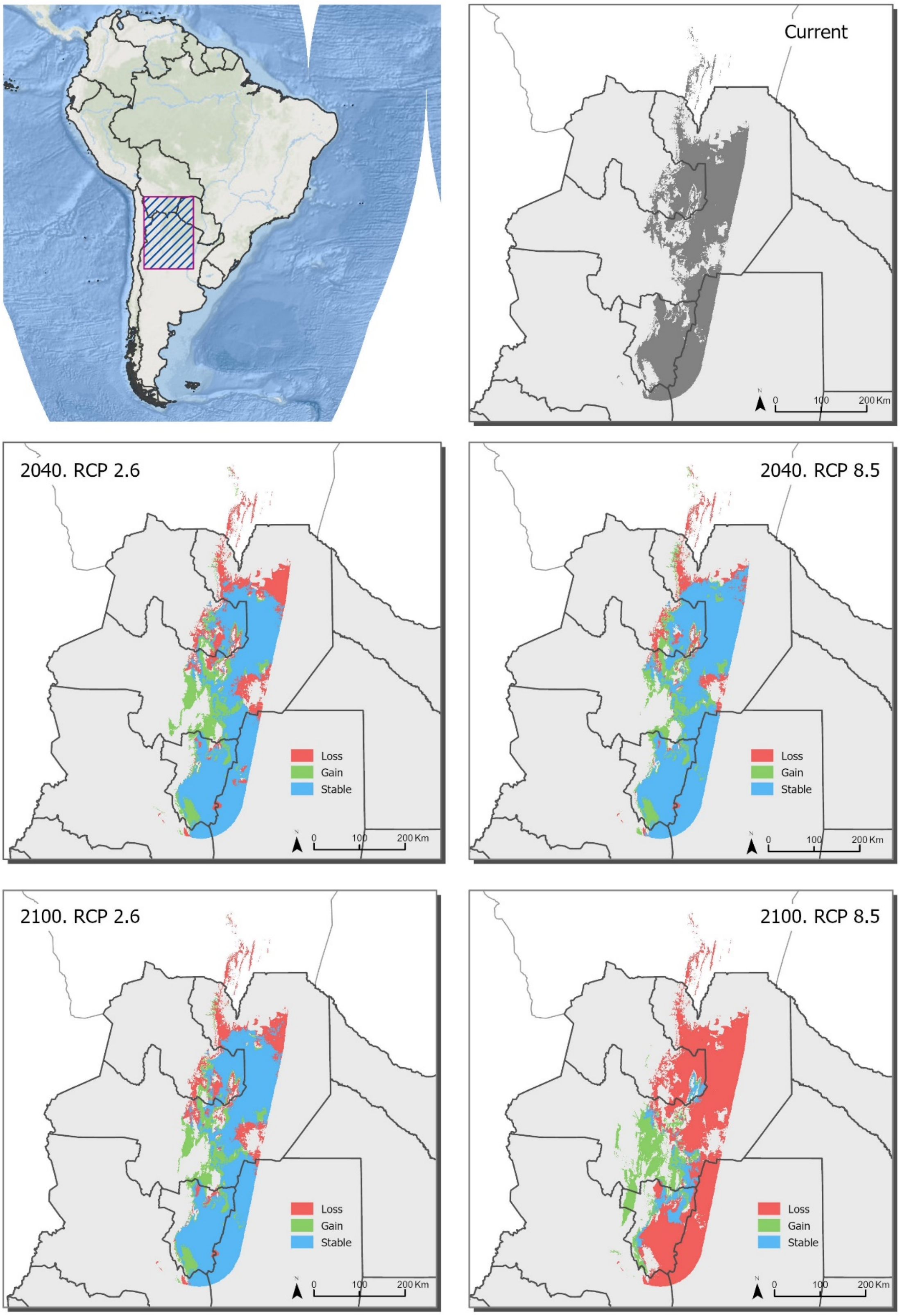

Fig. 7. Changes in climatically suitable areas comparing present conditions with four future climate scenarios for *P. argentina*. Red indicates a loss in suitability compared to the present, green indicates a gain in suitability and sky blue indicates stable suitability.

DISCUSSION

Systematic account

In NW Argentina, two species of *Phyllocycla* inhabits sandy bottomed rivers, *P. argentina* and *P. basidenta*. *Phyllocycla viridipleuris* was reported as present in Salta province but with no certainty on locality (Lozano et al. 2020). If this species is present, it is surely rare, we have examined 45 adult specimens from this and neighboring areas, with no matches with this species. The specific characters of the larval exuvia of reared males of *P. basidenta* were used to confirm that the reared females were of that same species. Female adult of *P. basidenta* is similar to the male, except that bluish pigments in the head are not present (only green pigments, instead), and the pale stripes on dorsum of thorax are extended medially (similar to *P. argentina*), but not reaching median carina. Thus, the female of *P. basidenta* cannot be readily separated from the sympatric *P. argentina* using the coloration of dorsum of thorax (as in males). Instead, both species can be distinguished by length and color of pterostigma (long and yellowish in *P. argentina*, short and brownish in *P. basidenta*), the shape of occipital plate (stout in *P. basidenta*, slender in *P. argentina*), color of metepimeron (dark in *P. basidenta*, pale in *P. argentina*) and the length and shape of vulvar lamina (0.3x length 9th st. in the former, 0.2x in the later). Additionally, the female of *P. basidenta* can be separated from *P. viridipleuris* by the absence of lateral dilatation on abdominal segment 8 (same in *P. argentina*, moderately developed in *P. viridipleuris*, Belle 1970). Finally, the apical rim of segment 10 in the female of *P. basidenta* is not differentiated from the remaining of the segment, as in other species of the genus, and it is only marked by a weak line.

The larvae of *P. basidenta* can easily be distinguished from that of the sympatric *P. argentina* by abdominal coloration (dark marks present on dorsum of abdomen in *P. argentina*). Other characters include (in bracket data from *P. argentina*): movable hook slightly longer and less pronouncedly curved (stouter and curved), last antennomere slender (stouter), posterolateral spines on abdominal segments 7–9 (on 6–9). The mediodorsal hooks are not useful instead, since both species present medial hooks on segments 3–9, with larger ones on s. 3–4 (*P. basidenta*) or 3–5 (*P. argentina*). Rodrigues Capítulo (1983) reported dorsal hooks from segments 3 to 5 only, we do not know if they were not seen by this author (hooks on 6–9 are tiny and hard to see, seeming a stout triangular spine) or represents intraspecific variation.

The larva of *P. viridipleuris* was described by Belle (1992) from a reared male exuvia from Minas Gerais (Brazil). Similar to *P. basidenta*, it shows lateral spines on abdominal segments 7–9, and a similar prementum and labial palp with slender movable hook (see Carriço et al. 2011). Belle (1992) also reported that prementum length was 1.5 times its width (1.3 in *P. basidenta*) and in his figure 1 the movable hook is as long as outer margin of palp (in *P. basidenta* the hook is 1/6 longer than this margin). Belle also reported dorsal tubercles on abdominal terga 3-7 in *P. viridipleuris*, but as they diminish in size posteriorly, it is not certain if its absence on 8-9 could be accurately used to distinguish this species from *P. basidenta* (showing very small tubercles on these segments, frequently hidden by dirt). From the picture of the male exuvia presented in Belle (1992, fig. 40) it is evident that the tubular segment 10 of the abdomen is much slender (ratio length segment 10/total length abdomen = 0.37) than in *P. basidenta* (this same ratio = 0.25). Finally, the exuvia described by Belle is 34 mm in length, much larger than our largest specimen of *P. basidenta* (29.5 mm). The same mandibular formula was reported for *P. gladiata* (Carriço et al. 2011), *P. argentina* (Rodrigues Capítulo 1983 and here) and *P. basidenta*. We found a small variation in *P. argentina*, with three m denticles in right mandible instead of two as reported by Rodrigues Capítulo (1983). Other species of *Phyllocycla* known in this stage did not mentioned the mandibular formula in descriptions.

Distribution

Our data, by expanding the known distribution of both species and demonstrating some continuity between the present and future potential area, support the proposed IUCN categorization for *P. argentina* and *P. basidenta* conservation status, both of which have been assessed as Least Concern (von Ellenrieder 2009; Lozano 2021). It is noteworthy that the projected range for both species is conserved or even increases in almost all future scenarios except the most drastic one. However, this area, although not decreasing, shows a significant shift towards higher altitudes. This has been reported for other odonates (Domisch et al. 2011; Collins and McIntyre 2015) including a species of Gomphidae (Soendgerath et al. 2012). *Phyllocycla* larvae live buried in sand and silt (de Assis et al. 2004), dominant sediments in the piedmont rivers they currently inhabit. However, these sediments decrease with altitude in the studied region (Pero et al. 2020), which could become limiting for future scenarios.

Phyllocycla argentina exhibits a positive relationship with BIO4, indicating a preference for areas characterized by climatic seasonality, a key feature of the Yungas. This variable, or more precisely, related variables such as BIO5 (maximum temperature of the warmest month) and BIO6 (minimum temperature of the coldest month), have been shown to be dominant drivers shaping the distribution of aquatic insects in the Yungas, as highlighted by Buitrago-Guacaname et al. (2024). In contrast, *P. basidenta* appears to be negatively affected by greater thermal fluctuations, as suggested by its negative relationship with BIO2 and BIO3 and habitat suitability.

Weather patterns may play a crucial role in determining the climatic range of species, directly impacting the timing and frequency of suitable oviposition days (Thompson 1990), which in turn affects population fecundity and long-term survival. Notably, areas predicted to be suitable in future scenarios are characterized by increased precipitation and frequent cloud cover, resulting from orographic and adiabatic processes (Viale et al. 2019). Therefore, weather conditions may also have a negative impact on the species' persistence. In the worst long-term scenario, the survival of both species is not assured, as a loss of between 60 and 90% of habitat suitability is predicted. In the case of *P. argentina*, which occupies other areas outside of this analysis, future studies including its entire range could modify this conclusion. However, this is not the case for *P. basidenta*, which is endemic to the studied region. Considering that lotic species are tracking climate change more slowly than lentic species, this adds greater concern for their survival (Hof et al. 2012).

Finally, other topic to be considered is the effectiveness of protected areas in safeguarding invertebrate species. A small percentage of their present suitable habitat is within protected regions, and this proportion remains stable across future scenarios. Relying solely on present conservation zones may be insufficient to ensure the long-term survival of these species, highlighting the need for adaptive management strategies that consider future habitat shifts.

CONCLUSIONS

We describe, for the first time, the female adult and larva of the large clubtail dragonfly *Phyllocycla basidenta*. Geographical records from larval specimens are easier to obtain through biodiversity monitoring, while adults are more difficult to collect and thus less common in collections. Using this new information, we evaluated the current and future distribution of this species alongside the partly sympatric *Phyllocycla argentina*. Our findings suggest that suitable habitats may shift to higher altitudes under moderate climate change, while significant habitat loss is expected under more severe warming scenarios. Climate change threatens both species as their habitats shift to elevated regions, making conservation efforts crucial in areas projected to remain suitable in the future. This study emphasizes the critical role of scientific museum collections in providing essential data for conservation and ecological research

Acknowledgments: We would like to express our gratitude to the International Dragonfly Foundation for their generous support of our collecting trips. We are additionally grateful to Daniela Gómez and Gabriela Fontanarrosa for field assistance, and to Sebastián Albanesi for curating specimens in the Instituto de Biodiversidad Neotropical odonatological collection. Finally, we acknowledge the continuous support provided by CONICET (National Council of Scientific Research, Argentina).

Authors' contributions: All authors contributed to the study conception and design. Material preparation and data collection were performed by Carlos Molineri and José Rodríguez. Ecological Niche Models analysis were performed by Carolina Nieto. The first draft of the manuscript was written by Carlos Molineri and Carolina Nieto, all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Competing interests: The authors have no relevant financial or non-financial interests to disclose.

Availability of data and materials: Data supporting the results and analysis in the article are included in Supplementary information.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Almeida M V, Pinto AP, Carvalho ADL, Takiya DM. 2013. When rare is just a matter of sampling: unexpected dominance of clubtail dragonflies (Odonata, Gomphidae) through different collecting methods at Parque Nacional da Serra do Cipó, Minas Gerais State, Brazil. Rev Bras Entomol **57:**417–423. doi:10.1590/S0085-56262013005000042.

APN (Administración de Parques Nacionales). 2024. Áreas protegidas de Argentina. *In*: Sistema de Información de Biodiversidad. Available at: https://mapas.apn.gob.ar/catalogue/#/search/?f=dataset. Accessed 15 Oct. 2025.

Araújo MF, De Marco P, Juen L, et al. 2020. Vulnerability of *Phyllocycla* Species (Odonata: Gomphidae) to Current and Planned Anthropic Activities by the Brazilian Government. Neotrop Entomol **49:**24–32. doi:10.1007/s13744-019-00714-4.

Belle J. 1970. Studies on South American Gomphidae (Odonata) with special reference to the species from Surinam. Stud Fauna Sur Guy **43:**1–158.

Belle J. 1988. A synopsis of the species of *Phyllocycla* Calvert with descriptions of four new taxa and a key to the genera of Neotropical Gomphidae (Odonata, Gomphidae). Tijdschr Entomol **131:**73–102.

Belle J. 1992. Studies on ultimate instar larvae of neotropical Gomphidae, with the description of *Tibiagomphus* gen. nov. (Anisoptera). Odonatologica **21:**1–24.

Carriço C, Costa JM, Santos TC, Anjos-Santos D. 2011. Description of the Last Instar Larva of *Phyllocycla gladiata* (Hagen in Selys)(Anisoptera: Gomphidae). EntomoBrasilis **4:**26–29. doi:10.12741/ebrasilis.v4i1.99.

Collins SD, McIntyre NE. 2015. Modeling the distribution of odonates: a review. Freshwat Sci **34:**1144–1158. doi:10.1086/682688.

de Assis JC, Carvalho AL, Nessimian JL. 2004. Composição e preferência por microhábitat de imaturos de Odonata (Insecta) em um trecho de baixada do Rio Ubatiba, Maricá-RJ, Brasil. Rev Bras Entomol **48:**273–282. doi:10.1590/S0085-56262004000200017.

Domisch S, Jähnig SC, Haase P. 2011. Climate-change winners and losers: stream macroinvertebrates of a submontane region in Central Europe. Freshwat Biol **56:**2009–2020. doi: 10.1111/j.1365-2427.2011.02631.x.

Elith J, Kearney M, Phillips S. 2010. The art of modelling range-shifting species. Methods Ecol Evol **1:**330–342.

Hassall C. 2012. Predicting the distributions of under-recorded Odonata using species distribution models. Insect Conserv Diver **5:**192–201. doi:10.1111/j.1752-4598.2011.00150.x.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. Int J Climatol **25:**1965–1978.

Hof C, Brändle M, Dehling DM, Munguía M, Brandl R, Araújo MB, Rahbek C. 2012. Habitat stability affects dispersal and the ability to track climate change. Biol Lett **8:**639–643. doi:10.1098/rsbl.2012.0023.

Cobos ME, Peterson AT, Barve N, Osorio-Olvera L. 2019. kuenm: an R package for detailed development of ecological niche models using Maxent. PeerJ **7:**e6281. doi:10.7717/peerj.6281.

Lozano F. 2021. *Phyllocycla argentina*. *In*: The IUCN Red List of Threatened Species 2021: e.T49254472A49255625. Available at: https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T49254472A49255625. Accessed 28 Jun. 2024.

Nava-Bolaños A, Vrech DE, Peretti AV, Córdoba-Aguilar A. 2021. Argentinian odonates (dragonflies and damselflies): current and future distribution and discussion of their conservation. J Threat Taxa **13:**19448–19465. doi:10.11609/jott.7166.13.11.19448-19465.

Needham JG. 1940. Studies on Neotropical Gomphine dragonflies (Odonata). Trans Amer Ent Soc **65:**363–394.

Osorio-Olvera L, Lira-Noriega A, Soberón J, Peterson AT, Falconi M et al. 2020. ntbox: An r package with graphical user interface for modelling and evaluating multidimensional ecological niches. Methods Ecol Evol **11:**1199–1206. doi:10.1111/2041-210X.13452.

Pero EJI, Georgieff SM, Gultemirian L, Romero F, Hankel GE, Domínguez E. 2020. Ecoregions, climate, topography, physicochemical, or a combination of all: Which criteria are the best to define river types based on abiotic variables and macroinvertebrates in neotropical rivers? Sci Total Environ **738:**140303. doi:10.1016/j.scitotenv.2020.140303.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecol Modell **190:**231–259. doi:10.1016/j.ecolmodel.2005.03.026.

Rodrigues Capítulo A. 1983. La ninfa de *Phyllocycla argentina* (Hagen in Selys) 1878 (Odonata, Gomphidae). Rev Soc Ent Arg **42:**267–271.

SERNAP (Servicio Nacional de Áreas Protegidas). 2023. Áreas protegidas de Bolivia. *In*: Ministerio de Medio Ambiente y Agua. Available at: https://geo.gob.bo/catalogue/#/datasets. Accessed 15 Jun. 2025.

SIGA (Sistema de Información Geográfico Ambiental). 2024. Áreas protegidas de Argentina. *In*: Fundación ProYungas. Available at: https://siga.proyungas.org.ar/. Accessed 15 Jun. 2025.

Soberon J, Peterson AT. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inform **2:**1–10. doi:10.17161/bi.v2i0.4.

Soendgerath D, Rummland J, Suhling F. 2012. Large spatial scale effects of rising temperatures: modelling a dragonfly's life cycle and range throughout Europe. Insect Conserv Diver **5:**461–469. doi:10.1111/j.1752-4598.2011.00182.x.

Viale M, Bianchi E, Cara L, et al. 2019. Contrasting climates at both sides of the Andes in Argentina and Chile. Front Environ Sci **7:**1–15.

von Ellenrieder N. 2009. *Phyllocycla basidenta*. *In*: The IUCN Red List of Threatened Species 2009: e.T158730A5275075. doi:10.2305/IUCN.UK.2009-2.RLTS.T158730A5275075.en. Accessed 28 Jun. 2024.

von Ellenrieder N, Garrison RW. 2007. Dragonflies of the Yungas (Odonata): a field guide to the species from Argentina. Pensoft publishers, Bulgaria.

Supplementary materials

Table S1. Model performance of candidate models according to regularization multiplier (RM) and feature classes (FC, l: linear, q: quadratic, p: product, t: threshold, h: hinge). The selection criteria were partial ROC (pROC), omission rate and AIC. The chosen model is highlighted. (download)

Table S2. Estimates of relative contributions of the environmental variables to the Maxent model. Values shown are averages over replicate runs. (download)

Table S3. Area estimated by ecological niche model for *P. basidenta* at five different times. (download)

Table S4. Area estimated by ecological niche model for *P. argentina* at five different times. (download)

Fig. S1. *P. basidenta*. Response curves. (download)

Fig. S2. Estimate of the potential geographic distribution of *P. basidenta* and projections acrossfour future climate scenarios. The gradient indicates the habitat suitability for the species, with red indicating higher suitability. (download)

Fig. S3. *P. argentina*. Response curves. (download)

Fig. S4. Estimate of the potential geographic distribution of *P. argentina* and projections across four future climate scenarios. The gradient indicates the habitat suitability for the species, with red indicating higher suitability. (download)