

SHORT COMMUNICATION

Insect Conservation
and Diversity

Invasive insect colonisation shapes the population distribution of an island-endemic scaly cricket

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Editor: Alan John Stewart and **Associate****Editor:** Seán Gary Brady**Abstract**

1. To what extent can island-native insect populations be shaped by non-native insects? The Ascension Island scaly cricket *Discophallus ascension* (Orthoptera: Mogoplistidae) of volcanic Ascension Island in the South Atlantic is abundant on young coastal lava flows. I aimed to assess whether non-native insect colonisation modified the population distribution of this island-endemic insect.
2. I trapped insects across 12 sampling blocks/transects spanning coastal and inland sand and lava flows up to 534 000 years in age. I modelled the abundance of *D. ascension* and compared predicted population distributions with and without the presence of two significant invasive insect taxa: the tropical house cricket *Gryllobates sigillatus* (Orthoptera: Gryllidae) and ants (Hymenoptera: Formicidae).
3. The invasive insect species disproportionately colonised older and inland lava flows. On flows <10,000 years in age and within 20 m of the coastline, *D. ascension* population size with invasive insect presence was predicted to be 48.7% relative to without. On flows >10,000 years in age or beyond 20 m inland, *D. ascension* population size with invasive insect presence was predicted to be just 12.1% relative to without. This suggested that the current *D. ascension* distribution is partly a result of habitat preference, but largely residual of invasive insect colonisation on older and inland flows.
4. This study demonstrates that apparent habitat specialism of island-endemic insects may instead indicate extirpation from other habitats by invasive species. Landscape heterogeneity can facilitate some degree of refuge from invasive species that may be slower or unable to colonise certain habitats.

KEYWORDS

ants, competition, habitat specialism, invasion ecology, island ecology, Orthoptera, population change, predation, species conservation, species distributions

INTRODUCTION

Non-native species introductions are among the most important global threats to insects (Wagner et al., 2021). Oceanic islands, which accommodate high levels of species endemism (Kier et al., 2009), are

highly vulnerable to negative impacts of species introductions (McGlynn, 1999; Suarez et al., 2009). A subset of introduced species can be considered 'invasive' when they inflict negative impacts where they establish, and such invasive species are responsible for 90% of extinctions on islands (Roy et al., 2024). Distributions and ecologies of

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endemic insects are often poorly understood but are important for species conservation on degraded islands (Gray et al., 2019). This includes knowledge of how and where non-native insects may displace native species (Fortuna et al., 2022). Many insects endemic to oceanic islands are threatened by invasive species and confined to small areas of habitat (Sharp & Gray, 2025). There are few case studies examining the extents to which limited ranges of island-endemic insects are shaped by non-native species colonisation.

Ascension Island is a volcanic island in the South Atlantic Ocean (7.95° S, 14.36° W) and is just one million years in age (Jicha et al., 2013; Nielson & Sibbett, 1996). Lava flows comprise around 57.1% of the land area (derived from Nielson & Sibbett, 1996). The island's youngest lava flows are just a few hundred years in age (Preece et al., 2018) and the oldest are approximately 791,000 years in age (Nielson & Sibbett, 1996). The landscapes comprise early successional and limited native animal and plant diversity (Ashmole & Ashmole, 1997; Duffey, 1964), and many introduced species (Sharp & Tawatao, 2023; Sherwood et al., 2024a; Sherwood et al., 2024b; Sherwood & Sharp, 2023). The Ascension Island scaly cricket, *Discophallus ascension* Gorochov 2009 (Orthoptera: Mogoplistidae), is endemic and has previously been reported only from the youngest and most barren lava flows on Ascension Island (Ashmole & Ashmole, 1997) – arguably the most ecologically inaccessible sites on the island for their lack of loose substrate, near-complete absence of vegetation and extreme surface exposure to sunlight. By contrast, the older flows comprise further-eroded substrate that may be more readily colonisable by non-native generalist species, including spreading non-native vegetation (Sharp et al., 2025) and insects (Chin et al., 2024). *Discophallus ascension* feeds preferentially on crab carcasses among other animal protein sources (Chin et al., 2024) and the single present terrestrial crab species, hare-lipped land crab *John-garthia lagostoma* Milne-Edwards 1837, utilises much of the volcanic lowlands (Hartnoll et al., 2010). Furthermore, *D. ascension* will oviposit in both fine volcanic sediment and shell sand (Chin et al., 2024) and thus is not tightly tied to coastlines for reproduction as some other scaly crickets are (Vahed, 2019). *Discophallus ascension* has no known ecological niche requirement that confines the species specifically to young or coastal lava flows.

Non-native species colonisation may have shaped populations of *D. ascension*. Established introduced species that either actively compete for limited resources with or predate directly on *D. ascension* must, by definition, reduce its survival. The three established introduced insect species previously found to be of potential competitive or predatory threat to *D. ascension* are: the tropical house cricket *Grylloides sigillatus* Walker 1869, longhorn crazy ant *Paratrechina longicornis* Latreille 1802, and American cockroach *Periplaneta americana* Linnaeus 1758 (Chin et al., 2024). *Grylloides sigillatus* and *P. americana* have been established on Ascension Island since at least the 19th century (Dahl, 1892) and *P. longicornis* since 1958 (Duffey, 1964). Each of *G. sigillatus*, *P. longicornis*, and *P. americana* were found to be attracted to and feed on the native crab and fish carcasses favoured by *D. ascension* on Ascension Island lava flows. *Paratrechina longicornis* and *P. americana* were observed also directly killing and feeding on

live crickets deployed as an experimental surrogate for *D. ascension* (Chin et al., 2024). All three species are globally widespread (Ma et al., 2019; Otte, 2006; Wetterer, 2008), but only *P. longicornis* (as a household and agricultural pest; Wetterer, 2008) and *P. americana* (as a household pest and disease vector; Ma et al., 2019) are considered globally invasive. If in direct active competition with and thus reducing individual survival of *D. ascension*, *G. sigillatus* might be considered an invasive species on Ascension Island also. These non-native generalist species may be able to colonise older lava flows but be unable to persist on younger flows due to their comparative barrenness and harsh environmental conditions.

Ascension Island's simple and degraded lava flow ecosystems present an ideal case study for quantifying the relative importance of non-native insect colonisation on an endemic insect. This is because, firstly, the ages of Ascension Island's lava flows describe a convenient linear gradient in habitat related to erosion and presumed ecological accessibility. Secondly, the focal endemic species of this case study, *D. ascension*, appears to be relatively generalist in its ecology. Thirdly, non-native insects are thought to compete with and predate on *D. ascension* on lava flows (Chin et al., 2024), and thus present a plausible threat to *D. ascension* populations. I aimed to assess whether non-native insects significantly shaped *D. ascension* populations. I sampled *D. ascension*, predicted the species' population distribution from non-native insect presence and habitat variables, and mapped the relative population of *D. ascension* both with and without non-native insects. I hypothesised that *D. ascension* populations were more so impacted by non-native insect colonisation on older and inland lava flows, and that the species has been extirpated from older lava flows by non-native insects.

METHODS

I sampled *D. ascension*, *G. sigillatus*, ants (there are 17 species on Ascension Island and all are non-native; Sharp & Tawatao, 2023) and *P. americana* across Ascension Island in January 2023 (Sharp, 2024; S1). Sampling locations were purposefully placed across the island area and across a range of habitats to facilitate prediction and mapping of *D. ascension* population distribution. The locations were separated into seven blocks and five transects spanning lava flows of various ages, and sand sites around the island (S2). There were a total of 83 trapping locations. Sand sites were sampled as a non-lava control – they were the only habitats other than lava flows which were present around the island, both coastal and inland, and therefore represented the most appropriate comparison to test whether *D. ascension* distribution was linked to lava habitat or coastline. Five coastal habitat blocks were established at points on the coastline where lava flows, sandy beaches and sea converged. These blocks were designed to differentiate fine-scale occurrence of insects across habitats and thus confirm or refute that the sampled insects favoured lava flows. At each coastal habitat block, one central trap was set approximately 4 m from the waterline (to avoid disruption by breaking waves) where the sand and lava met the sea. From that central trap,

two more were set extending outwards into each of the sand, lava and edge habitats. Traps (seven per coastal habitat block) were separated by 20 m, so that the three outermost trap locations were approximately 40 m from the central point. The exact shapes of each coastal habitat block depended on the natural convergence of habitats. Five lava transects extended inland into lava flows. Pairs of traps, 20 m apart, were set at the coastline (around 4 m from the waterline), 20 m inland, 100 m inland and 500 m inland on each lava flow transect (eight traps per transect). In addition, there were two inland habitat blocks that were both approximately 2500 m inland: one on a lava flow and one on a large sand patch. Inland habitat blocks comprised four individual traps each set in a square with sides of 20 m. The selected inland sampling distances of 4, 20, 100, 500 and 2500 m inland represented an exponential gradient of order 5, with distances equal to $5^{0.86}$, $5^{1.86}$, $5^{2.86}$, $5^{3.86}$ and $5^{4.86}$ m. Sampled lava flow ages ranged from <1000 to 534,000 years in age (S2).

Scaly crickets are cryptic and difficult to detect (Berville et al., 2012; Ingrisch, 2006), so I used purpose-designed baited traps to attract them. The traps comprised 700 mL plastic collection bottles (intended for a malaise trap) which had 1 cm diameter holes drilled at 5 cm intervals around the circumference. Three rings of holes separated by 3.5 cm were drilled around the middle of each bottle, leaving approximately 5 cm of the bottom intact to be part-filled with 70% ethanol for specimen preservation. A 50 mL bait container was suspended inside each bottle and filled up to three-quarters with a rancid meat bait of mashed hot dog. The traps were deployed on lava flows by part-burying them in coarse rocks (>5 cm in approximate diameter). With many points of contact between rocks and the bottle, there were numerous access points whereby insects could fall through the holes in the vertical walls of the bottle from outside. As the traps sat atop the undisturbed substrate and the surrounded rocks formed makeshift ramps upwards and into the bottle, the traps sampled insects moving only on the substrate surface. In sand habitats, the traps were buried up until the first ring of holes so that they were level with and easily accessible from the substrate surface also. Traps were deployed for only 24 hours or a single nighttime period of insect activity (*D. ascension* is nocturnal; Chin et al., 2024) – I intended to deploy traps at each site for the minimum duration necessary to quantify *D. ascension* relative population and minimise losses from their populations. Trapping for additional nighttime periods would have undoubtedly collected a higher number of *D. ascension* individuals, but was unnecessary for fitting strong statistical models (see Results and Discussion). From each trap, I recorded the abundance of *D. ascension* captured and the presence/absence of *G. sigillatus*, *P. americana*, and ants. I disregarded abundance of the non-native insects primarily because the study aims concerned habitat colonisation, but also because these taxa were mostly trapped in either large numbers (for example, a swarm of ants) or complete absence – this rendered quantification of abundance statistically problematic.

I analysed the data using R version 4.3.1 (R Core Team, 2023) and the *lme4* package to fit mixed-effect models (Bates et al., 2015). In aim of mapping the population distribution of *D. ascension*, I first fitted a mixed-effects Poisson generalised linear model predicting abundance at individual trap scale with block/transect included as a

random intercept, and forward-selected fixed terms according to corrected Akaike Information Criteria (AICc; as recommended for small sample sizes by Burnham & Anderson, 2002). All models described the trap location with sand presence/absence (binary, present = 1) and lava presence/absence (also binary, present = 1) in place of fixed intercepts, and these variables were not selected for. Edge habitat was coded as being both sand (value 1) and lava flow (also value 1). Additional fixed parameters were: distance inland of the sampling location from the coast (log-transformed to base 5), the interaction between distance inland and lava presence, lava age (only where lava was present), the interaction between distance inland and lava age, and the presence/absence of each of *G. sigillatus*, *P. americana* and ants. The next requirement for mapping the *D. ascension* population distribution was to predict the occurrence of the non-native insect taxa selected for in the model of *D. ascension* abundance. To do so, I fitted mixed-effects logistic regression models predicting occurrence with block/transect included as a random intercept. The candidate terms were the same as for *D. ascension* and were also selected via AICc but excluded the presence/absence of non-native insects. During all model selection procedures, the Variance Inflation Factor (VIF) was calculated between explanatory fixed variables to check for collinearity (Dormann et al., 2013; Naimi et al., 2014). Post-hoc pairwise differences in marginal means were estimated between sand, edge and lava flow for each fitted model using the *emmeans* package (Lenth, 2024) to identify potential habitat preference at fine spatial scales.

I used the fitted models to extrapolate the occurrence of non-native insects impacting *D. ascension* abundance across Ascension Island, and next extrapolate *D. ascension* population distribution given the presence or absence of non-native insects. I calculated distance inland across the entire island area and manipulated spatial data using the *terra* package (Hijmans, 2025). Many of Ascension Island's lava flows were dated by either Jicha et al. (2013) or Preece et al. (2018). For those that had not been dated, I assigned them the median value of other dated formations fitting the same three-tier age categorisation that Nielson and Sibbett (1996) delineated by physical structure and mapped across Ascension Island. Using this information, I predicted the probability of colonisation (0–1) by the modelled non-native insect taxa. With these additional maps, I predicted the relative abundance of *D. ascension* with and without the presence of non-native insects. Relative abundance was scaled between 0 and 1, where 1 was the maximum estimated in the absence of non-native insects. Calculations of per-area difference in *D. ascension* relative abundance with and without non-native insects were used to estimate island-scale effects on populations. Bootstrapped confidence intervals were calculated by sampling fixed parameter estimates from the *D. ascension* mixed model 1000 times from their multivariate distribution and recalculating estimates of proportional abundance change.

RESULTS AND DISCUSSION

I collected 2076 arthropods, of which 299 were crickets. This number included 194 endemic *D. ascension* from 23 traps and 104 non-native

G. sigillatus from 33 traps. *Dis ascension* was detected from coast to 500 m inland. A single individual of the non-native Canarian tiny cricket *Cycloptiloides canariensis* Bolívar 1914 was trapped also but was not included in analyses because of its low abundance. Ants were detected at 14 and *P. americana* at 11 of the trap locations. The ants comprised *Monomorium subopacum* Smith 1858, *P. longicornis*, *Pheidole megacephala* Fabricius 1793, and *Solenopsis globularia* Smith 1858. The maximum variable VIF, 5.65 (S3), was less than the critical value of 10, which could be considered to indicate that collinearity between predictor variables was reasonably low (Dormann et al., 2013).

Discophallus ascension population distribution was related to both habitat variables and non-native insect presence (Figure 1; Table 1; model selection: S3). The species preferred edge habitat over sand (marginal means Z ratio: $p < 0.001$; S4), and in turn lava over edge ($p < 0.05$). It was trapped in higher abundance close to the coast ($p < 0.001$) and on younger lava flows ($p < 0.05$), but abundance was higher inland on older flows compared with younger ($p < 0.001$). These results confirmed that *D. ascension* is associated with lava

flows, but also suggested that the previously documented occurrence of *D. ascension* on youngest flows (Ashmole & Ashmole, 1997) unlikely represented habitat specialism. This follows known *D. ascension* ecology – the species scavenges on animal protein including crab and beached fish and can oviposit on fine sediment (Chin et al., 2024). Those resources are largely absent from young inland flows of coarse volcanic rock. Carcass resources are probably scarcer inland, but land crabs are still present (Hartnoll et al., 2010) and further-eroded volcanic substrate may provide pockets of sediment suitable for oviposition. Older inland lava flows may therefore be suitable for *D. ascension* habitation, at least in low abundance. *Discophallus ascension* was trapped in significantly lower abundance where *G. sigillatus* ($p < 0.001$) or ants ($p < 0.05$) were present. *Periplaneta americana* presence was selected against inclusion in the model via AICc (S3). *Discophallus ascension* populations therefore appeared to be reduced by *G. sigillatus* and ant colonisation but not by *P. americana*.

Grylloides sigillatus exhibited no preference between sand, edge or lava flows (marginal means Z ratio: $p > 0.05$; S4) but occurred more

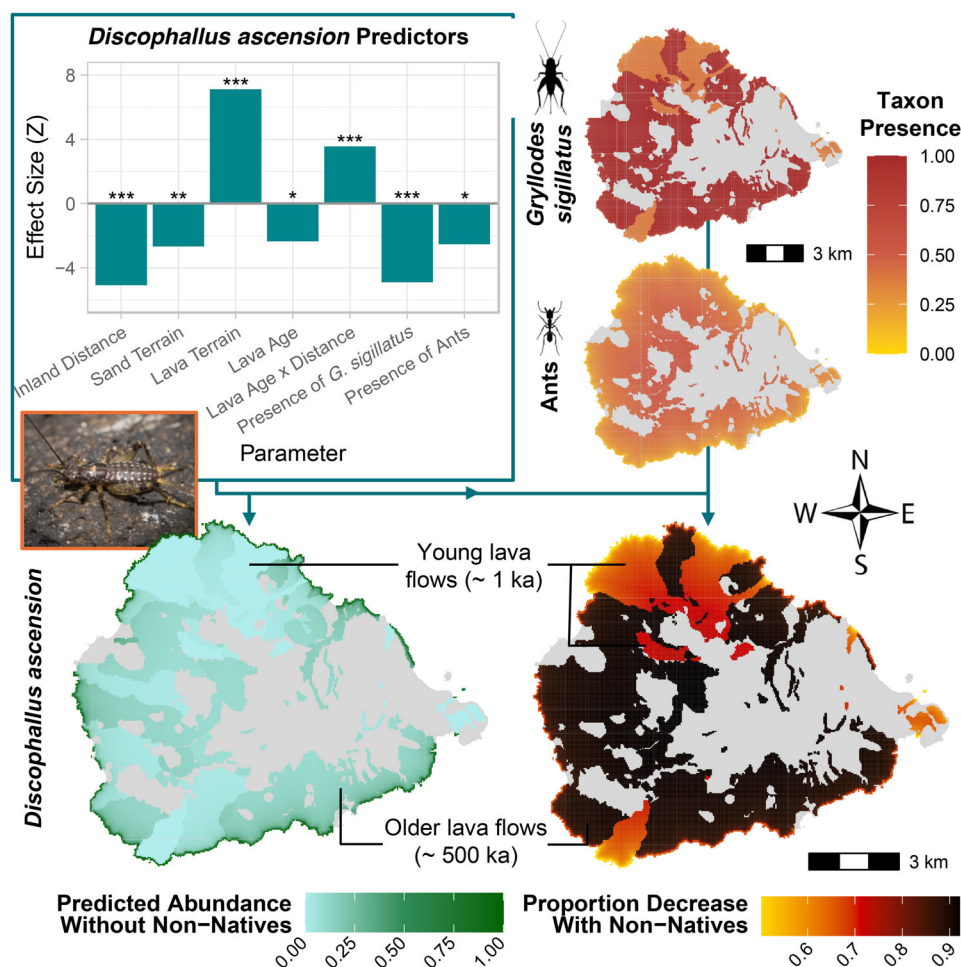


FIGURE 1 Predicted impact of non-native *Grylloides sigillatus* and ants on *Discophallus ascension* populations on Ascension Island's lava flows (all non-grey areas). The bar plot (top-left) summarises the parameter estimates predicting *D. ascension* abundance. Significance of parameters at the $p < 0.05$, $p < 0.01$ and $p < 0.001$ levels are represented by *, ** and *** respectively. The maps for *G. sigillatus* and ants (top-right) report predicted probability of presence. The *D. ascension* maps report predicted relative abundance without both *G. sigillatus* and ants (bottom-left) and the proportional decrease in *D. ascension* with predicted presence of those two non-native taxa (bottom-right).

TABLE 1 Mixed-model parameter estimates predicting non-native insect presence/absence (PA) and *Discophallus ascension* abundance from habitat variables.

Species predicted	Fixed model term	Estimate	SE	Z	p
<i>Gryllobates sigillatus</i> (PA – mixed-effects logistic model)	Sand	−0.68	0.59	−1.16	0.248
	Lava	−0.85	0.47	−1.83	0.067
	Lava age × distance inland	0.41	0.16	2.63	0.009
Ants (PA – mixed-effects logistic model)	Sand	−2.05	0.77	−2.67	0.008
	Lava	−3.22	0.72	−4.50	<0.001
	Distance inland	0.65	0.21	3.09	0.002
<i>Discophallus ascension</i> (Abundance – mixed-effects Poisson model)	Sand	−0.52	0.19	−2.67	0.008
	Lava	4.68	0.66	7.12	<0.001
	Distance inland	−3.27	0.64	−5.08	<0.001
	<i>Gryllobates sigillatus</i> presence	−2.02	0.41	−4.91	<0.001
	Ant presence	−0.97	0.38	−2.54	0.011
	Lava age	−0.88	0.37	−2.36	0.018
	Lava age × distance inland	0.99	0.28	3.56	<0.001

Note: Each taxon was predicted by a separate model. All models included site as a random intercept, and all estimates are on the log link scale.

frequently inland on older lava flows compared with younger flows ($p < 0.01$; Figure 1; Table 1; model selection: S3). Ants were trapped least often on edge habitat (sand – edge & edge – lava marginal means Z ratio: $p < 0.05$) and occurred more frequently inland ($p < 0.01$; Figure 1; Table 1; model selection: S3). Both non-native taxa were therefore able to inhabit lava flows and could be considered more so as habitat generalists for their colonisation of sand habitats. *Gryllobates sigillatus* in particular was predicted to have colonised a large area of Ascension Island's lava flows – over 72% of total lava flow area had over 90% probability of *G. sigillatus* occurrence (Figure 1). The disproportionate presence of these taxa inland and on older flows (*G. sigillatus* only) suggests that those habitats are more readily colonised than younger and coastal flows.

Across Ascension Island's lava flows and sand habitats, I predicted the total population size of *D. ascension* with non-native *G. sigillatus* and ant presence to be just 12.8% (bootstrapped 95% CI: 5.2%–30.6%; Figure 1) compared with their predicted population size without. There was a significant difference in effect between lava flow habitats (bootstrapped $p < 0.001$). On lava flows younger than 10 ka in age and within 20 m of the coastline, *D. ascension* population size was predicted to be 48.7% (95% CI: 37.9%–62.8%) relative to the predicted *D. ascension* population size in the absence of *G. sigillatus* and ants. Across flows either older than 10 ka in age or further than 20 m from the coastline, *D. ascension* population size was predicted to be just 12.1% (95% CI: 5.0%–27.6%) relative to the predicted *D. ascension* population size in the absence of *G. sigillatus* and ants. These estimates indicated that *D. ascension* populations were more so impacted by colonisation on older and inland lava flows compared with young coastal flows.

Gryllobates sigillatus appears to exert a negative impact on *D. ascension* populations, especially on Ascension Island's expansive older and coastal flows. The non-native cricket has been observed

competing for the protein resources favoured by *D. ascension* (Chin et al., 2024). It appears likely that *G. sigillatus* reduces *D. ascension* populations through resource competition, and thus should be considered invasive on Ascension Island. Ants exerted a negative impact on *D. ascension* mostly inland. They were previously observed both directly preying on and competing with experimental live surrogates for *D. ascension* (Chin et al., 2024). Ants were predicted to have a lesser impact on *D. ascension* populations than *G. sigillatus* and are known to be widely detrimental to native island ecosystems where introduced (Krushelnicky & Gillespie, 2010; O'Dowd et al., 2003; Wetterer & Lester, 2012). *Periplaneta americana* was estimated to have the least impact on *D. ascension* populations from the three non-native taxa tested. The species likely persists at relatively low abundance and exerts limited competitive or predatory pressure on endemic insect populations.

These results and prior findings (Chin et al., 2024) together indicate that *D. ascension* inhabits young coastal lava flows largely in refuge from resource competition with and predation by invasive insects. Given the statistical significance ($p < 0.05$) of *G. sigillatus* and ant presence in reducing *D. ascension* abundance, and the very high (87.2%) predicted population reduction of *D. ascension* on older and inland lava flows relative to non-native insect absence, I accept my initial hypothesis. Populations of *D. ascension* appear to be shaped by invasive species colonisation such that the species has largely been extirpated from older lava flows. It could be concluded that invasive species colonisation exerts comparable influence to habitat preference on the population distribution of this island-endemic insect. What may initially be perceived as habitat specialism, specifically on young and coastal lava flows in this case, could result instead from invasive species colonisation. Nonetheless, habitat structure proved to be vital to endemic species survival in this case study. That is because without habitat heterogeneity in the form of young and old

lava flows, there may not have been suitable refuge for *D. ascension* from non-native insects. This study shows that invasive insect colonisation can be a strong determinant of island-endemic insect populations, but habitat heterogeneity may be key to conserving insect biodiversity on oceanic islands degraded by invasive species.

AUTHOR CONTRIBUTIONS

Adam Sharp: Conceptualization; investigation; writing – original draft; writing – review and editing; visualization; validation; methodology; software; formal analysis; project administration; resources; supervision; data curation.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data used in this analysis are freely available at <https://zenodo.org/records/11793944>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Supporting Information.

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