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Congruence of detection probabilities and co-occurrence of threatened Afromontane damselflies with diverging functional traits (Odonata: Chlorocyphidae, Coenagrionidae)

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Abstract

The biodiversity crisis is exceptionally severe in the freshwater systems of the highly threatened Afromontane region. We estimated abundance, occupancy and detection probabilities and studied functional traits of ecological significance for adults and larvae of Kenya Jewel (*Platycypha amboniensis* Martin, 1915) and Giant Sprite (*Pseudagrion bicoerulans* Martin, 1907) in Mount Kenya Forest. Our estimates of abundance were based on replicated counts, while occupancy and detection probabilities were estimated using a single-season, two-species occupancy formulation. We found that detection probabilities of one species were influenced by the detection probabilities of the other, but conversely, occupancy was not. This was supported by morphological traits, as the larvae of *P. amboniensis* are adapted to rocky and fast-flowing lotic streams, while *P. bicoerulans* is adapted to vegetated, littoral, and slow-moving reaches of the same streams. This means that, while these species have different adaptations, their co-occurrence depends on the heterogeneity of the microhabitats. We recommend implementation of ecosystem restoration approaches that will contribute to maintain habitat complexity and therefore increase the resilience of these co-occurring species to future environmental changes.

Implications for conservation: The occurrence of Kenya Jewel was not influenced by

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the occurrence of Giant Sprite, and there was neither competition nor niche overlap. This aligns with the differences in ecological adaptations based on the functional morphology of adults and larvae. This evidence is useful for restoration of the ecosystem to ensure that these species are conserved concurrently in their range of co-occurrence.

Keywords: occupancy probability; co-occurrence; larval morphology; functional traits; conservation; ecosystem restoration.

Introduction

Insects provide a continuum of ecosystem services that are critical for human welfare and survival (Samways et al. 2020). These services include food provisioning, nutrient cycling and decomposition of organic matter, pollination, control of pests, and use in ecological monitoring (May 2019, Samways et al. 2020). Lately, there has been a dramatic decline in insect populations and diversity around the globe, which has inspired multiple conservation actions (Hallmann et al. 2017, Forister et al. 2023). These efforts are urgent because population dynamics of insects can easily translate to instability of aquatic and terrestrial ecosystems (Mendes et al. 2017, May 2019).

Conservation of threatened insects is shifting from identification of causes of population decline to searching for mechanisms to address effects and understanding the intrinsic responses of the populations to ecosystem restoration (Lambret et al. 2023, Webster et al. 2023). This approach is required to inform current conservation endeavours and model future population recovery under extreme scenarios and across vast landscapes (Kawahara et al. 2021). However, this effort is limited by the paucity of reliable data on the functional traits of species, population abundances and species interactions within microhabitats (Khelifa et al. 2021, Viza et al. 2023). Exploring this diversity is particularly problematic for aquatic insects because they have complex life history traits that involve metamorphosis and the use of different habitats for their larval and adult stages (Stoks and Córdoba-Aguilar 2012, Kietzka et al. 2021). The population decline of aquatic insects can be attributed to these intricate life cycles, making them vulnerable to pressures from both aquatic and terrestrial habitats (Samways 2008, Pires et al. 2020, Silva et al. 2021).

The highest diversity of threatened dragonflies and damselflies (*Odonata*) in Africa is concentrated in the tropical forests and highlands (Clausnitzer et al. 2012). Habitat loss resulting from deforestation in the Afromontane radiation (isolated high-altitude regions of the African tropical realm, *sensu* Hořák et al. 2023) and human activities such as water abstraction impact both the terrestrial and aquatic phases of odonate species (Samways 2008; Clausnitzer et al. 2011; Clausnitzer et al. 2012; Hořák et al. 2023). Damselflies (*Zygoptera*) and dragonflies (*Anisoptera*), being amphibious in nature and charismatic players in the food web as top predators of aquatic and terrestrial invertebrates and prey for vertebrates, are potent ecological indicators owing to their sensitivity to different stressors (May 2019). The knowledge of their ecology and diversity is crucial to develop conservation measures for their populations (Dijkstra et al. 2014). Much of the current work on odonate populations in East Africa has focused on life history, biogeography and taxonomy (Clausnitzer et al. 2011, Njoroge et al. 2017). These include the characterisation of extinction risk based on trends in population abundance, geographical distribution, and habitat fragmentation (Clausnitzer et al. 2012).

The information on species abundances is important for their conservation, regardless of their threat status (Baker et al. 2019, Hogreve and Suhling 2022). Detection probabilities of species (likelihood of a species being present) help scientists and practitioners to create awareness, in research planning, and to inform interventions such as ecological restoration (Redford et al. 2013). Equally, knowledge on species co-occurrence can be used to understand how animal communities function, such as revealing patterns in competition and niche overlap when several threatened species are involved (Steenweg et al. 2019). The knowledge of species-specific functional traits of larvae and adult damselflies that can contribute to population resilience of threatened species is limited. This study seeks to answer the research questions: how do abundances and ecologically significant morphological traits vary between two threatened damselfly species, and how does habitat influence their patterns of co-occurrence? For this purpose, we estimated the abundance, detection and occupancy probabilities of Giant Sprite, *Pseudagrion bicoerulans* Martin, 1907 (Odonata: Coenagrionidae), and Kenya Jewel, *Platycypha amboniensis* Martin, 1915 (Odonata: Chlorocyphidae), in Mount Kenya Forest. We further describe and compare functional traits of ecological significance based on the morphology of the adults and final stadium instar larvae of these two damselfly species.

Materials and methods

Study species

We studied two threat-defined and range-restricted species of damselflies (Figure 1). *Platycypha amboniensis* is endemic to the Central Highlands of Kenya and is highly dependent on montane forest and considered a sub-montane relict species among dancing jewels (Clausnitzer et al. 2011). Little is known about its reproductive ecology, behaviour, and life history, even though it is a very rare and highly threatened species (Dijkstra and Clausnitzer 2014). The species is classified in the IUCN Red List as Critically Endangered (CR) due to extensive habitat loss as a result of forest clearance within regions it is dependent upon (Clausnitzer 2018, Clausnitzer et al. 2011). The male of this species has bright orange tibiae that are slightly flattened and white interiorly, sky-blue abdominal segments (S5–S10), and large, bulbous eyes (Dijkstra and Clausnitzer 2014).

Similarly, *P. bicoerulans* is endemic to streams in the mountains of Kenya, Tanzania, and Uganda. The species is classified as Vulnerable (VU) in the IUCN Red List (Clausnitzer, 2018). It was termed 'the most alpine of African Odonata' because it occurs in heather and Afroalpine zones higher than 3000 m above sea level (Clausnitzer et al. 2011). The species has high intraspecific genetic diversity and three subspecies: *P. b. bicoerulans* (Central Kenya), *P. b. elgonensi* (West Kenya and East Uganda), and *P. b. kilimanjaricus* (North Tanzania), widespread across high-elevation forests in East Africa (Dijkstra et al. 2007). Males of this species are distinguished by a bright yellow to orange labrum and orange post-ocular spots, a green-striped black thorax, pruinescent abdominal segments (S1–S2, S9–S10), and clasper-like cerci (Dijkstra and Clausnitzer 2014).

Figure 1. Threatened Afromontane damselflies in Kenya: (a) *Platycypha amboniensis* Martin, 1915, male; (b) *P. amboniensis,* copulation; (c) *Pseudagrion bicoerulans*

Martin, 1907, copulation; (d) *P. bicoerulans,* male.

Study area

We conducted this study in Kangaita Forest Station (Kirinyaga County) and Irangi Forest Station (Embu County) (Figure 2). These forest stations are part of the Mount Kenya Forest Reserve, which is a protected area in the Central Highlands of Kenya (Nyongesa and Vacik 2019). This study area is classified as lower montane humid forest and is renowned for its agro-ecological value and high diversity of woody plant species, birds, and mammals (Zhou et al. 2018, Onditi et al. 2022). The drainage pattern is dendritic, with all streams forming tributaries of the Tana River. Water is directly abstracted in large quantities from these streams for domestic use, municipal supply, micro-hydropower stations, and small- and large-scale irrigation schemes.

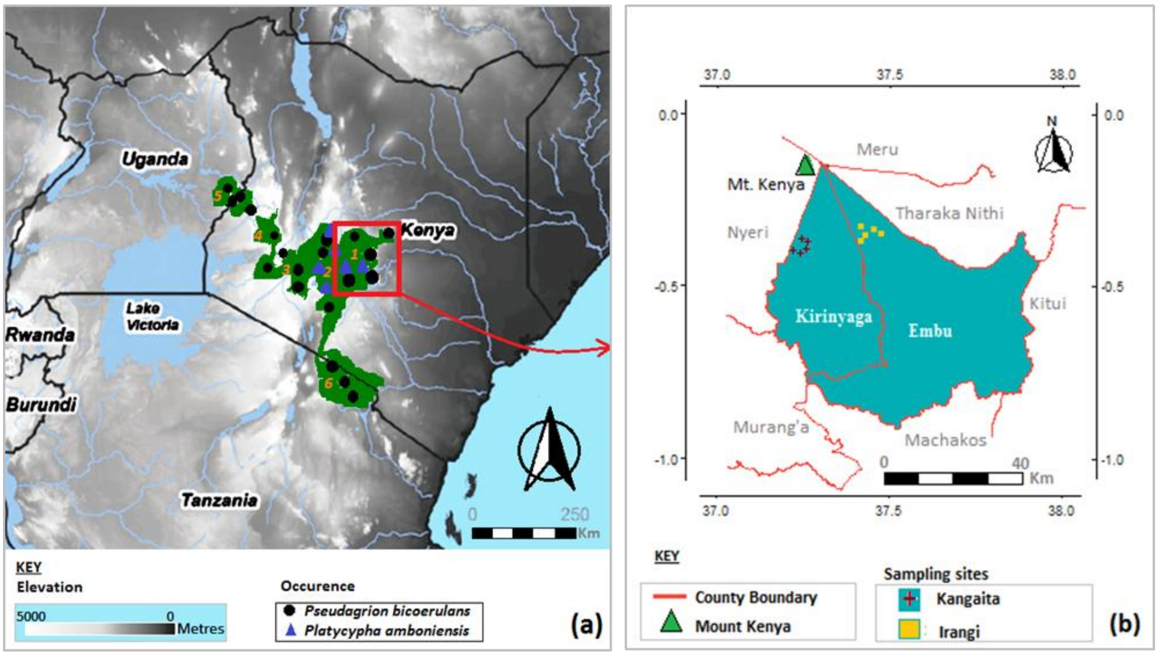

Figure 2: (a) Map showing the distribution of *Pseudagrion bicoerulans* Martin, 1907 (shaded green) and the occurrence of *P. bicoerulans* (black dots) and *Platycypha amboniensis* Martin, 1915 (blue triangles) along the elevation gradient in Afromontane forests of East Africa: (1) Mt Kenya, (2) Aberdare Ranges, (3) Mau Forest Complex, (4)

Nandi Hills, (5) Mt Elgon, and (6) Mt Kilimanjaro and Mt Meru; (b) map of Kirinyaga and Embu Counties (shaded blue) showing the location of Mount Kenya and sampling sites in Kangaita Forest (red crosses) and Irangi Forest (yellow squares).

Sampling

The sampling period ranged from September 2022 to March 2023 and is considered in this study a 'single season', which runs across two dry periods interspaced with a period of short rains. It is possible that the adults and final instar larvae encountered during this study belong to the same generation. Sampling sites were selected randomly from a list of first-level and second-level streams (five in Kangaita and five in Irangi). At each sampling point, three transects of 100 m in length and covering the width of the stream channel (up to 10 m) were established along each stream following the method of Batista et al. (2021). Sampling of adults and larvae (including exuviae) was undertaken at four sampling occasions (interval: 9–17 days) along each transect at twenty-metre intervals, starting at zero, which translates to five full-width belt transects (FWBT) on each transect (Darshetkar et al. 2023), equivalent to 200 m^2. The following water quality parameters were measured using a multi-parameter portable meter (Suzhou Holi, China): dissolved oxygen (DO), electrical conductivity (EC), oxidation-reduction potential (ORP), pH, total dissolved solids (TDS), and temperature. Turbidity was measured using a nephelometer (BD PhoenixSpec™, South Africa).

Sampling was consistent with the guidelines for handling living insects (Montegomery et al. 2021; Cezário et al. 2021). On each sampling occasion, two observers were involved and took turns in data entry and observation. The sampling period was mostly sunny, and the water was shallow. All adult damselflies and larvae (including exuviae) encountered at each interval were counted. Evidence of the presence of adults was confirmed by the presence of damselflies perching on the rocks, twigs overhanging the stream, emergent vegetation, and driftwood. No attempts were made to search for adult damselflies beyond the riverbanks. Exuviae were found by locating suitable emergence sites mostly on emergent vegetation, driftwood, and exposed rocks. Collected exuviae were placed in Falcon tubes and stored in a freezer in order to prevent damage by inadvertently trapped insects and spiders and the growth of mould. After at least 12 hours of freezing, the exuviae were dried and mounted.

Larvae were collected by sinking a dip net into the water and scooping debris at the edges of the stream (targeting *P. bicoerulans*). Movable rocks along the river were also lifted or overturned and checked for clinging or crawling damselfly larvae (targeting *P. amboniensis*). These were then returned to position at the point of collection. Adults were collected with a professional sweep net (38 cm diameter, 86 cm depth, and 100 cm handle). Specimens were placed in specimen jars and washed in acetone or preserved in absolute ethanol. The following parameters were measured for adult damselflies: abdomen length, body length, hind femur length, thorax length, wing area, wing length, wing perimeter, and wing width. The following parameters were measured for larvae: abdomen length, appendages, body length, gonapophyses, hind femur length, prementum, and wing sheath.

Data analyses

The pairwise correlation between water properties was calculated using Pearson correlation coefficients. The difference in functional traits between males and females was estimated using an independent samples t-test. The replicated count data (pooled to stream level and treated separately for adults and larvae of both species) were averaged as daily abundance with standard error (mean ± SE). A ratio was calculated by dividing the mean daily abundance of larvae by that of adults. An independent sample t-test was used to determine if there were significant differences in means. These tests were carried out in R version x64: 4.0.3 (R Core Team 2020). Further, we used linear mixed-effects models to test for differences in traits with species, stage, and sex as fixed effects and traits as a random intercept, using the lme4 package (Kuznetsova et al. 2017). We then conducted post hoc Kenward–Roger tests to assess pairwise differences between species, stage, and sex, using the emmeans package (Lenth 2024). The trait-specific effect sizes (ES) were calculated as the mean difference between species per trait, grouped by developmental stage and standardised by the trait-specific standard deviation (SD) in dplyr (Wickham et al. 2019).

Species abundance data denoted as presence-absence at each sampling interval and organised into pairs (*P. amboniensis* adult + *P. bicoerulans* adult; *P. amboniensis* larvae + *P. bicoerulans* larvae) were compiled to fit the formulation of two-species single-season occupancy models (Richmond et al. 2010). This model accepts detection histories of each species at each site across sampling occasions (0 indicating non-detection and 1 indicating detection). The model assumes that one of the species in pairwise interactions is dominant while the other is subordinate (Kleiven et al. 2023; Lonsinger 2022). Three parameters were used to estimate occupancy: ψA—occupancy probability of species A (*P. amboniensis*); ψBA—occupancy probability of species B (*P. bicoerulans*) in the presence of species A; and ψBa—occupancy probability of species B in the absence of species A. These were used to test the hypothesis that the occupancy probability of *P. amboniensis* is not dependent on the presence of *P. bicoerulans* (ψBA ≠ ψBa).

Five parameters were estimated for detection probability, namely: pA—detection probability of species A in the absence of species B; pB—detection probability of species

B in the absence of species A; rA—detection probability of species A in the presence of species B; rBA—detection probability of species B when species A is present and detected; rBa—detection probability of species B when species A is present but not detected. These were used to test hypotheses that 1) the detection probability of *P. amboniensis* is not dependent on the presence of *P. bicoerulans* (pA $\neq$ rA) and 2) the detection probability of *P. bicoerulans* is not dependent on the presence and detection of *P. amboniensis* (pB $\neq$ rBA). The model also estimates derived parameters of occupancy probability: ψB—probability of occupancy for species B, regardless of occupancy status of species A; ψAB—probability of both species being present. The species interaction factor (SIF or γ) was used to measure co-occurrence, where $\gamma = 1$ means that the two species occur independently of each other, $\gamma < 1$ means that the two species avoid each other and $\gamma > 1$ means that there is overlap in the co-occurrence of the two species (Lonsinger 2022).

A logit link function was used to model the occupancy and detection of both species in the program MARK (White and Burnham 1999). This was conducted separately for pairs of adults and larvae. A total of 32 predetermined models were developed to include combinations of constant occupancy probability ψ(.), variable occupancy probability ψ(t), constant detection probability p(.), and variable detection probability p(t). All candidate models were ranked from highest to lowest based on their Akaike's Information Criteria modified for c-hat (QAICc) values and the AIC weights. The top-ranked model has a model likelihood of one (1), the lowest QAICc, and presents the best combination of parameters (ψA, ψBA, ψBa, rA, pA, pB, rBa, rBA).

Results

The physico-chemical water properties for each stream are shown in Table 1. There was no significant correlation between dissolved oxygen (DO) and oxidation-reduction potential (ORP) and no correlation between turbidity and pH. In contrast, EC was strongly positively correlated with TDS (r = 0.93) and negatively correlated with ORP (r = -0.78). Temperature was negatively correlated with pH (r = -0.72), while ORP was negatively correlated with TDS (-0.79). Several moderate and weak relationships were found, such as the inverse between temperature and DO (Supplementary Table S1).

Table 1

The abundance of both adults and larvae differed between species (t = -3.99, df = 33.76, p-value < 0.001). The damselflies, *P. amboniensis* and *P. bicoerulans,* were encountered in the study area a total of 3,605 times. These included 871 adults and 613 larvae of *P. amboniensis* and 906 adults and 1,215 larvae of *P. bicoerulans*. Additionally, the ratio of adults and larvae at sampling sites differed between species (t = 3.68, df = 40.4, p-value < 0.001). The average number of individuals encountered across sampling occasions was (mean ± SE) 19.85 ± 2.00, 16.70 ± 1.89, 22.00 ± 2.29, and 33.20 ± 2.98 for *Platycypha amboniensis* adults, *P. amboniensis* larvae, *Pseudagrion bicoerulans* adults, and *P. bicoerulans* larvae, respectively, in Irangi Forest; 23.70 ± 2.11, 13.95 ± 0.79, 23.30 ± 2.64, and 27.55 ± 1.86 for *P. amboniensis* adults, *P. amboniensis* larvae, *P. bicoerulans* adults, and *P. bicoerulans* larvae, respectively, in Kangaita Forest (Figure 3). This translates to a density of 0.218 sqm^{-1}, 0.153 sqm^{-1}, 0.227 sqm^{-1}, and 0.308 sqm^{-1} of *P. amboniensis* adults and *P. amboniensis* larvae, *P. bicoerulans* adults, and *P. bicoerulans* larvae, respectively.

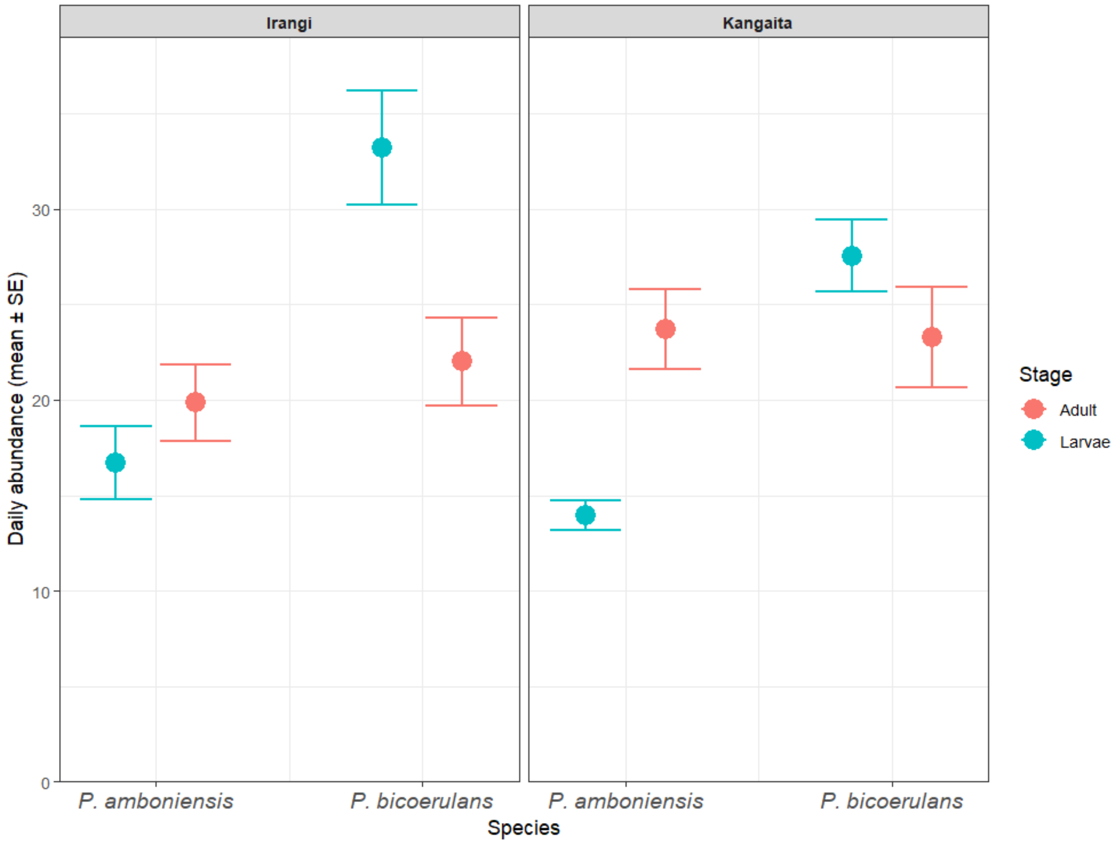

Figure 3. Point range diagram of daily abundance (mean ± SE) for adults and larvae of montane damselflies *Platycypha amboniensis* Martin, 1915 and *Pseudagrion bicoerulans* Martin, 1907 in Kangaita and Irangi Forests, Mount Kenya.

The most parsimonious models (Table 2) estimated the probability of occupancy for *P. amboniensis* adults paired with *P. bicoerulans* adults and *P. amboniensis* larvae paired with *P. bicoerulans* larvae but showed no evidence that occupancy of either was influenced by occupancy of the other (Table 3). The best-supported model for adult occurrence had an AICc value of 645.11, a weight of 0.356, and the model likelihood reduced dramatically to 0.058 in the sixth model (ΔAICc = 5.703). The best-supported model for larvae co-occurrence had an AICc value of 603.84, a weight of 0.333, and the model likelihood reduced to 0.086 in the sixth model (ΔAICc = 4.907).

Table 2

There was no evidence that occupancy of *P. amboniensis* was affected by the presence of *P. bicoerulans* (Table 3). The species' had high probabilities of occupancy (0.915–1.00) regardless of whether the other species was present or not present ($\psi A = \psi BA = \psi Ba = \psi B \cong 1.00$); while the probability of both species being present was 0.926 ± 0.044 for larvae and 0.888 ± 0.043 for adults. The two species were present and detected independently ($\gamma = 0.999 \pm 0.002$). There was evidence that the presence of *P. amboniensis* affected the presence and detection probability of *P. bicoerulans*. The detection probability for larvae of *P. amboniensis* was higher when the adults of *P. bicoerulans* were absent ($pA = 0.473 \pm 0.39$). The detection probability of *P. bicoerulans* larvae was lowest when the larvae of *P. amboniensis* were present ($pB = 0.14 \pm 0.589$). There was support that the detection probability of *P. amboniensis* adults was influenced by the detection probability (but not presence) of *P. bicoerulans* ($rA \neq pA$). The detection probability for adults of *P. amboniensis* was higher when the adults of *P. bicoerulans* were absent ($pA = 0.625 \pm 0.122$).

Table 3

There was a significant difference between males and females of *P. amboniensis* for abdomen length, body length, wing area, and wing length. No significant differences were found for hind femur length, thorax length, wing perimeter, and wing width (Table 4). There was no evidence that the adult males and females of *P. bicoerulans* differed significantly. The differences and similarities in the morphology of *P. amboniensis* and *P. bicoerulans* larvae and the associated ecological adaptations are summarised in Table 5.

Table 4

Table 5

Using a linear mixed-effects model, we found that *P. bicoerulans* varied significantly from *P. amboniensis*, with an estimated difference in overall trait values of 5.42 units (SE = 0.59, t = 9.17, p < 0.001). The developmental stage was a strong predictor of trait variation (t = 5.94, p < 0.001), while sex had a smaller but significant effect, with females differing from males by 1.40 units (SE = 0.70, t = 2.01, p = 0.045). Trait-specific effect sizes (ES) were positive (i.e., *P. bicoerulans* > *P. amboniensis*) in wing sheath length (ES = 1.74), adult body length (ES = 1.89), adult abdomen length (ES = 1.99), larva body length (ES = 1.85), larva abdomen length (ES = 1.69), appendage length (ES = 1.26), and wing area (ES = 1.17). Negative effect sizes were recorded for thorax length (ES = -1.80), hind femur length (ES = -0.996), and labium length (ES = -0.798). The wing length, wing perimeter, and wing width contributed less to overall species separation.

Discussion

The studied streams in the Afromontane forests offer a highly heterogeneous environment that can support the co-occurrence of both damselfly species. This environmental complexity creates a range of microhabitats, allowing species with differing ecological requirements to co-occur. Such variability provides opportunities for niche differentiation, which may explain the high local diversity often observed in montane stream systems (Matomela et al. 2021, Masese et al. 2023). This study contributes towards understanding the patterns of co-occurrence and structure of Afromontane damselfly communities as mediated by species-specific adaptations to varying microhabitats. As expected, *P. b. bicoerulans* (*sensu stricto*) occur in the same streams occupied by *P. amboniensis* in the Central Highlands of Kenya. These species belong to distinct lineages that have followed different evolutionary trajectories for an extended period (Njoroge et al. 2017, Dijkstra et al. 2014).

The abundances of these threatened damselflies in the studied Afromontane streams were relatively stable over the sampling period, which suggests that these habitats provide suitable conditions for their survival. The larvae of *P. bicoerulans* were detected mostly on sites with slower water flows and higher abundances of emergent vegetation characterised by warm waters and low abundances of total dissolved solids. This microhabitat specialisation is probably the reason why *P. bicoerulans* is easily displaced by competitive lowland species (Clausnitzer et al. 2011). The overall detection probability for larvae was lower than that for adults in the presence of *P. amboniensis*. The adults of *P. amboniensis* were common in areas with driftwood, while larvae were detected mostly where the stream was rocky and fast-flowing. The result from the single-season, two-species occupancy model means that there was neither competition nor niche overlap in the occupancy of *P. amboniensis* adults and *P. b. bicoerulans* adults, as well as *P. amboniensis* larvae and *P. bicoerulans* larvae. It is noteworthy that the method assumes population closure (*sensu* Richmond et al. 2010), which has limitations when associated with open populations (Lonsinger 2022, Kleiven et al. 2023).

The distribution and structure of *Odonata* assemblages in streams can be predicted using their functional traits (Silva et al. 2021). The morphological traits in *Odonata* larvae contribute to the requirements for larval survival, such as breathing, feeding, and predator avoidance (Matomela et al. 2021). The independent co-occurrence of *P. amboniensis* and *P. bicoerulans* can be explained in terms of their feeding ecology. This is because there are different prey items in the littoral zone and fast-flowing sections, with specialised morphological features that aid the processing of these prey items. The mouthparts of *P.*

amboniensis and *P. bicoerulans* differ in shape, size, and structure; the significance is that it enhances foraging success in varying microhabitats. The general morphology of larval mouthparts in *Odonata* is grossly similar, meaning that these small morphological variations are insightful to explain ecological adaptations with regard to food intake in littoral and benthic zones (Büsse and Gorb 2018, Büsse et al. 2021). The presence of labial palps with long hooks in *P. amboniensis* is likely an adaptation for better grasping of prey, while the prementum with wide labial palps that have setae in *P. bicoerulans* increases the sensitivity of the prehensile mask. In addition, the presence of a well-developed hypopharynx enhances overall food acquisition in *P. amboniensis,* as its muscles have been associated with the opening of the labium (Büsse and Gorb 2018).

The littoral and benthic regions of lotic streams differ in their mechanisms of retaining dissolved oxygen, which can be attributed to the diversity of shapes of gaseous exchange features like caudal lamellae (Mendes et al. 2017). Damselflies have evolved autotomy, where caudal lamellae are self-amputated to escape predators (Black et al. 2019, Pernecker et al. 2020). The drab colour and detritus particles attaching to the setae of *P. amboniensis* make it well camouflaged, while the swimming capabilities of *P. bicoerulans* make it easy to escape predators. A robust and cylindrical body shape (*P. amboniensis*) is preferred in microhabitats with a higher proportion of stone and gravel substrate (Pires et al. 2020); that is also utilised by burrowing predators such as gomphids—mostly *Notogomphus* Selys, 1858 and *Paragomphus* Cowley, 1934. On the other hand, an elongate body (*P. bicoerulans*) is suited for refuge among vegetation and litter, where climbing and sprawling predators live—mostly *Pinheyschna* Peters & Theischinger, 2011; *Zygonyx* Hagen, 1867; and *Atoconeura* Karsch, 1899. Siltation of the streams leads to sedimentation that homogenises substrates, excluding larvae that depend on substrates in favour of burrowing species (Dalzochio et al. 2018, Mühlenhaupt et al. 2022). Alteration of habitat has consequences on abundance (Dalzochio et al. 2020) and size structures of multiple co-occurring species (Oliveira-Junior et al. 2021). This affects species simultaneously and shifts in favour of species that have evolved in heterogeneous environments (Matomela et al. 2021, Samways 2008).

The observed differences in gonapophyses of *P. amboniensis* and *P. bicoerulans* at emergence suggest different emergence and maturation times. Early larval development provides an advantage by allowing faster growth and quicker maturation of adults, potentially influencing reproductive timing and success. The female gonapophyses are highly developed because these species have endophytic oviposition, where females deposit their eggs within plant tissues by means of a well-developed ovipositor (Johnston et al. 2025). It is also noteworthy that larval behaviour and adult behaviour in these damselflies are intertwined, where, for instance, the site of oviposition and habitat for early larval development is chosen by the adult. This compensates for higher activity, which results in a higher growth rate but increases predation risk in damselfly larvae (Mühlenhaupt et al. 2022) and predicts developmental plasticity in changing environments such as drying pools (Pernecker et al. 2020). This can be used to explain why adult detection probability differed from that of larvae within a shared habitat.

This study sheds light on stage-specific differences in the occupancy and detection probabilities of adults and larvae of co-occurring species. The sensitivity of Afromontane forests is due to their distinct vegetation types that are ecologically meaningful for the terrestrial adult Odonata (Dijkstra and Clausnitzer 2006, Clausnitzer et al. 2011). However, owing to the complex life history traits that involve metamorphosis and use of different habitats for larvae and adults (Steenweg et al. 2019, Hogreve and Suhling 2022), stability of these populations can be regulated at different developmental stages (Lambret et al. 2023). Adults select the most suitable oviposition sites, and therefore, the presence of many adults on a site of oviposition means that a large number of larvae are recruited. The emergence of a large number of larvae translates into a high density of adults from certain sections. Larvae disperse by swimming or drifting, especially downstream, whereas adults fly to more suitable microhabitats for oviposition (Johnston et al. 2025). Combining co-occurrence analysis with functional traits is a useful tool for detecting species that rely on similar ecological conditions and identifying important habitats that support rare species and enhance the survival of endangered damselflies (Steenweg et al. 2019, Cerini et al. 2023).

Implications for conservation

The East African Montane Forests, Ethiopian Highlands, Eastern Arc, and Coastal Forest Mosaics are regions of conservation value due to the large number of threatened species in these regions (Clausnitzer 2003, Clausnitzer et al. 2011). The sensitivity and diversity of threatened species also coincide with the patterns of endemism (Dijkstra et al. 2007). Habitat specialists (species that occur in a small geographical range) are highly susceptible. These include those that are confined to mountain peaks and those living in highly fragmented landscapes (Clausnitzer et al. 2011, 2012). Despite this study showing that these species are present and co-occur in Mount Kenya, this population remains isolated from other highland regions like the Aberdare Ranges (Dijkstra et al. 2007, Njoroge et al. 2017, Clausnitzer 2018). This risk of continued habitat isolation and fragmentation means that even when a population is seemingly stable in a restricted range, it is still vulnerable to stochastic events like extreme weather and genetic effects such as bottlenecks and inbreeding depression that hasten biotic attrition (Dijkstra et al. 2007, Webster et al. 2023).

Species in the Afromontane streams are adapted to live in clear waters with little natural silting, while species that occur downstream tend to be more tolerant of human disturbance and natural silting from storms (Deacon and Samways 2021). The larvae are critical for conservation because a great proportion of *Odonata* larvae do not emerge or develop to adulthood, and this number may rise with increased human pressure on these habitats caused by multiple factors (Kietzka et al. 2021, Silva et al. 2021, Lambret et al. 2023). These include soil erosion and siltation caused by deforestation and livestock grazing along riverbanks and invasive alien trees that affect freshwater systems through synergistic effects (Samways 2008).

Dynamics of water abstraction from small montane streams (first- and second-level) may prevent threatened species (such as *P. amboniensis* and *P. bicoerulans*) from becoming abundant and encourage generalist species. Water abstraction affects abundances of many species groups, including fish (Merciai et al. 2017) and dragonflies (Consoli et al. 2021). Damming of waterways can locally impoverish riverine fauna, affect water flow, create lentic conditions in lotic systems, and induce long-term changes in odonate assemblages (Samways 2008). In this study, these newly created spaces appear to favour occupancy by *P. bicoerulans* but fail to guarantee that these microhabitats are suitable for both species' long-term survival and co-occurrence. Without restoring river structure, when a dam is left to follow natural succession and becomes fully vegetated, it is likely to limit the abundance of specialists in favour of widespread generalists (Merciai et al. 2017). Similarly, the silt that accumulates on the ponds is often released into the stream and washed downstream, which alters water chemical properties and occasionally causes algal blooms (Matomela et al. 2021, Munyai et al. 2025). The effects of these recurrent small-scale events, though barely detected in the short term, affect local species co-occurrence and can alter community structure in the long term (Consoli et al. 2021, Masese et al. 2023, Bakare et al. 2024).

Dragonflies and damselflies are agile organisms because they require more than one ecosystem to become mature adults, and it is necessary to define stage-specific and species-specific threats in order to evaluate extinction probabilities (Steenweg et al. 2019, Hogreve & Suhling 2022, Viza et al. 2023). For instance, habitat loss—the sole threat highlighted in the IUCN Red List for *P. amboniensis* and *P. bicoerulans*—is a broad term in the context of odonates and other freshwater invertebrates (*sensu* Forister et al. 2023) and fails to account for all life stages. Co-occurrence patterns segregated by life stages can be used as a baseline for both aquatic and terrestrial ecosystem restoration because they provide information about the stability of ecosystems in their entirety and the dynamics of larger insect communities (Mendes et al. 2017, Steenweg et al. 2019, Oliviera-Junior et al. 2021, Cranston et al. 2023, Piczak et al. 2024). Environmental properties such as water quality and distribution of microhabitats influence species co-occurrence and interactions as indicators of successful wetland restoration (Pires et al. 2020, Cerini et al. 2023, Munyai et al. 2025).

The approach used in this study has wide applications because it reveals the life-history mechanisms that determine species survival under increasing human encroachment by connecting co-occurrence patterns of threatened damselflies with their functional traits and abundances (Clausnitzer et al. 2011, Redford et al. 2013, Cerini et al. 2023, Cranston et al. 2023). It has been shown that even when protected areas are rarely designed with the conservation of insects in mind (e.g., Chowdhury et al. 2023), the conservation of threatened species can be achieved through the conservation of targeted non-threatened species (Hallman et al. 2017, Baker et al. 2019). This work complements other studies by providing a practicable perspective for planning conservation and restoration of human-dominated landscapes in a rapidly changing world (Samways et al. 2020, Kawahara et al. 2021, Piczak et al. 2024).

Conclusion

Two threatened Afromontane species co-occur but utilise different microhabitats. These distantly related damselfly species are a good case for comparative studies because their distinct morphological differences are evident and adequate to infer variation in life history. Combining occupancy modelling with functional traits of sympatric species is a useful way to understand potential interaction between species. While this study is not adequate to decipher the historical pathways that influenced the evolution of these traits, it reveals adaptations to different microhabitats and the co-occurrence of threatened damselflies in montane streams. In order that such species are conserved simultaneously, there is a need to ensure habitat heterogeneity as a common ground for ecosystem restoration when multiple threatened species are involved.

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Author contributions

Conceptualisation: AMK, AWK, and MNG; methodology: AMK, IWN, and AWK; formal analysis: AMK; data collection: AMK, AWK, and MNG; data curation: AMK; writing—original draft preparation: AMK and IWN; writing—review and editing: AWK, MNG, and AWG; visualisation: AMK; supervision: AWK and MNG; funding acquisition: AMK, IWN, AWK, AWG, and MNG. All authors have read and agreed to the published version of the manuscript.

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Supplementary material

Data and analysis are available in Supplementary material S1.

Data availability

All data that were generated and analysed in this study have been included in the article and/or its supplementary material.

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Disclosure statement

The authors declare no conflict of interest.

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Tables

Table 1: Mean and range (min-max) of water quality parameters measured from sampling sites at forest streams in Kangaita and Irangi Forests, Mount Kenya

Stream	DO (mg/L)	EC (µS/cm)	ORP (mV)	pH	TDS (ppm)	Temperature (°C)	Turbidity (NTU)
Ciaminogia	3.90 (3.9–3.9)	36.00 (32–42)	183.00 (159–208)	7.84 (7.68–7.93)	18.33 (17–21)	18.00 (16.7–18.9)	8.34 (3.43–15.53)
Rwamuthambi	4.18 (3.6–4.6)	26.50 (26–27)	270.50 (247–294)	7.86 (7.86–7.89)	13.00 (13–13)	14.60 (13.9–15.3)	4.22 (2.64–6.52)
Mukengeria	3.90 (3.8–4.2)	15.30 (14–16)	334.00 (153–585)	7.99 (7.75–8.14)	7.33 (7–8)	15.17 (14.1–16.5)	7.39 (2.77–15.63)
Ruiru	4.40 (4.2–4.6)	38.60 (34–42)	189.00 (163–212)	7.32 (7.11–7.56)	15.25 (14–17)	14.52 (13.7–16.3)	11.38 (2.92–16.06)
Rundu	4.56 (4.1–4.9)	50.40 (46–68)	215.20 (135–381)	7.67 (6.61–8.26)	25.60 (23–35)	19.02 (17.1–22.1)	4.02 (0.65–8.35)
Ena	5.56 (5.2–5.9)	40.75 (23–64)	232.50 (204–273)	7.92 (7.22–8.53)	20.75 (13–32)	13.15 (12.2–14.6)	4.69 (3.10–6.90)
Karutune	4.65 (4.6–4.7)	42.25 (36–46)	174.60 (108–248)	7.94 (7.14–8.65)	21.60 (17–24)	15.85 (13.9–18.3)	4.32 (2.27–6.20)
Kiye	5.05 (4.4–5.7)	37.80 (16–47)	185.80 (163–201)	7.91 (7.21–8.40)	24.80 (12–48)	17.92 (12.9–22.8)	5.07 (3.72–6.52)
Nyanjara	6.25 (6.2–6.3)	34.50 (18–48)	265.75 (208–373)	8.11 (7.75–8.37)	21.00 (17–23)	13.20 (12.5–13.9)	4.55 (3.40–6.50)
Thambana	3.95 (3.6–4.3)	38.60 (32–45)	199.00 (124–257)	7.95 (7.43–8.64)	21.20 (18–26)	12.56 (10.5–14.3)	3.73 (2.39–5.60)

Note: Abbreviations: DO: Dissolved Oxygen, EC: Electrical Conductivity, ORP: Oxidation-Reduction Potential, pH, TDS: Total Dissolved Solid

Table 2. Candidate models used to evaluate co-occurrence and detection probability of *Platycypha amboniensis* Martin, 1915, and *Pseudagrion bicoerulans* Martin, 1907, using a two-species conditional occupancy model.

Occupancy	Detection	AICc	ΔAICc	Weight	Likelihood	Num. Par
Co-occurrence between larvae of *P. amboniensis* and *P. bicoerulans*						
ψA(.) ψBA(.) ψBa(.)	pA(.) pB(.) rA(.) rBA(.) rBa(t)	645.11	0	0.356	1	9
ψA(.) ψBA(.) ψBa(t)	pA(.) pB(.) rA(.) rBA(.) rBa(.)	645.61	0.504	0.276	0.777	8
ψA(.) ψBA(t) ψBa(.)	pA(.) pB(.) rA(t) rBA(.) rBa(.)	647.44	2.331	0.111	0.312	9
ψA(t) ψBA(.) ψBa(.)	pA(.) pB(.) rA(.) rBA(t) rBa(.)	647.67	2.562	0.099	0.278	9
ψA(.) ψBA(t) ψBa(t)	pA(.) pB(t) rA(.) rBA(.) rBa(.)	647.75	2.640	0.095	0.267	10
ψA(t) ψBA(t) ψBa(.)	pA(t) pB(.) rA(.) rBA(.) rBa(.)	650.81	5.703	0.020	0.058	11
Co-occurrence between adults of *P. amboniensis* and *P. bicoerulans*						
ψA(.) ψBA(.) ψBa(.)	pA(.) pB(.) rA(.) rBA(.) rBa(t)	603.84	0	0.333	1	7
ψA(.) ψBA(.) ψBa(t)	pA(.) pB(.) rA(.) rBA(.) rBa(.)	604.19	0.357	0.278	0.837	5
ψA(.) ψBA(t) ψBa(.)	pA(.) pB(.) rA(t) rBA(.) rBa(.)	606.29	2.455	0.097	0.298	8
ψA(t) ψBA(.) ψBa(.)	pA(.) pB(.) rA(.) rBA(t) rBa(.)	606.43	2.592	0.091	0.274	9
ψA(.) ψBA(t) ψBa(t)	pA(.) pB(t) rA(.) rBA(.) rBa(.)	608.58	4.739	0.031	0.094	10
ψA(t) ψBA(t) ψBa(.)	pA(t) pB(.) rA(.) rBA(.) rBa(.)	608.72	4.907	0.029	0.086	8

Notes: ψA = occupancy of species A; ψBA = occupancy of species B in the presence of species A; ψBa = occupancy of species B in the absence of species A on the site; rA = detection probability of species A in the presence of species B; pA = detection probability of species A in the absence of species B; pB = detection probability of species B in the absence of species A; rBA = detection probability of species B when species A is present and detected; rBa = detection probability of species B when species A is present but not detected.

Table 3. Estimates of occupancy (ψ), detection probability (p and r), and species interaction factor (SIF or γ) for *Platycypha amboniensis* Martin, 1915, and *Pseudagrion bicoerulans* Martin, 1907, determined using a two-species conditional occupancy model with data from Irangi and Kangaita Forests in Mount Kenya

	Larvae			**Adults**		
Co-occurrence	Estimate	SE	Range	Estimate	SE	Range
ψA	0.995	0.049	(0.884–1.000)	0.915	0.061	(0.695–0.981)
ψBA	0.969	0.060	(0.377–0.999)	0.971	0.032	(0.787–0.997)
ψBa	1.000	0.000	(1.000–1.000)	1.000	0.000	(1.000–1.000)
pA	0.473	0.390	(0.040–0.951)	0.625	0.122	(0.256–0.744)
pB	0.140	0.589	(0.000–1.000)	0.504	0.497	(0.252–0.966)
rA	0.334	0.036	(0.268–0.408)	0.338	0.065	(0.225–0.478)
rBA	0.429	0.117	(0.227–0.657)	0.328	0.090	(0.181–0.524)
rBa	0.401	0.048	(0.311–0.499)	0.308	0.076	(0.183–0.473)
γ	0.999	0.002	(0.995–1.002)	0.997	0.002	(0.998–1.001)
ψB	0.960	0.042	(0.736–0.995)	0.973	0.018	(0.922–0.993)
ψAB	0.926	0.044	(0.781–0.978)	0.888	0.043	(0.853–0.984)

Notes: ψA, ψBA, ψBa, rA, pA, pB, rBa, and rBA as used in Table 3; γ = co-occurrence ($\gamma = 1$ means independence, $\gamma < 1$ = avoidance, and $\gamma > 1$ = overlap); ψB = probability of occupancy for species B, regardless of occupancy of species A; ψAB = probability of both species being present.

Table 4: Morphological traits of adults and larvae of *Platycypha amboniensis* Martin 1915 and *Platycypha bicoerulans* Martin 1907 from Irangi and Kangaita Forests in Mount Kenya.

Stage	**Species**	**Trait**	**Female**	**Male**	**N**	**Mean**	**T-test**	**df**	**p-value**
Adult	*P. amboniensis*	Abdomen length	17.80 (17.5–18.2)	19.95 (18.9–21.2)	19	19.37	-8.09	11.95	>.001
		Body length	29.70 (28.2–30.8)	33.32 (32.1–35.1)	19	32.35	-5.67	4.70	0.003
		Hind femur length	5.58 (4.9–6.6)	5.49 (4.9–6.2)	19	5.51	0.21	3.31	0.847
		Thorax length	8.55 (7.7–9.4)	8.79 (7.9–10.1)	19	8.74	-0.52	3.82	0.629
		Wing area	100.94 (87.28–120.32)	84.37 (68.91–93.68)	65	87.42	4.78	11.77	>.001
		Wing length	27.83 (25.73–30.34)	25.81 (24.64–27.24)	65	26.18	3.47	24.86	0.002
		Wing perimeter	80.96 (71.96–90.35)	72.27 (62.01–127.43)	65	73.87	1.97	31.46	0.058
		Wing width	5.76 (5.19–6.36)	5.49 (4.69–9.25)	65	5.54	1.18	3.11	0.320
	P. bicoerulans	Abdomen length	33.40 (32.2–35.7)	34.36 (32.3–36.0)	9	33.93	-0.88	6.47	0.411
		Body length	42.70 (40.9–47)	43.54 (41.7–46.2)	9	43.17	-0.51	4.80	0.634
		Hind femur length	4.88 (4.3–5.4)	5.00 (4.3–5.3)	9	4.94	-0.40	5.63	0.704
		Thorax length	6.85 (6.6–7.3)	6.48 (5.6–7.3)	9	6.64	1.13	6.25	0.299
		Wing area	98.87 (85.37–105.89)	101.68 (74.81–127.06)	75	101.12	-1.37	39.20	0.178
		Wing length	26.58 (24.9–27.91)	26.83 (23.85–29.62)	75	26.78	-0.52	19.95	0.610
		Wing perimeter	82.15 (61.85–139.56)	84.99 (61.34–145.48)	75	84.42	-0.35	25.39	0.726
		Wing width	6.11 (5.36–6.65)	6.16 (5.15–8.24)	75	6.15	0.64	6.86	0.541
Nymph	*P. amboniensis*	Abdomen length	10.43 (9.2–11.2)	10.23 (9.6–10.7)	7	10.34	0.35	4.96	0.741
		Appendages	5.73 (5.3–6.2)	5.77 (5.4–6.2)	7	5.74	-0.13	4.69	0.902
		Body length	22.63 (22.1–23.5)	22.30 (22.1–22.7)	7	22.49	0.91	4.79	0.407
		Gonapophyses	1.98 (1.8–2.1)	-	4	-	-	-	-
		Hind femur length	5.85 (5.5–6.6)	5.67 (5.3–6.0)	7	5.77	0.57	5.00	0.596
		Prementum	3.63 (3.6–3.7)	3.80 (3.8–3.8)	7	3.70	-7.00	3.00	0.006
		Wing Sheath	5.50 (5.4–5.7)	5.57 (5.4–5.8)	7	5.53	-0.48	3.36	0.662

P. bicoerulans	Abdomen length	12.27 (12.1–12.5)	12.27 (11.7–12.6)	6	12.27	0.00	2.69	1
	Appendages	6.77 (6.4–7)	6.67 (6.1–7.0)	6	6.72	0.29	3.44	0.786
	Body length	25.47 (25.1–26)	25.50 (25.1–25.9)	6	25.48	-0.09	3.89	0.930
	Gonapophyses	1.97 (1.9–2.1)	0.87 (0.8–1.0)	6	1.42	11.67	4.00	>.001
	Hind femur length	5.30 (5.2–5.5)	5.40 (5.3–5.6)	6	5.35	-0.71	4.00	0.519
	Prementum	3.40 (3.3–3.5)	3.67 (3.3–4.0)	6	3.53	-1.26	2.32	0.318
	Wing Sheath	6.27 (6.1–6.6)	6.40 (6.2–6.7)	6	6.33	-0.59	3.97	0.587

Table 5. Similarities and differences in larval morphology of *Platycypha amboniensis* Martin 1915 and *Pseudagrion bicoerulans* Martin 1907 and functional traits that account for ecological adaptations

Morphology	**Functional traits**	**Ecological adaptations**
P. amboniensis		
General habitus	The body is short, stout, cylindrical, and setose; muddy brown to dark brown; the legs are long.	Larvae sit and wait to ambush prey; their stout body and long legs are suitable for clinging to stones and gravel substrates. Setae attract mud or debris for camouflage in dark/brown environments.
Mouthparts	Labium brown without setae, labial palps with long hooks, mandibles setose and heavily sclerotised, hypopharynx well developed	Labium colour blends with the environment, hooks for grasping prey, and strong mouthparts for processing food with hard cuticles.
Caudal lamellae	Epiproct rudimentary; paraprocts elongate, triquetral, setose and spinose	Long lamellae with spines are used for autotomy to escape predators.
Gonapophyses	Well developed in female, marginal in male	Fast development of larvae
P. bicoerulans		
General habitus	The body is elongate, cylindrical, pale or dark brown; the legs are short.	Larvae actively search for prey; their colour blends with litter and vegetation in the littoral zone.
Mouthparts	Labium long, pale to translucent, with premental/labial setae; labial palps wide	Pale colour of labium for 'invisibility' while ambushing prey, wide labial palps for better clutching of larger prey, and setae enhance sensitivity.
Caudal lamellae	Epiprocts and paraprocts are elongate, leaf-like, flattened, and pigmented.	Lamellae are used for swimming, respiration among vegetation, agonistic display among conspecifics, and autotomy to escape predators.
Gonapophyses	Well developed in male and female	Quick maturation of adults