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LETTER

Migratory monarchs that encounter resident monarchs show life-history differences and higher rates of parasite infection

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Abstract

Environmental change induces some wildlife populations to shift from migratory to resident behaviours. Newly formed resident populations could influence the health and behaviour of remaining migrants. We investigated migrant–resident interactions among monarch butterflies and consequences for life history and parasitism. Eastern North American monarchs migrate annually to Mexico, but some now breed year-round on exotic milkweed in the southern US and experience high infection prevalence of protozoan parasites. Using stable isotopes (δ^2H, δ^{13}C) and cardenolide profiles to estimate natal origins, we show that migrant and resident monarchs overlap during fall and spring migration. Migrants at sites with residents were 13 times more likely to have infections and three times more likely to be reproductive (outside normal breeding season) compared to other migrants. Exotic milkweed might either attract migrants that are already infected or reproductive, or alternatively, induce these states. Increased migrant–resident interactions could affect monarch parasitism, migratory success and long-term conservation.

Keywords

Asclepias curassavica, cardenolide profile, *Danaus plexippus*, migrant–resident interactions, *Ophryocystis elektroscirrha*, partial migration, reproductive diapause, stable isotopes, tropical milkweed.

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INTRODUCTION

Wildlife populations that engage in partial migration include both migrant and resident individuals, with migrants moving between habitats seasonally and residents remaining in the same area throughout the year (Newton 2008; Chapman *et al.* 2011a,b). Migrants and residents often differ in reproductive behaviour, body size, predation risk, and in some cases, pathogen infection (Adriaensen & Dhondt 1990; Hendry *et al.* 2004; Hebblewhite & Merrill 2009; Altizer *et al.* 2011). Seasonal migrants and residents can interact and share habitat for part of the year, as reported for Canada Geese (*Branta canadensis*), wildebeest (*Connochaetes taurinus*) and other species (Caccamise *et al.* 2000; Chapman *et al.* 2012; Estes 2014), and such interactions are likely widespread across taxa, given the high incidence of partial migration in wildlife populations (Chapman *et al.* 2011a). However, the ecological implications of migrant–resident interactions represent a critical knowledge gap in migration biology (Brodersen *et al.* 2008; Chapman *et al.* 2011a,b). Migratory animals that share habitat with residents could encounter additional resources or mates, but they might also experience greater exposure to natural enemies or factors that alter their behaviour and movement.

Examining the ecological consequences of migrant–resident relationships could be important for the conservation of migratory species (Chapman *et al.* 2011a), many of which are now threatened (Wilcove & Wikelski 2008). Residency is becoming more common in some populations (Berthold 1999; Griswold *et al.* 2011), as birds, ungulates and other animals establish or expand resident sub-populations due to habitat alteration, climate change or supplemental feeding (Sutherland 1998; Fiedler 2003; Partecke & Gwinner 2007; Jones *et al.* 2014). For instance, a partially migratory population of Great Bustards (*Otis tarda*) in Europe has increasingly shown resident behaviours, a change linked to high mortality of migrants on power lines (Palacín *et al.* 2017). Bats, storks, waterfowl, and numerous other species are showing similar increases in residency (Baskin 1993; Tortosa *et al.* 1995, 2002; Van Der Ree *et al.* 2006). Quantifying the extent to which migrants overlap with and respond to growing resident subpopulations could help improve population projections and inform whether interactions with residents require mitigation.

One critical question is whether residents increase pathogen infection risk for migrants that encounter them. Theoretical models and empirical studies have demonstrated greater infection prevalence for residents compared to migrants in some cases (Cross *et al.* 2010; Akbar *et al.* 2012; Poulin *et al.* 2012; Qviller *et al.* 2013; Hall *et al.* 2014). Seasonal migration can reduce pathogen transmission through several mechanisms, including by periodically enabling migrants to escape parasite-contaminated habitat (*migratory escape*; Folstad *et al.* 1991; Loehle 1995) and by causing disproportionate mortality or loss of infected individuals during strenuous journeys (*migratory culling*; Bartel *et al.* 2011). In contrast, resident

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populations do not experience these processes and, as a result, can suffer higher parasite burdens – with the potential for transmission to migrants (Hines *et al*. 2007; Cross *et al*. 2010; Hill *et al*. 2012).

Another important question is whether resident animals and their habitats alter migrant behaviour, particularly movement. This might occur if resident areas induce migrants to curtail their journeys or modulate the physiological states that facilitate migration. For instance, changes in climate and food have enabled some bird populations to shorten their migrations, using new wintering sites closer to breeding grounds (Elmberg *et al*. 2014; Teitelbaum *et al*. 2016). Sites with year-round residents (providing mates and breeding habitat) might similarly allow shortened migrations. Furthermore, resources at resident sites could modify the physiological states that help animals undertake and survive strenuous journeys (e.g., atrophy of non-essential organs; Dingle 2014). Past work suggested that many migrants initially ignore environmental stimuli that could interrupt migration (Kennedy 1985; Dingle 2014), but this remains understudied and may be different for males (Gatehouse 1997). Moreover, persistent exposure to attractive resources and heightened risks of migratory journeys might modify this.

Here, we focus on the widely recognised monarch butterfly (*Danaus plexippus*), whose annual migration has been well studied (Figure S1), to investigate whether migrants in Texas encounter residents *en route*, and to ask whether differences in infection status or reproductive behaviour are associated with these interactions. To conserve energy for migration, most (although not all) monarchs postpone reproduction during fall and enter a hormonally induced state called reproductive diapause (Herman 1973; Brower *et al*. 1977) as they travel to overwintering sites in central Mexico (Urquhart & Urquhart 1978). In spring, these same monarchs break reproductive diapause, mate, and return to the southern US to lay eggs on milkweed; their progeny and grand-progeny continue northward to recolonise the breeding range (Malcolm *et al*. 1993; Miller *et al*. 2012; Flockhart *et al*. 2013). Past work indicated that this annual journey reduces monarchs' infection prevalence from the specialist protozoan *Ophryocystis elektroscirrha* (OE), through migratory culling and migratory escape (Bartel *et al*. 2011; Altizer *et al*. 2015; Flockhart *et al*. 2018). However, some monarchs now breed year-round in the southern US and do not migrate (Howard *et al*. 2010; Batalden & Oberhauser 2015). Surveys of volunteers indicate that monarch winter-breeding occurs almost exclusively on exotic tropical milkweed (*Asclepias curassavica;* Satterfield *et al*. 2016; D.A. Satterfield and S.A. Altizer, unpublished), which is often planted in gardens, does not senesce during fall like most native milkweeds, and can provide food year-round for larval monarchs in warm climates (Batalden & Oberhauser 2015; Satterfield *et al*. 2015, 2016). Reports from citizen scientists (Howard *et al*. 2010) and a survey of historical documents (Satterfield *et al*. 2015 Supplementary Material) suggest that the planting of tropical milkweed and year-round monarch breeding has become common in recent decades, potentially linked to warmer winters. Previously, we found that resident monarchs in the southern coastal US experience significantly higher OE infection prevalence compared to migrants, likely because of loss of the migratory mechanisms that typically control disease (Satterfield *et al*. 2015, 2016). The impacts of resident monarchs on the infection risk and movement behaviour of migrants have not previously been investigated.

We conducted field sampling and chemical analyses of wild butterflies to ask: (1) Do migrant and resident monarchs share habitat during fall and spring migrations? (2) Are fall migrants that encounter sites with resident monarchs more likely to harbour parasites? (3) Are fall migrants at resident sites more likely to be reproductively active (typically associated with non-migratory behaviour), and do they show evidence of abandoning migration to remain at these locations? We assigned resident and migrant status based on analyses of stable isotope composition to estimate natal origins (using isoscapes based on Malcolm *et al*. 1993; Hobson *et al*. 1999; Dockx *et al*. 2004; Flockhart *et al*. 2013) and cardenolide fingerprints (milkweed secondary compounds) to infer natal host plant species (Malcolm *et al*. 1989). We also collected data on OE infection status, morphometrics and reproductive behaviour. We hypothesised that if migratory monarchs pass through resident sites *en route* to and from overwintering locations, migrants could acquire parasites from residents. Migrants that are reproductively active (primarily in spring but also sometimes in fall) could also lay eggs on parasite-laden tropical milkweed, leading to high infection risk for offspring. Furthermore, encounters with resident monarchs or tropical milkweed might prompt fall migrants in diapause to become reproductive and to halt their journeys (Batalden & Oberhauser 2015).

MATERIAL AND METHODS

Parasite biology

Transmission of OE in monarchs occurs from adults to caterpillars, when infected butterflies (covered with millions of dormant spores on the outside of their bodies) scatter parasites onto eggs or milkweed leaves (McLaughlin & Myers 1970). Caterpillars ingest the spores, and parasites replicate internally. Infected adults can transfer dormant spores to other adults (e.g., during mating), although spores must be consumed by a larva to initiate infection. Infections can lower pupal survival and reduce adult lifespan, body size, mating success, and flight performance (Bradley & Altizer 2005; de Roode *et al*. 2007, 2009).

Field collections and capture-mark-recapture study

To investigate migrant–resident interactions, we sampled a total of 508 adult monarchs and 56 larval monarchs in Texas across nine sites (Fig. 1; Fig. S1), exhibiting either: (a) seasonal monarch activity, where migrants stop to refuel but where monarch breeding does not occur during Dec–Feb (hereafter called *seasonal stopover sites*), or (b) year-round monarch activity, where residents are known to breed during winter on tropical milkweed (hereafter called *year-round breeding sites*). Monarchs inhabit year-round breeding sites throughout the year, but not always continuously if food depletion or hard freezes cause local extinction–recolonisation cycles. Both site types provide flowering nectar plants as stopover resources for migrants, which travel primarily either

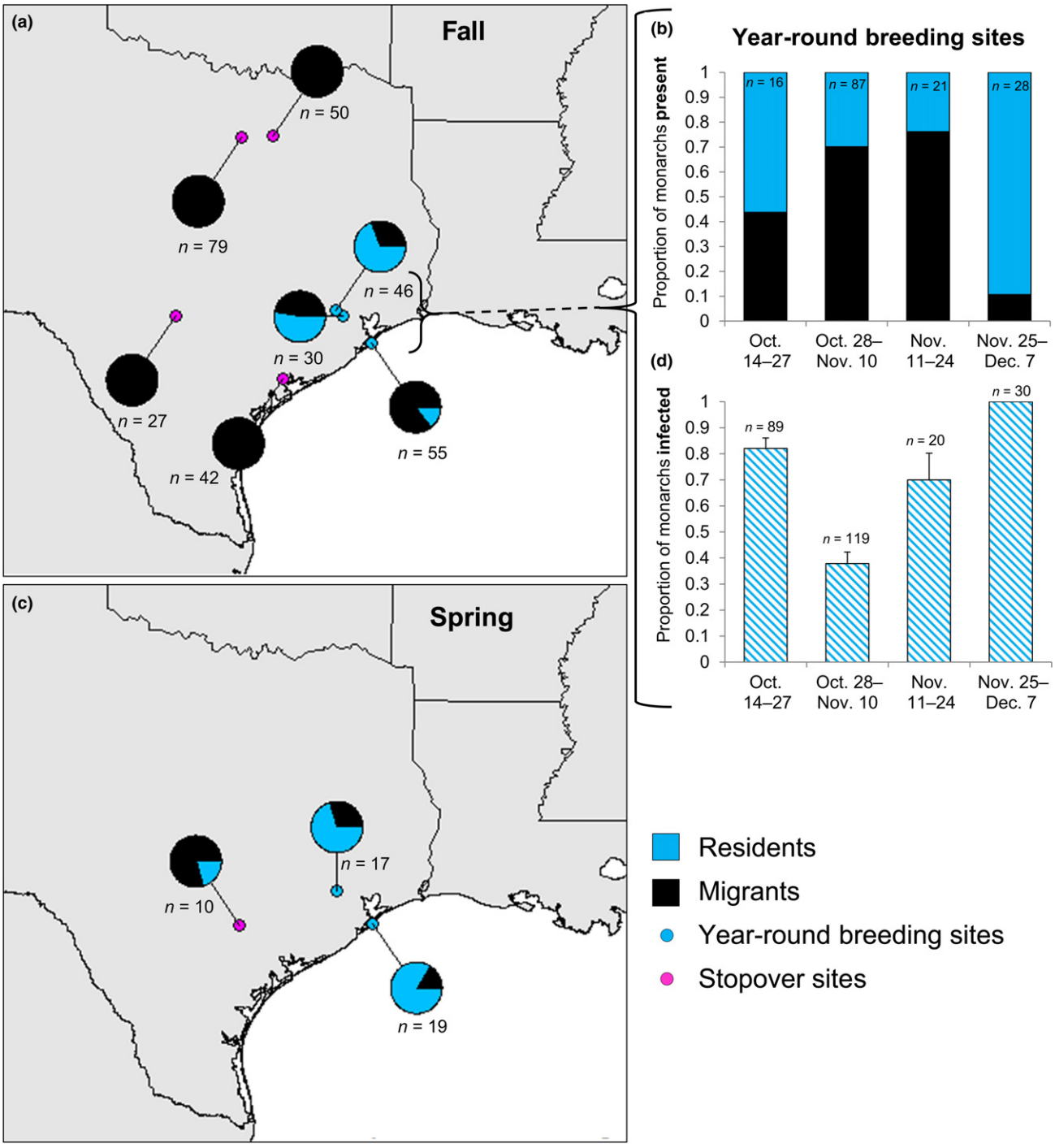

Figure 1 Map of sampling locations in Texas, USA from (a) fall 2014 and (c) spring 2015, with the proportion of sampled adult monarchs that were assigned migrant status (black) or resident status (blue) at *year-round breeding sites* (blue points) and *seasonal stopover sites* (pink points). (b) Temporal changes in the proportion of migrants vs. residents at year-round breeding sites during the fall. (d) Temporal changes in infection prevalence of adult monarchs at year-round breeding sites during the fall.

along the central flyway (extending from the Midwest through central Texas) or the coastal flyway (extending from the Atlantic and Gulf coasts through coastal Texas), where resident monarchs reside (Calvert & Wagner 1999; Howard & Davis 2008). In fall (starting in the peak migration period for each location), we collected 345 adult monarchs across four seasonal stopover sites (N = 200; average of 50/site) and three year-round breeding sites (N = 145; average of 48/site) during Oct–Dec 2014. We also tagged and released an additional 113 adults in a capture-mark-recapture study at three year-round breeding sites (Oct 14–Dec 5) to observe whether migrants halted migration. Adults were tagged before, during and after peak migration period to estimate monarchs' duration of stay, changes in mass, and site fidelity

(Supporting Information B). During spring migration (April 2015), we collected 50 adult monarchs and 56 immature stages from two seasonal stopover sites ($N = 12$ adults from one site; $N = 29$ larvae/singly-laid eggs from *A. viridis* or *A. asperula* from two sites) and three year-round breeding sites ($N = 38$ adults; $N = 27$ pupae or larvae from *A. curassavica* across three sites). Monarchs collected as eggs/larvae were reared in individual containers and fed greenhouse-grown, parasite-free *A. incarnata* (after consuming their natal leaves). Forty eggs/larvae (of 56) survived to adulthood. As detailed below, we assessed captured-and-released butterflies ($N = 113$) for infection status, sex and forewing length. We assessed collected monarchs ($N = 395$) for infection status, sex, forewing length, natal origin, and reproductive status (for fall butterflies), except where noted in Supporting Information A.

Infection status

We examined all adult monarchs for OE infection by pressing clear adhesive tape (1.5 cm) against the abdomen (as in Altizer *et al.* 2000). We viewed samples at 60× to observe parasite spores. Based on prior laboratory work, samples with ≥ 100 spores were classified as infected, indicating infections acquired as larvae. Samples with < 100 spores were classified as uninfected, and most likely resulted from adults acquiring dormant spores from other infected adults during mating or other contact (as opposed to monarchs that ingested spores as larvae, which develop much higher infection loads; Altizer *et al.* 2004; de Roode *et al.* 2009). We assessed immature monarchs for infection at adulthood.

Reproductive status

We evaluated reproductive status for a subset of fall-collected monarchs ($N = 300$ of 345 fall monarchs). We expected that most fall monarchs would be in reproductive diapause, but that a small fraction would exhibit reproductive activity, as shown previously (Calvert 1999; Zalucki & Rochester 1999; Goehring & Oberhauser 2002; Borland *et al.* 2004); reproductive individuals could be older summer-breeding monarchs, or migrants (bound for the southern US or Mexico) in a reproductive state. We examined reproductive activity across both site types, allowing us to compare the background level of reproductive activity for monarchs sampled at seasonal stopover sites to those at year-round breeding sites. Within 5 days of capture, wild-caught females were dissected ($N = 106$ across seven sites) to observe the presence or absence of mature eggs in ovaries (Oberhauser & Hampton 1995). Wild-caught males were placed in mesh cages either outdoors ($N = 163$) or in incubators set to outdoor photoperiod and temperatures ($N = 31$) to observe mating with laboratory-reared females over 8–10 days, or until monarchs experienced 7 days at > 21 °C. We categorised females with mature eggs and males that mated as reproductively active (Supporting Information C).

Natal origins: Stable isotope and cardenolide analyses

We used chemical markers to assign wild butterflies ($N = 390$, of 395 total adults collected in fall and spring) as 'migrant' or 'resident' and to obtain natal origin information (Fig. 2). Stable hydrogen (δ^2H) and carbon ($\delta^{13}C$) isotope composition from wing chitin has been used to estimate geographic regions of natal origin (Wassenaar & Hobson 1998; Miller *et al.* 2012; Flockhart *et al.* 2013; Altizer *et al.* 2015). Mean δ^2H patterns in precipitation (δ^2H_p; amount-weighted mean growing season values) decrease with increasing latitude; these patterns are integrated into the plant tissue eaten by larvae and retained in monarch wing membranes (Hobson *et al.* 1999). Monarchs from northern latitudes have more depleted (negative) values of δ^2H. Mean $\delta^{13}C$ values vary longitudinally in milkweeds, and $\delta^{13}C$ measurements enhance geospatial natal assignment maps (Wassenaar & Hobson 1998; Hobson *et al.* 1999). Wings were stored at −20 °C and prepared (as in Flockhart *et al.* 2013) by washing right hindwings with 2 : 1 chloroform-methanol and weighing and loading wing pieces into capsules. We used an elemental analyser coupled with a continuous-flow isotope ratio mass spectrometer to obtain wing δ^2H and $\delta^{13}C$ following calibration with laboratory standards (Supporting Information D).

Next, we examined cardenolide profiles in wings to determine whether natal host plants were native or tropical milkweed (*A. curassavica,* which feed resident monarchs). In North America, monarch larvae can feed on dozens of milkweed species with varying toxic cardenolides (cardiac glycosides) that are retained in wing tissue (Zalucki *et al.* 2001; Agrawal *et al.* 2012). Thus, chromatography can determine natal host plant species and inform resident and migrant classifications (Malcolm *et al.* 1993; Dockx 2012). *A. curassavica* has high concentrations of diverse cardenolides compared to native milkweeds, such as *A. incarnata* or *A. syriaca,* which support the vast majority of migrants (Seiber *et al.* 1986). To obtain cardenolide profiles, we pulverised right forewings, extracted cardenolides in methanol, dried samples and re-suspended extracts in methanol with a known cardenolide standard (digitoxin). We then used Acquity ultra-performance liquid chromatography (UPLC; Waters Corp, Milford, MA, USA) with a Luna C(18) column (Phenomenex, Torrance, CA, USA) and a photodiode array detector to assess cardenolide concentration, non-polarity (retention time per peak) and diversity (Supporting Information E). We used non-metric multidimensional scaling (NMDS) to represent each cardenolide profile with two Cartesian coordinates. Monarchs with cardenolide concentrations of zero were automatically assigned as migrants (and excluded from NMDS analyses), as these butterflies could not have originated from *A. curassavica*.

Resident and migrant classifications

Based on δ^2H and cardenolide profiles ($N = 390$), we classified monarchs as residents or migrants with two approaches: (1) decision rules developed from previous knowledge about monarch biology and chemical patterns; and (2) a discriminant analysis developed from known resident and migrant monarchs, using δ^2H values, cardenolides and wing length. This dual approach allowed us to assess monarchs based on previously established findings as well as recent data from wild-caught individuals. In subsequent analyses, we only included

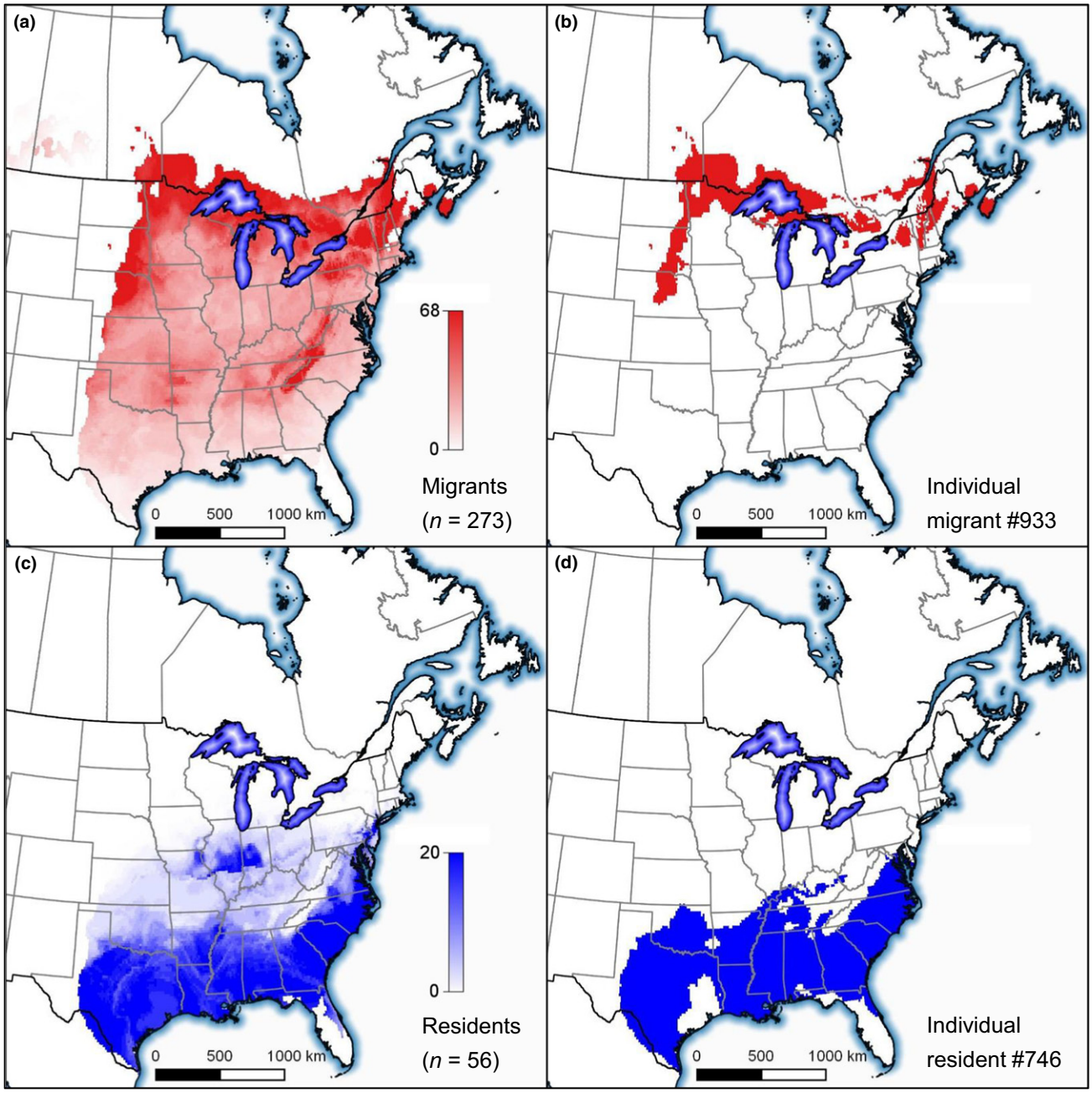

Figure 2 Assigned natal origins based on δ^2H and $\delta^{13}C$ values for (a) monarchs classified as migrants in our analyses ($N = 273$), captured in Texas during fall 2014; (b) monarch #933, an individual classified as a migrant and shown here as an example of a migrant that departed a northern area and was sampled at a year-round breeding location; (c) monarchs classified as residents in our analyses ($N = 56$), captured in Texas during fall 2014; and (d) monarch #746, an individual classified as a resident and shown here as an example.

individuals for which both classification methods agreed (96.7% of samples; $N = 377$ of 390).

In the decision-rules method, we classified monarchs using the following assumptions:

(i) Monarchs were assigned as migrants if they originated from northern latitudes, defined here as corresponding to wing δ^2H <-111‰. This value was informed by previously described monarch δ^2H isoscapes (Hobson *et al.* 1999) and is three standard deviations below the mean δ^2H value for a set of known resident monarchs ($N = 25$ individuals collected from Texan year-round-breeding sites as late-instar larvae/pupae, with average δ^2H=−91‰; range: −76‰ to −104‰; Figure S5). (ii) Of the remaining (southern) individuals, monarchs with cardenolide profiles matching *A. curassavica* were residents. To meet this criterion, a butterfly's NMDS cardenolide coordinates fell within a defined '*A. curassavica* polygon', previously constructed from a separate set of laboratory-raised and field-collected monarchs known to be fed *A. curassavica* ($N = 134$ monarchs; Figure S6). (iii) Monarchs with cardenolide NMDS coordinates falling outside the *A.*

curassavica polygon (> 3 SD's from the cluster means) were considered migrants, as they likely originated from native milkweed. This assumption was tested previously with additional laboratory-raised and field-collected monarchs from known milkweed species (N = 214 monarchs; Figure S6). (iv) Any remaining wild monarchs (N = 11) were deemed unclassifiable and removed from further analyses.

For the discriminant analysis approach, we used 25 known residents (described above) and 84 known migrants (collected at Mexican overwintering sites in Feb 2013 and for which we had previously attained δ^2H values; A. Fritzsche McKay and S.A. Altizer, unpublished) as training data to build discriminant functions including total cardenolide concentration, cardenolide NMDS coordinates, δ^2H values and forewing length (using the *MASS* package in R 3.2.3). Values of δ^{13}C were not available for known migrants. Results indicated that cardenolide concentration was the strongest predictor of resident versus migrant status (Wilk's lambda=0.52, $F_{1,107}$=262.5, $P < 0.001$). Wing δ^2H was informative although not significant (Wilk's lambda=0.15, $F_{1,107}$ = 2.00, P = 0.16, NS). Cardenolide NMDS coordinates and forewing length were not significant predictors of migratory status. Next, to classify wild monarchs, we pre-grouped individuals as residents if cardenolide NMDS values fell within the *A. curassavica* polygon and δ^2H values indicated southern origins (> −111‰; see above). We used the discriminant functions to classify remaining butterflies, placing monarchs into groups with high posterior probabilities (> 0.9). One monarch with a posterior probability < 0.7 was unclassifiable. We proceeded with the 377 monarchs (of 390) for which assignments agreed using both methods.

Geospatial natal assignment maps

We created geospatial natal origin maps using both δ^2H and δ^{13}C values (Fig. 2). We used a multivariate normal probability assignment to calculate posterior probability densities of natal origin for geographically indexed cells across eastern North America (described in Flockhart *et al.* 2013); expected values were based on previously developed δ^2H and δ^{13}C isoscapes for monarchs (Hobson *et al.* 1999). We then reclassified the probability surface to a binary surface (pixels assigned 1 or 0) for each individual, using a 2 : 1 odds ratio whereby the upper third of the probability surface was deemed the region of natal origin.

Data analysis

We used logistic regression to examine how migratory status (migrant vs. resident) varied by site type (seasonal stopover vs. year-round breeding) and time period during fall (divided into five 14-day intervals). Next, we examined differences in reproductive and infection status between migrants and residents. We used a generalised linear mixed model (GLMM) with binomial error distribution to test effects of migratory status, sex and a migratory-status-by-sex interaction on reproductive state during the fall (reproductive or in diapause), with site as a random variable (for N = 286 fall monarchs for which all needed data were available). A second GLMM with the same model structure examined predictors of binary infection status (N = 329). Sample sizes for analyses are described in Supporting Information A.

We next focused only on monarchs assigned as migrants, to ask whether fall migrants were more likely to be reproductive or parasitised at year-round breeding sites compared to stopover sites. We assessed predictors of reproductive status using a third GLMM with binomial error and fixed factors for site type, sex and their interaction (N = 237). We also included δ^2H (a proxy for latitude) as a continuous variable to observe from which regions reproductive migrants originated. Site was a random variable. Infection status of fall migrants was analysed using a fourth GLMM with the same model structure (N = 273). Non-significant terms were eliminated.

For monarchs in the capture-mark-recapture study, we recorded duration of stay and used Bayesian hierarchical Cormack-Jolly-Seber models to estimate site fidelity of presumed migrants versus residents at year-round breeding sites (Supporting Information B). We conducted statistical analyses in R 3.2.3.

RESULTS

Co-occurrence of residents and migrants

Across all sites and sampling periods, we detected 290 migrant and 87 resident monarchs (total N = 377). During fall, the proportion of migrants vs. residents differed significantly by site type (χ^2 = 46.19, df = 1, $P < 0.0001$) and changed nonlinearly with time (χ^2 = 37.35, df = 4, $P < 0.0001$). At seasonal stopover sites, we detected only migrants (N = 198, Fig. 1a), and at year-round breeding sites, we assigned 57% of sampled monarchs as migrants and 43% as residents (N = 131; Fig. 1a). The proportion of migrants at year-round breeding sites increased from Oct through mid-Nov, before sharply declining (Fig. 1b).

Small sample sizes collected during spring (when monarchs disperse and are more difficult to capture) again showed that migrants and residents shared habitat (Fig. 1c). At year-round breeding sites in April, we assigned 24% of sampled monarchs as migrants and 76% as residents (N = 38). At the single seasonal stopover site sampled for adults in spring, we detected eight migrants and two residents.

Reproductive activity

Resident monarchs were more likely to be classified as reproductive (47%; N = 49) than were migrants (18%; N = 237; χ^2=6.08, df = 1, P = 0.01; Fig. 3a) during fall. Across all samples, males were more likely to be reproductive than were females (χ^2=7.55, df = 1, P = 0.006). Sex differences in reproductive status were especially strong among migrants, with 4% of females and 26% of males being reproductive. Sex differences were present but less pronounced among residents (migratory-status-sex interaction: χ^2=4.63, df = 1, P = 0.03).

Fall migrants sampled at year-round breeding sites were three times more likely to be reproductively active (35%; N = 69) than migrants at seasonal stopover sites (11%; N = 169; χ^2 = 5.06, df = 1, P = 0.02; Fig. 3a). Male

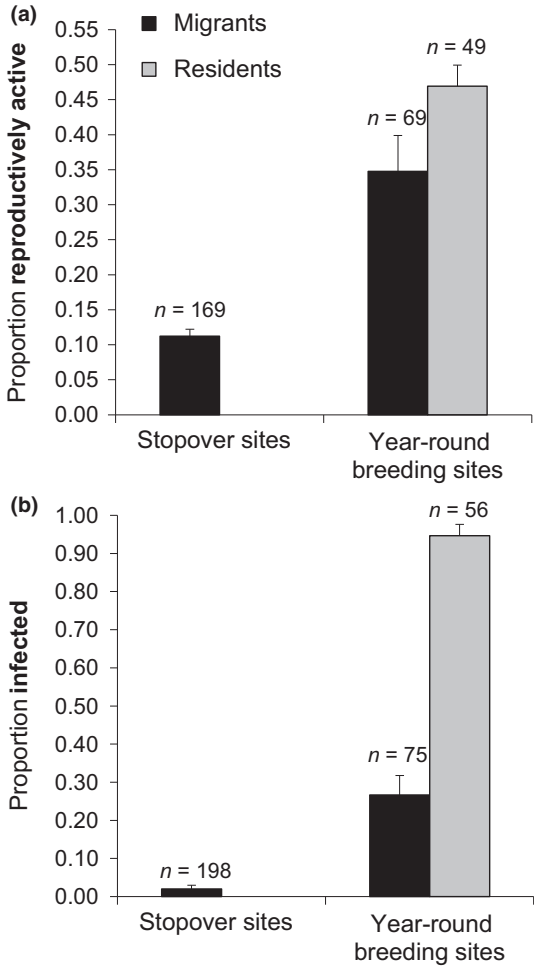

Figure 3 (a) Reproductive activity and (b) infection prevalence among fall migrants and residents sampled at seasonal stopover sites and year-round breeding sites. Resident monarchs were more likely to be reproductive and to be infected than were migrants; residents were only observed at year-round breeding sites during fall, and no residents were observed at seasonal stopover sites. Migratory monarchs sampled at year-round breeding sites were significantly more likely to show reproductive activity and OE infections than were migrants sampled at seasonal stopover sites.

reproductive activity was again significantly higher compared to females ($\chi^2 = 9.98$, df = 1, $P = 0.002$; Fig. 4). Migrants sampled at year-round breeding sites were predominantly male (unlike at seasonal stopover sites), but the interaction term between site type and sex was not a significant predictor of reproductive status. Hydrogen isotope values (correlated with natal origin latitude) did not predict reproductive status.

Infection risk

During fall, 95% of resident monarchs ($N = 56$) and 9% of migrants ($N = 273$) were infected with OE. Thus, migratory status was the strongest predictor of infection in fall ($\chi^2 = 21.51$, df = 1, $P \ll 0.001$; Fig. 3b). Infection status did not differ by sex. Importantly, migrants were 13 times more likely to be infected at year-round breeding sites (27%; $N = 75$) than at seasonal stopover sites (2%; $N = 198$;

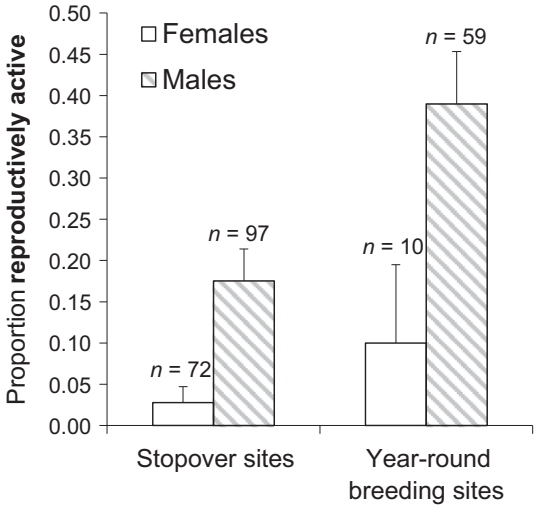

Figure 4 Proportion of fall migrant monarchs that were reproductively active by sex and site type. Migrants were more likely to be reproductive at year-round breeding locations with tropical milkweed as compared to seasonal stopover locations. Males were significantly more likely to be reproductive, regardless of site type.

χ^2=14.03, df = 1, $P = 0.0002$; Fig. 3b), and infected migrants were more likely to originate from southern latitudes (less negative δH^2; $\chi^2 = 16.12$, df = 1, $P < 0.001$). As fall progressed, the total proportion of butterflies infected at year-round breeding sites initially decreased, as healthy migratory monarchs arrived and 'diluted' site prevalence, and later increased, as migrants departed and infected residents remained (Fig. 1d).

In spring, resident monarchs continued to show high infection prevalence (71%; $N = 31$) relative to migrants (24%; $N = 17$). For larvae sampled during spring, infection prevalence was higher at year-round breeding sites (41%; $N = 27$) compared to sites with seasonal milkweed only (0%; $N = 13$).

Monarch movement behaviour at year-round breeding locations

The capture-mark-recapture study included 113 monarchs not used in natal origin assignments. Because most of these monarchs were not recaptured, migratory status could not be confirmed, and we proceeded with capture-mark-recapture analyses (Supporting Information B) by assuming that infected monarchs were likely residents ($N = 100$) and uninfected monarchs were likely migrants ($N = 37$), based on infection patterns noted earlier. We recaptured 40% of 'presumed residents' and 8% of 'presumed migrants' at least once. This limited dataset suggests that most migrants continued migrating, but a small fraction halted their journeys.

An additional 24 individuals were marked, recaptured, collected and later used in natal origin analyses (described above); we assigned 12 as migrants, nine as residents and three as unclassifiable. Of the 12 migrants, 11 stayed at the same year-round breeding site for 7 days or more (five remained >20 days) and had presumably terminated migration. Migrants that stayed at year-round breeding sites were all male; they also tended to be reproductively active (6 out of

9 assessed), infected with OE (10 of 12) and originated from more southern latitudes (mean $\delta^2H = -95‰$, range = −126 to −80‰).

DISCUSSION

Migratory monarchs sampled in Texas during both spring and fall shared habitat with resident monarchs, which breed year-round and harbour high protozoan infection prevalence. Although the majority of monarchs classified as migrants were non-reproductive and free of infections (conditions that support successful migration), migratory monarchs captured at year-round breeding sites showed a higher propensity for reproduction and a higher probability for infection, compared to migrants sampled at seasonal stopover sites (with no resident monarchs). Most migrants that visited year-round breeding sites (with resident monarchs) continued to migrate; however, a small fraction remained in these gardens for days or weeks. In spring, monarchs migrating northward to lay eggs shared breeding habitat with residents, both at seasonal sites with native milkweed and at year-round breeding sites with exotic milkweed, where infection risk for larval monarchs is high.

Two possibilities could explain why migrants sampled at year-round breeding locations were more likely to show reproductive activity. First, exposure to tropical milkweed in the fall might induce monarchs to break reproductive diapause (Batalden & Oberhauser 2015), which is thought to be induced and maintained by decreasing day length and temperatures combined with exposure to ageing milkweed (Goehring & Oberhauser 2002). Unlike the vast majority of native milkweeds that senesce during fall, tropical milkweed continues to grow during winter in some areas. It is unclear whether exposure to actively growing milkweed over a matter of days could induce a physiological change as strong as reproductive development (Batalden & Oberhauser 2015), although adult monarchs can break diapause quickly following exposure to warm temperatures and longer photoperiods (Herman 1981). A second explanation could be that these sites attract the small proportion of migrants that are not in diapause and already reproductively active (Herman 1981; Brower 1985; Goehring & Oberhauser 2002; Borland *et al*. 2004). Habitats with warm temperatures and viable host plants might recruit these reproductive migrants to join resident populations. Our results cannot distinguish between these two explanations.

The higher infection probability among migratory monarchs sampled at year-round breeding sites (compared to seasonal stopover sites) could result from butterflies acquiring dormant parasite spores, possibly from heavily infected residents attempting to mate with them (which can, in some cases, cause moderate spore loads, as shown in captive experiments; de Roode *et al*. 2009), or from contact with contaminated milkweeds. We observed, for instance, eight confirmed migrants nectaring or landing on tropical milkweeds, which are often covered in parasites at year-round breeding locations (Altizer *et al*. 2004). Alternatively, higher infection prevalence among migrants at year-round breeding sites could occur if tropical milkweed gardens disproportionately attract migrants that are already infected. Past work showed that infected females preferentially oviposit on tropical milkweeds, which offer highly toxic cardenolides that reduce parasite load in larval offspring (Lefèvre *et al*. 2010). Moreover, infected monarchs cannot fly as well as healthy monarchs (Bradley & Altizer 2005) and are less likely to migrate successfully to Mexico (Bartel *et al*. 2011; Altizer *et al*. 2015), and thus, might possibly abandon migration when given opportunities for immediate reproduction.

Of particular concern is whether spring migratory monarchs returning from Mexico lay eggs on milkweeds contaminated with parasites from infected residents. This could increase infection risk for migrants' offspring. Our results suggest that shared habitat use creates the potential for pathogen spillover from resident to migrant butterflies. At year-round breeding sites, where infection risk is extremely high (Satterfield *et al*. 2015), we observed six resident and four migrant females (chemically confirmed) ovipositing on *A. curassavica*. Additional data are needed to assess movements of infected residents in spring, when monarchs are more dispersed and could experience different frequencies of resident-migrant interactions. Some spring residents appear to visit seasonal sites with native milkweeds (Fig. 1c), on which they may deposit eggs and potentially parasites; we observed one confirmed resident ovipositing on *A. asperula*. If migrants and residents share breeding habitat frequently, infection levels could rise among the first generation of spring monarchs, most of which are produced along the Gulf coast before travelling north to recolonise the breeding range (Malcolm *et al*. 1993; Miller *et al*. 2012).

Migratory monarchs have undergone an 84% decline in eastern North America (1996-2015), thought to be caused by multiple factors, including habitat loss, throughout their annual migratory cycle (Akbar *et al*. 2012; Brower *et al*. 2012; Vidal & Rendon-Salinas 2014; Flockhart *et al*. 2015; Semmens *et al*. 2016; Marini & Zalucki 2017; Thogmartin *et al*. 2017). Threats for monarchs during fall migration are particularly difficult to measure but could be significant (Ries *et al*. 2015; Inamine *et al*. 2016). Understanding the types of habitats through which migratory monarchs travel, and how these influence their health, behaviour, and migratory success, could inform conservation actions. Results here indicate potential consequences for some migratory monarchs that share habitat with residents, and represent the first quantification of migrant–resident interactions within the monarchs' core migratory range. Previous work showed that fall migrant monarchs can enter areas with resident monarchs in Cuba and South Florida, but these locations are peripheral to the major flyways, and monarchs from these locations are unlikely to interact with migrants that reach Mexico (Dockx *et al*. 2004; Knight & Brower 2009; Dockx 2012). Our study presents evidence that either (A) year-round breeding sites with tropical milkweed disproportionately attract infected and reproductively active migrants, in which case migrants' offspring produced at these sites will face high infection risk, or alternatively, (B) year-round breeding sites induce some fraction of migrants to break reproductive diapause, which could interrupt migration or lower its success. In either case, these findings and other studies (Batalden & Oberhauser 2015; Satterfield *et al*. 2015) collectively provide evidence that native,

seasonal milkweeds – rather than exotic, year-round milkweeds – could best support monarch migration. We recommend that future efforts to restore pollinator habitat in eastern North America focus on native species and, when possible, avoid further planting of tropical milkweed. In locations where tropical milkweed is already present, it should be cut back monthly throughout fall and winter to limit monarch winter-breeding and its associated parasite transmission risk.

While we concentrated on monarchs, the co-occurrence of resident and migrant conspecifics is likely common in wildlife populations across taxa. Furthermore, as many migratory species shift towards shorter migrations or non-migratory behaviours in response to human activities (Satterfield *et al*. 2018), migrant–resident interactions may become more frequent in the future. This study addresses an imperative question in light of these changes: What are the consequences of expanding resident populations for migratory animals already facing multiple stressors? Our work suggests that, for some populations, the health and migratory success of migrants might be influenced by interactions with conspecific residents. Our findings underscore growing scientific support for prioritizing the preservation not only of migratory species themselves, but also of their behaviours and propensities for migration, which can reduce infectious disease risk and contribute to ecosystem function (Altizer *et al*. 2011; Bauer & Hoye 2014).

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AUTHORSHIP

DAS, SA, and JCM designed the study; DAS conducted fieldwork. MDH, HS, DAS and JCdR conducted cardenolide analyses; KAH, DTTF, DRN and DAS conducted isotope work; DTTF and DRN developed natal origin maps. DAS, JCM and SA conducted statistical analyses. DAS and SA wrote the manuscript with revisions from all authors.

DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.3jv3435

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SUPPORTING INFORMATION

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

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