A fresh look at the biodiversity lexicon for fiddler crabs (Decapoda: Brachyura: Ocypodidae). Part 2: Biogeography

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ABSTRACT

Fiddler crabs (Ocypodidae Rafinesque, 1815) occupy most tropical and semitropical coastlines worldwide where they are keystone species and ecosystem engineers. I present updated ranges for all 105 species and explore both global and local patterns to establish a baseline distribution as species ranges begin to shift with climate change. Globally, the average number of species per occupied coastline is five, with only limited allopatry observed within the group. Cohesive species assemblages were used to define four zoogeographic fiddler realms containing 24 provinces and transitional zones. These regions can serve as units of study when trying to explore which factors influence the distribution of coastal species.

Key Words: *Afruca, Austruca, Cranuca*, ecology, *Gelasimus, Leptuca, Minuca, Paraleptuca, Petruca*, phylogeography, zoogeography, *Tubuca, Uca, Xeruca*

INTRODUCTION

Fiddler crabs (Ocypodidae Rafinesque, 1815) are a charismatic group of globally distributed brachyuran crabs, popular with both scientists and amateur naturalists due to their colorful markings, aggressive waving and fighting behaviors, and the extreme claw asymmetry found in males. Fiddler crabs are generally considered a keystone species of intertidal wetlands, serving as essential ecosystem engineers (Burns, 1976; Haines, 1976; Moore, 1991; Jones *et al.*, 1994; Kostka *et al.*, 2002; Curran & Martin, 2003; Smith *et al.*, 2003; Guest *et al.*, 2004; Kristensen & Alongi, 2006; Ferreira *et al.*, 2007; Lim & Heng, 2007; Cannicci *et al.*, 2008; Kristensen, 2008; Penha-Lopes *et al.*, 2009; Wang *et al.*, 2010; Bartolini *et al.*, 2011; Chowdhury *et al.*, 2012; Ohzono & Miura, 2012; Sayão-Aguiar *et al.*, 2012; Diele *et al.*, 2013; Andreetta *et al.*, 2014; Chatterjee *et al.*, 2014; González-Ortiz *et al.*, 2014; Fanjul *et al.*, 2015; Nobbs & Blamires, 2015; Smith & Green, 2015; Citadin *et al.*, 2016; Correia & Guimarães, 2016; Vu *et al.*, 2017; Booth *et al.*, 2019; El-Hacen *et al.*, 2019; Moore, 2019), whose activities effect oxygenation of sediment, soil drainage, belowground decomposition, and both above- and belowground biomass (Katz, 1980; Holdredge *et al.*, 2010; Thomas & Blum, 2010; Gittman & Keller, 2013; Michaels & Zieman, 2013). The scope of these activities is likely mediated through both population density and local species (alpha) diversity (Katz, 1980; DePatra & Levin, 1989; Citadin *et al.*, 2018; Raposa *et al.*, 2018; Moore, 2019).

Fiddler crabs also serve as a primary food source for a wide range of vertebrate and invertebrate taxa (Raut, 1943; Kushan, 1979; Subramanian, 1984; Petit & Bildstein, 1987; Zwarts & Dirksen, 1989, 1990; Zwarts, 1990; Zwarts & Blomert, 1990; Grant, 1992; Turpie & Hockey, 1993; Lee & Kneib, 1994; McNeil & Rompré, 1995; McNeil *et al.*, 1995; Thibault & McNeil, 1995; De Santo *et al.*, 1997; Backwell *et al.*, 1998; Olmos *et al.*, 2001; Vannini *et al.*, 2001; Whitelaw & Zajac, 2002; Jennions *et al.*, 2003; Hugie, 2004; Martínez, 2004; Ribeiro *et al.*, 2004; Rulison, 2010; Rush *et al.*, 2010; Lourenço *et al.*, 2017; Alleman & Guillen, 2017), and are often viewed as a critical respondent to near-coast pollution events (Krebs & Burns, 1977; Burns & Teal, 1979; Lee *et al.*, 1981; Deecaraman & Fingerman, 1985; Shafer & Hackney, 1987; Snowden & Ekweozor, 1987, Jacob, 1988; Snowden & Ekweozor, 1990; Burger *et al.*, 1991, 1992; Burger & Gochfeld, 1992; Teal *et al.*, 1992; Culbertson, 2008; Chase *et al.*, 2013; Zengel *et al.*, 2016; Deis *et al.*, 2017; Damare *et al.*, 2018; Franco *et al.*, 2018).

Although adult fiddler crabs are semiterrestrial and generally limited to the intertidal zone, dispersal in the group is driven almost entirely by their pelagic larvae, with abiotic factors such as tides, water temperature, and salinity likely to be among the critical factors controlling the coastline where juvenile crabs attempt to settle (Lambert & Epifanio, 1982; O'Connor & Epifanio, 1985; Epifanio, 1988; Epifanio *et al.*, 1988; Anger *et al.*, 1994; Christy, 2003; López-Duarte *et al.*, 2011; Levinton & Mackie, 2013; Simith *et al.*, 2014; Wieman *et al.*, 2014). As global ocean temperature increases, there is

already evidence that some species of fiddler crab are moving pole-ward (Johnson, 2014; Peer *et al.*, 2015; Rosenberg, 2018; Truchet *et al.*, 2019), suggesting that the distribution of species of this group may serve as a key indicator for wetland response to global climate change. Peer *et al.* (2018) present a recent review and study how both abiotic and biotic factors interact to control species presence and density in fiddler crabs. In order to construct and test better hypotheses about factors leading to the species distributions of fiddler crabs, we require a baseline description of that global distribution.

Crane (1975) was the first work to fully delve into the global distribution of fiddler crabs. Necessarily, her study was driven by and dependent on her taxonomic treatment, which recognized one genus, nine subgenera and 62 species (many of which contained subspecies). Crane (1975) described three primary geographic regions: the Indo-Pacific (later referred to generally as the Indo-West Pacific or IWP) (from East Africa to the Marquesas and Easter Island), the Americas, and the eastern Atlantic, containing four, three, and one endemic subgenera, respectively. Her ninth and largest subgenus was mostly restricted to the Americas, but with two species also found in the IWP. Within the Americas, the Atlantic and Pacific coastal species assemblages were almost entirely distinct, with only three species represented on both coasts by different subspecies. Crane further subdivided these large regions into smaller assemblages (largely ignored by subsequent researchers), including seven subdivisions within the IWP, three zones along the Pacific coast of the Americas, and four zones along the Atlantic coast of the Americas. Crane favored an IWP origin of the genus, with two trans-Pacific migrations, one to colonize the Americas (and later across the Atlantic to West Africa) and a later return trip of members from one of the American-derived clades.

Few studies have explored the global distributions of these crabs subsequent to the major work of Crane (1975). Beyond a few studies which re-examined the phylogeographic origin of the genus (Salmon & Zucker, 1988; Levinton *et al.*, 1996; Sturmbauer *et al.*, 1996; Beinlich & von Hagen, 2006), most biogeographic works on fiddler crabs have focused on regional and local patterns (Barnwell & Thurman, 1984; von Hagen & Jones, 1989; Apel & Türkay, 1999; Hopkins & Thurman, 2010; Shih *et al.*, 2010b; Bezerra, 2012; Thurman *et al.*, 2013; Hopkins *et al.*, 2016; Shih *et al.*, 2016a; Thurman *et al.*, 2017; Peer *et al.*, 2018;), with a large number of studies examining factors contributing to the local spatial distribution of species within specific sites (Ono, 1965; Macnae, 1967; Frith *et al.*, 1976; Icely & Jones, 1978; Thurman, 1998; Ravichandran *et al.*, 2001; Silva & de Almeida, 2002; Nobbs, 2003; Lim *et al.*, 2005; Bezerra *et al.*, 2006; Ohno *et al.*, 2006; An *et al.*, 2008; Diele *et al.*, 2010; Mokhtari *et al.*, 2015; Nobbs & Blamires, 2015, 2017) rather than more generally among sites. One of the few global studies of the past 45 years explored the relationship between species richness and latitude, concluding that air and sea surface temperatures in early summer are a primary driver of diversity (Levinton & Mackie, 2013).

Three general advancements in our knowledge of fiddler crabs have occurred in the four-and-a-half decades since Crane (1975) that bear upon the issue of biogeography. First, substantial taxonomic revision has taken place, including reorganization of the subgenera into genera and an expansion of the recognized species to 105 (Shih *et al.*, 2016b; Rosenberg 2019), including descriptions of entirely new, often cryptic species; recognizing former subspecies as full species; and recognizing formerly synonymized species as distinct species. Second, phylogenetic methods and molecular data provide a framework for understanding the evolutionary relationships within fiddler crabs that was unavailable in 1975 (Crane presented dendrograms as hypotheses about relationships, based entirely on authorial expertise rather than data-based numerical methods). Third, substantially more data are available on the geographic distributions of individual species, enhanced by electronic databases such as Global Biodiversity Information Facility (GBIF) (www.gbif.org) and citizen-science and amateur naturalist

initiatives such as iNaturalist (www.inaturalist.org). Combined, these advances allow us to reexamine the global distribution of species, redefine zoogeographical species assemblages, and construct a biogeographic infrastructure for future distributional studies of the group.

DATA

Updated ranges for all 105 currently recognized extant species were created through literature surveys. When possible, the initial range was that supplied by Crane (1975), which was subsequently updated to reflect changes in taxonomic concepts, new observations, molecular analysis, and other considerations. Maps illustrating the range of each species, along with the references used to determine each are provided here as Supplementary material maps. These maps are also available from https://www.fiddlercrab.info and will be updated on that site as new information is discovered.

Raw land and sea map data were derived from the Natural Earth large scale (1:10 m) data sets, version 4.0.0 (https://www.naturalearthdata.com/). Coastlines as used in this study include a combination of both the "Coastline" (including major islands) and "Minor Island" data sets. Country borders displayed on maps are derived from the "Admin 0 – Countries" data set but are not part of any analysis.

Coastline length was determined from these map data as the sum of spherical (geodesic) distances between adjacent coordinates describing the coastline. It is worth noting that "coastline length" is a classic example of a fractal dimensional problem (Richardson, 1961; Mandelbrot, 1983), where estimated length continually increases with the accuracy of measurement, such that infinitesimally small measurements would lead to infinitely long coastlines. Thus, any estimated lengths used here are at most only meaningful as direct comparisons at the underlying scale of measurement (in this case, the 1:10m-based dataset).

Obligate intertidal and coastal species such as fiddler crabs have a somewhat unusual element to what one would consider their species range in that over any significantly large scale the range would usually be functionally one-dimensional (along the coasts), rather than the two-dimensional overlay more common for land or aquatic organisms. Thus, it does not make much sense to express the size of a fiddler crab range by area, but rather as some measure of linear distance; an exception might be argued for an island-dense area such as Indonesia and the Philippines, but this is clearly the exception rather than the rule. I estimated the extent of species' ranges using multiple measures, including 1) the sum of inhabited coastline length, 2) the latitudinal range, and 3) the longitudinal range.

GLOBAL PATTERNS

Fiddler crabs are ubiquitous along non-rocky tropical and subtropical coastlines throughout the world (Fig. 1), with occasional extensions further into temperate zones (latitudinal range is approximately 38° south to 43° north). Fiddler crabs are so common across tropical and subtropical coastlines, that it may be more meaningful to discuss where they are not found rather than where they are found. Three examples illustrate three likely explanations of the absence of fiddler crabs in our records.

1. *False positives:* the Hawaiian Islands. Limited reports of fiddler crabs from the Hawaiian Islands (Owen, 1839; Kingsley, 1880) appear to be based on errors in collection location (Crane, 1975; Castro, 2011) as fiddler crabs are otherwise not know from these well-studied islands. Given the apparent suitability of the habitat, the absence of fiddler crabs in the Hawaiian Islands is likely due to a combination of historical stochasticity and the extreme isolation of the islands (the closest islands to Hawaii known to have fiddler crabs are the Marshall Islands, Wake Island, and the Gilbert
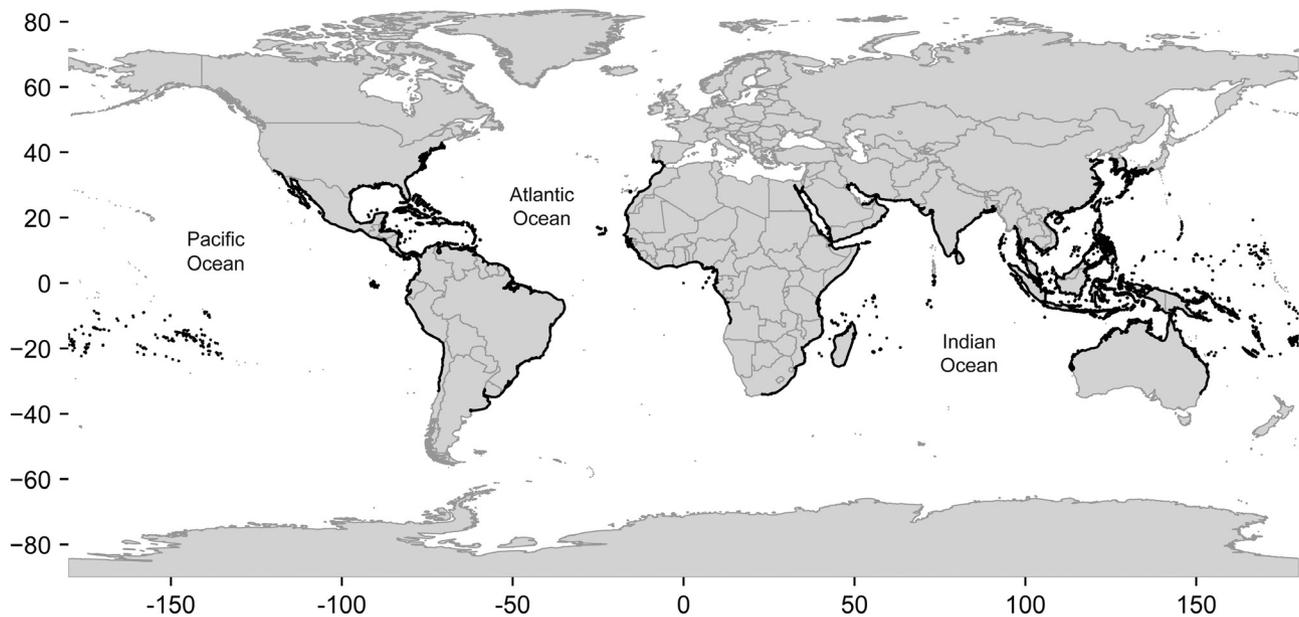
Figure 1. Global coastline occupancy of fiddler crabs.

Islands of Kiribati, each approximately 2,400 km distant), as fiddler crabs appear to have only made the full trans-Pacific crossing (east to west) once (Levinton *et al.*, 1996). Historical references to fiddler crabs in New Zealand (Kirk, 1880; Filhol, 1885a, b), which is otherwise at the southern edge of suitable fiddler crab habitat, are also likely due to similar errors in geographic collection location (Bennett, 1964). Reports of fiddler crabs from clearly unsuitable habitat, e.g., Vancouver, Canada (Bate, 1866), the interior of the Amazon (Doflein, 1899), and the Adriatic Sea (Stossich, 1878), may represent errors in geographic collection location or mistaken taxonomic identification.

2. *True negatives:* the southwestern coast of the Persian Gulf, including Saudi Arabia, Bahrain, Qatar, and southwestern United Arab Emirates. Although fiddler crabs are known from the northwestern, northern, and eastern parts of the Persian Gulf, they appear to be entirely absent from the southwestern coast (Apel & Türkay, 1999; Naderloo, 2017), corresponding to a general decline in brachyuran diversity within this area. This pattern is thought to be due to the unusually high salinity of this region (Apel & Türkay, 1999), reaching > 40 psu, which is beyond the range generally tolerated by fiddler crabs (Crane, 1975). It should be noted that laboratory experiments on adult individuals from numerous species reveal at least short-term tolerance to substantially higher salinities than those found in the Persian Gulf (Zanders & Rojas, 1996; Khanyile, 2012; Peer *et al.*, 2015); it may be that larvae have lower tolerance to high salinity, preventing recruitment, or that the apparent tolerance in adults degrades over longer-term exposure.

3. *False negatives (?):* Northeastern Bay of Bengal. In the Bay of Bengal, fiddler crabs are found along the entire east coast of India as far north as the Sundarban of Bangladesh, along the west coast of Thailand and southern Myanmar, and on the Andaman and Nicobar Islands. There are no reports of fiddler crabs along the northeastern part of the Bay, from eastern Bangladesh through northern Myanmar (Rakhine state and Ayeyarwardy region). It is noteworthy, however, there are also no coastal surveys which fail to find fiddler crabs in this region (unlike in the previous Persian Gulf example). This area appears to be particularly poorly studied for coastal Crustacea in general (although the possibility of obscure gray literature, such as local government surveys, theses, and dissertations cannot be ruled out), and it is possible (and has

historically been assumed) that fiddler crabs are present. The lack of data on fiddler crabs in this region is of particular importance because this coast is likely part of the boundary between the Indian Ocean and Pacific Ocean species clusters (or more narrowly, the Indian Subcontinent Province and the Sumatra and Malay Peninsula Transition Zone, see below) and knowing which species were present would aid in understanding how the species of these regions overlap. This "empty" area also marks the boundary between the recent taxonomic split of *Austruca variegata* (Heller, 1862) (western Bay of Bengal) and *A. bengali* (Crane, 1975) (southeastern Bay of Bengal) (Shih *et al.*, 2019); if these species were found to be sympatric, it would likely be in this unexplored area.

The presence of fiddler crabs in some other areas is less certain. For example, the range maps include four species along the coast of Cambodia, but I have been unable to find any clear scientific record of any species of fiddler crabs from the country. But because these four species are generally thought to be present in both Vietnam to the east and Thailand to the west, they are assumed to also occupy the intervening coastline of Cambodia. Other similar examples include the Pacific coast of Guatemala, the southeastern coast of the Arabian Peninsula that abuts the Arabian Sea (Oman and Yemen), and northern and northeastern Somalia. Species surveys in all of these areas could be of interest as each is near the boundary of accepted species ranges and/or occupies a potential transitional region between different species assemblages.

This lack of collection data is a place where citizen science initiatives can sometimes prove useful. iNaturalist includes more than 4,500 worldwide observations of fiddler crabs. These include an observation (*Austruca* Bott, 1973) from the east coast of Oman along the Arabian Sea, and another observation (*Austruca*) in Cambodia near the border with Thailand. Two stray observations do not completely fill in these areas, and identification to species via photo is often difficult, if not impossible, but these observations indicate that fiddler crabs are not entirely absent from these under-explored coastlines. In rare instances, these citizen science initiatives provide enough evidence for range expansions, such as the first observations of *Uca princeps* (Smith, 1870) moving northward from Mexico into the US (Rosenberg, 2018). As a follow-up to that work, additional observations of *U. princeps* in southern California, USA, have continued through the fall of 2019, indicating its presence was not a single-year aberration. The data in citizen science databases such as these do have to be

viewed with a critical eye and a dose of skepticism. The primary requirements for an observation to be deemed as "research grade" in iNaturalist are a date and location, evidence of the observation such as photos or recorded sounds, and having at least two-thirds of identifiers (minimum two) agreeing on the taxonomic identification. This is not an overly high bar and can be particularly susceptible to erroneous identifications, as taxonomic nomenclatural changes in the professional literature can take a long time to penetrate to local and amateur usage.

I downloaded every research-grade observation of fiddler crab species from iNaturalist and computationally compared it to my updated ranges, filtering for observations that fell outside of the accepted range. The taxonomic identification was wrong in some cases, and a correction was submitted to iNaturalist. In most cases the species identification was ambiguous; these observations could represent range expansions, or they could represent taxonomic confusion with a similar species known to occupy the observed location. In two instances, however, the identification was clear enough to slightly extend the observed range of two species: *Leptuca terpsichores* (Crane, 1941) northward into southern Guatemala and *Tubuca flammula* (Crane, 1975) eastward to the west coast of the Cape York Peninsula, Australia (see Supplementary material maps). It may be possible to derive additional range expansions from these data, but we have chosen to err on the side of caution.

In order to examine broad global diversity patterns, a $1 \times 1°$ grid was created in a 90° band (45° north to 45° south) over the surface of the planet. Each of the 32,400 cells was evaluated for the presence of coastline; cells without coastlines (purely ocean or purely land) were dropped from further analysis. For each of the 3,069 cells containing a coastline, the species present within the cell and the total length of coastline found within the cell were recorded. Of the 855 coastal cells with no observed species of fiddler crabs, 35% are at latitudes above 40°, 66% are above 35°, and 79% are above 30°. Of the 2,214 coastal cells with at least one species of fiddler crab, the mean species present per cell is 5.5 (median = 5), with a range of 1 to 34 (Fig. 2A). The six cells that exceed 30 species are found in Panamá, and include species from both the Pacific and Atlantic coasts. Ignoring these cross-isthmus counts, the highest density of species is found along the Pacific coasts of southern Costa Rica and Panamá, with 28 species present, 29 for the cell which includes Golfo Dulce, Costa Rica, only known location of *Minuca osa* (Landstorfer & Schubart, 2010). These extremely high densities are rare; 98% of the cells have 13 or fewer species and 70% have six or fewer. About 12% of the cells only had one species present. Half of these single-species cells represent the range of *Afruca tangeri* (Eydoux, 1835), while the others mostly appear to represent the latitudinal extremes of temperate zone-tolerant species or a random scattering
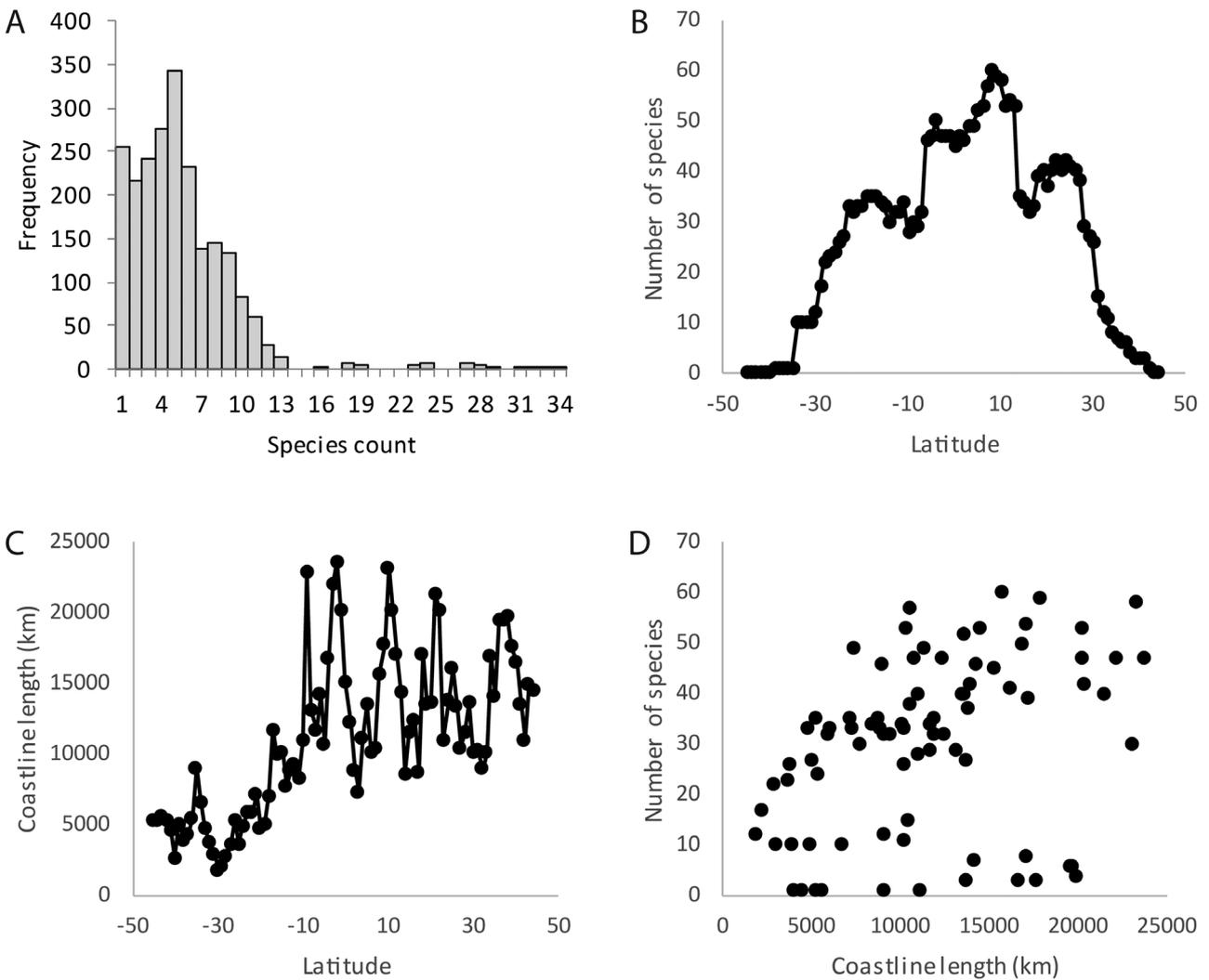
Figure 2. Global species counts in $1 \times 1°$ coastal cells. Histogram of species counts per coastal cell with at least one observed species (**A**); species presence by latitude (**B**); coastline length *versus* latitude (**C**); number of species per latitude *versus* coastal length (**D**).

of observations across isolated IWP islands, generally representing < 10% of a species total range.

Combining observations for cells of the same latitude approximately recreates one of the results of the analyses of Levinton & Mackie (2013), which indicated a peak global species richness in the tropics centering slightly north of the Equator, with roughly symmetric secondary peaks around 20–25° latitudes, with diversity rapidly declining as latitude increases beyond 25° (Fig. 2B). While the apparent symmetry of these secondary peaks is intriguing, it is not clear they represent anything other than a geographic fluke. An early hypothesis was that these secondary peaks represented a mixture zone of temperate and tropical species. Such could be the case in the western Atlantic, where the northern peak corresponds to where three separate regions intermix around the entrance of the Gulf of Mexico (see below), but does not appear to be a likely explanation for anywhere else in the Northern Hemisphere nor in the Southern Hemisphere, where the peak is more tropical than in the north. An alternative hypothesis is that these secondary peaks happen to represent areas where there is an unusual longitudinal stretch of continental coastlines. The analysis of Levinton & Mackie (2013) indicated that these secondary peaks may largely be driven by patterns in the IWP realm. The northern peak corresponds roughly to the northern edge of the Indian Ocean, and thus crosses coastlines in the Red Sea, Persian Gulf, northern Arabian Sea, and northern Bay of Bengal, as well as China and Taiwan, each of which has a somewhat different set of species. The southern peak intersects with the long coastline of northern Australia and thus includes a number of unique species not found outside the continent. The rough symmetry of these secondary peaks is most likely meaningless.

One obvious complicating factor of my analyses is that 1 × 1° cells represent different areas at different latitudes. As discussed above, however, because fiddler crabs are approximately functionally restricted to one-dimensional coastlines at global/continental scales (at a more local scale, distributions across estuaries and wetlands is clearly two-dimensional), the area is potentially of less concern than the amount of coastline found within each cell. An examination of the previous results with this factor in mind reveals little additional explanatory power (Fig 2C–D), an observation also made by Levinton & Mackie, 2013. In parallel with patterns of land area, there is generally more coastline in the Northern than the Southern Hemisphere (Fig 2C). A weak correlation ($r = 0.16$) exists between coastline length and species count per cell across the 2,214 cells with at least one species. Summed across latitude (skipping the extreme latitudes with zero species) the correlation between coastal length and species count is 0.35 (Fig 2D). While increasing coastline length does correspond to an increase in species count, the effect is weak relative to latitude. One likely reason coastline length lacks predictive ability is that not all coastlines are equally occupiable by fiddler crabs; fiddler crabs are almost entirely absent from rocky shores and high-energy sandy beaches. A more predictive model would need to include these and other factors (see below).

Sympatry among the species of fiddler crab on a macro scale is thus the rule rather than the exception. Only two of 105 species, *Afruca tangeri* and *Paraleptuca boninensis* (Shih, Komai & Liu, 2013; see Shih *et al.*, 2013), are allopatric with respect to other species of fiddler crabs across their entire range, and these have wildly different distributions from each other. *Afruca tangeri* is the only species in the eastern Atlantic, occupying the entire coast of Africa from Angola to Morocco, with a northward extension into southern Spain and Portugal. In contrast, *P. boninensis* is endemic to one of the Ogasawara Islands, Japan (approximately 1,000 km south of Tokyo) and the only species found on this island, although a number of other species are found in the broader western Pacific region.

Leptuca uruguayensis (Nobili, 1901; see Nobili, 1901a) is sympatric with up to nine species in the northern part of its range

(southern Brazil) but extends southwards (through Uruguay and into northern Argentina) into pure allopatry for more than half of its range. The few other species that extend into allopatry at latitudinal extremes for fiddler crabs (*e.g.*, *Minuca pugnax* (Smith, 1870) extending northward into New Hampshire, USA; *Leptuca crenulata* (Lockington, 1877) extending northward to Santa Barbara, California, USA; *L. stenodactylus* (H. Milne Edwards & Lucas, 1843) extending southward into Chile; *Austruca occidentalis* (Naderloo, Schubart & Shih, 2016; see Naderloo *et al.*, 2016) extending southward in South Africa) are still sympatric with other species over most (> 90%) of their range. Most fiddler crab species are essentially sympatric with others over their entire range.

In contrast, at the more local scale, species frequently sort into different parts of the local habitat (such as whether upper or lower intertidal, mud or sand, more or less brackish water) to display microallopatry, a widely studied phenomenon in fiddler crabs (Ono, 1965; Macnae, 1967; Frith *et al.*, 1976; Icely & Jones, 1978; Thurman, 1998; Ravichandran *et al.*, 2001; Silva & de Almeida, 2002; Nobbs, 2003; Lim *et al.*, 2005; Bezerra *et al.*, 2006; An *et al.*, 2008; Diele *et al.*, 2010; Mokhtari *et al.*, 2015; Nobbs & Blamires, 2015, 2017). Even when four or five species may be present at a given location, some of the species likely have little direct interaction due to different microhabitats. Exceptions have been noted, however, such as an observation by Barnes (2010) of six species regularly coexisting in 2 m² quadrats (with a seventh in 4 m²). The highest number of species worldwide is found along the Pacific coasts of Panamá and Costa Rica (see above). I observed over the course of three months in 1997 at least 14 species on a large mudflat adjacent to the Base Naval Vasco Nuñez de Balboa (formerly Rodman Naval Base) in Panamá (Rosenberg, 2000); J. Christy had earlier identified 16 species at this same site (personal communication). Although there was clear subdivision of the overall mudflat among the species, it was not unusual to see three or four species within a meter, and a photograph from that time reveals individuals of four of the small-size species of *Leptuca* Bott, 1973 within 10–15 cm from each other.

This local microallopatry highlights a secondary reason why coastline length is a poor determinant of species abundance. Coastal hydrogeological factors such as tidal height and sediment variation, uncorrelated with coastline length, create more potential ecological niches for local species differentiation and co-occurrence (Crane, 1975). Global-scale ecological niche modeling of coastal habitats and their relationship to fiddler species abundance is beyond the scope of this work but could represent a worthy future study.

PHYLOGEOGRAPHY

Crane (1975) considered a number of hypotheses about the historical zoogeography of fiddler crabs, but favored one in which fiddler crabs arose in the IWP and then spread eastward across the Pacific (via the Bering Bridge) into the Americas (and then later, across the Atlantic to Africa) during the Eocene-early Oligocene, with a return westward migration by one branch of the American-derived forms back into the IWP. Crane's hypothesis was largely driven by assumptions about primitive *versus* derived behaviors associated with narrow-front and broad-front subgenera, respectively. In contrast, Salmon & Zucker (1988) postulated early evolution of both narrow- and broad-front clades in the Tethys Sea until the late Oligocene, with members of both groups radiating into both the IWP and the Americas as the Tethys closed. The first molecular phylogeny of fiddler crabs (Levinton *et al.*, 1996) reversed Crane's hypothesis, indicating a more likely origin of fiddler crabs in the Americas, with one westward trans-Pacific crossing and radiation into the IWP species, along with one eastward trans-Atlantic crossing to western Africa. Beinlich & von Hagen (2006) largely rejected these molecular studies and

returned to a hypothesis similar to that of Crane (1975), arguing that morphological and fossil data (from non-fiddler crabs) suggest an Australian origin of fiddler crabs, which then expanded westward through "Wegener's Indo-Atlantic Ocean," separately for narrow-front and broad-front groups. Fiddler crabs would have expanded north along the east coast of Africa, then through a Tethyan passage into the Atlantic, circumventing the need for a Pacific crossing. This hypothesis is largely incongruent with all subsequent molecular phylogenetics of fiddler crabs (most recently Shih et al., 2016b), which continue to suggest the Americas as the most likely area of origin.

The base of the fiddler crab phylogeny has two key splits (Shih et al., 2016b). The first separates fiddler crabs into two groups: 1) Ucinae Dana, 1851, and/or Ocypodinae Rafinesque, 1815, consisting of Uca Leach, 1814 (found on both coasts of the Americas) and Afruca Crane, 1975 (restricted to the eastern Atlantic), possibly along with the ghost crabs (Ocypode Weber, 1795, found worldwide); and 2) Gelasiminae Miers, 1886, consisting of the remaining nine genera of fiddler crabs. The second major split separates Gelasiminae into two tribes with complete geographic separation: 1) Gelasimini Miers, 1886, consisting of the six IWP genera, and 2) Minucini Rosenberg, 2019, consisting of the three American broad-front genera. It should be noted that, just as with fiddler crabs, ghost crabs (Ocypode) appear to have two strongly supported clades with perfect geographic division, one for the three American species and one for the ~20 IWP species (Shih et al., 2016b).

Viewed from the standpoint of the geographic realms of fiddler crabs (see below), the Eastern Atlantic Realm contains only one monospecific genus, Afruca tangeri, whereas the Indo-West Pacific Realm contains only the six genera making up the tribe Gelasimini. The fiddler crabs of the two American realms (Eastern Pacific and Western Atlantic) do not form a single monophyletic unit, either across or within the two realms.

Three genera (Uca, Minuca Bott, 1954, and Leptuca) are found on both coasts of the Americas, with a fourth monospecific genus (Petruca Shih, Ng & Christy, 2015; see Shih et al. 2015) found only on the Pacific coast. No species is found on both coasts, however, suggesting the origin of all three (and particularly the separation of the more closely related Minuca and Leptuca) prior to the closing of the Isthmus of Panamá about 2.8 million years ago (O'Dea et al., 2016). All three genera contain trans-continental species pairs that seem to be closely related, suggesting potential vicariance speciation from the closing of the isthmus: Uca maracoani (Latreille, 1803) and U. insignis (H. Milne Edwards, 1852), Leptuca thayeri (Rathbun, 1900) and L. umbratila (Crane, 1941), and Minuca vocator (Herbst, 1804) and M. ecuadoriensis (Maccagno, 1928). Given that the Eastern Pacific Realm has about 50% more species than the Western Atlantic Realm (36 versus 21), one would expect species from these genera to also be unequally distributed between the realms. Both Uca (7 versus 2) and Leptuca (21 versus 9) are more speciose on the Pacific than the Atlantic coast, but Minuca (7 versus 10) is the opposite, albeit more evenly split than either of the other two. Species of Minuca represents 50% of the Atlantic species, but only 25% of the Pacific species. Most of these species of Minuca occupy the upper intertidal zone, in or above the edge of the mangroves (Crane, 1975; J. Christy, personal communication). In contrast, Leptuca and Uca occupy a wider variety of microhabitats which appear to be more readily available along the Pacific coast than the Atlantic. Whether the underlying mechanism controlling diversity is differential expansion into available ecological niches on the Pacific or differential extinction due to loss of such niches on the Atlantic is unclear.

Within the Indo-West Pacific Realm, two of the genera (Xeruca Shih, 2015 and Cranuca Beinlich & von Hagen, 2006) are monospecific and somewhat limited in distribution, whereas species of the other four genera (Gelasimus Latreille, 1817; Tubuca Bott, 1973; Austruca Bott, 1973; and Paraleptuca Bott, 1973) are generally found

throughout the entire realm. Although the faunal assemblages are largely distinct, there are species which overlap the subrealms described below. One subgenus, Tubuca (Australuca) Crane, 1975, is restricted to Australia, but otherwise there is little in the way of clear broad-scale phylogeography within the region.

A rough biogeographic pattern of community assemblage is nevertheless apparent. As mentioned above, the median number of species per 1 × 1° cells (with at least one species) is five; this number holds worldwide as well as in the IWP. Superficially, if one wanted to describe an average species assemblage of fiddler crab for any location in the IWP, one could assume it will contain one species from each of the subgenera Austruca (Austruca), Gelasimus (Gelasimus) and Tubuca (Tubuca), one species from the genus Paraleptuca, and one additional random species. While species within each of the four clades can be found in sympatry (particularly within the geographically/structurally complex, species-rich Malayan Archipelago), it appears that within-clade allopatry is more common, with within-clade species turnover more often leading to having only one species in any particular location.

ZOOGEOGRAPHICAL REGIONS

Just as taxonomists and systematists seek to organize organisms into a hierarchical nomenclatural framework, one of the primary goals of biogeography is to classify organisms into meaningful geographical units. These bioregionalization schemes play an important role in many disciplines, including conservation biology, historical and ecological biogeography, evolutionary biology, and macroecology, providing a geographic framework of hypotheses and operational units for analysis, study, or conservation (Morrone, 2009; Kreft & Jetz, 2010; Vilhena & Antonelli, 2015). Many studies have focused on higher taxonomic units or cross-taxonomic assemblages of species (e.g., Hagmeier & Stults, 1964; Holt et al., 2013), but the same principles can be applied at smaller taxonomic or spatial scales.

The regionalization scheme for fiddler crabs described here borrows from the Marine Ecoregions of the World (MEOW) (Spalding et al., 2007), although the specifics are somewhat different (see below). The scheme described here for fiddler crabs contains two main levels. The largest spatial units are referred to as "realms," large oceanic coasts, separated from other realms by continents, deep ocean basins, or colder temperate and arctic waters unsuitable for the survival of fiddler crabs, in contrast to the MEOW realms, many of which are trans-oceanic. Nested within the realms are "provinces" (Spalding et al., 2007: 575):

"Large areas defined by the presence of distinct biotas that have at least some cohesion over evolutionary time frames. Provinces will hold some level of endemism, principally at the level of species. Although historical isolation will play a role, many of these distinct biotas have arisen as a result of distinctive abiotic features that circumscribe their boundaries. These may include geomorphological features (isolated island and shelf systems, semienclosed seas); hydrographic features (currents, upwellings, ice dynamics); or geochemical influences (broadest-scale elements of nutrient supply and salinity)."

The provinces described for fiddler crabs follow this definition with a focus on cohesion of species co-occurrences and the use of distinctive abiotic features to demarcate boundaries whenever possible.

Parallel in size to the provinces, also being defined here are "transition zones," regions that clearly represent the faunal mixing of two or more neighboring provinces, rather than representing a unique entity on its own (although some of the transition zones contain unique endemic species). The provinces are not further divided into the equivalent of the small-scale "ecoregions" in the MEOW scheme, although subrealms or subprovinces are being suggested in a few cases.

Fiddler crabs fall into four realms, each with an entirely unique and non-overlapping set of species. The species and genera in two of the realms form monophyletic clades, while the other two realms share genera. A summary of all realms and provinces and their species is shown in Figure 3.

Eastern Atlantic Realm

The Eastern Atlantic realm consists of only one province as it contains only one species, *Afruca tangeri* in a monospecific genus. This northern edge of the province starts in southwestern Europe (southern Portugal and southwestern Spain) and extends
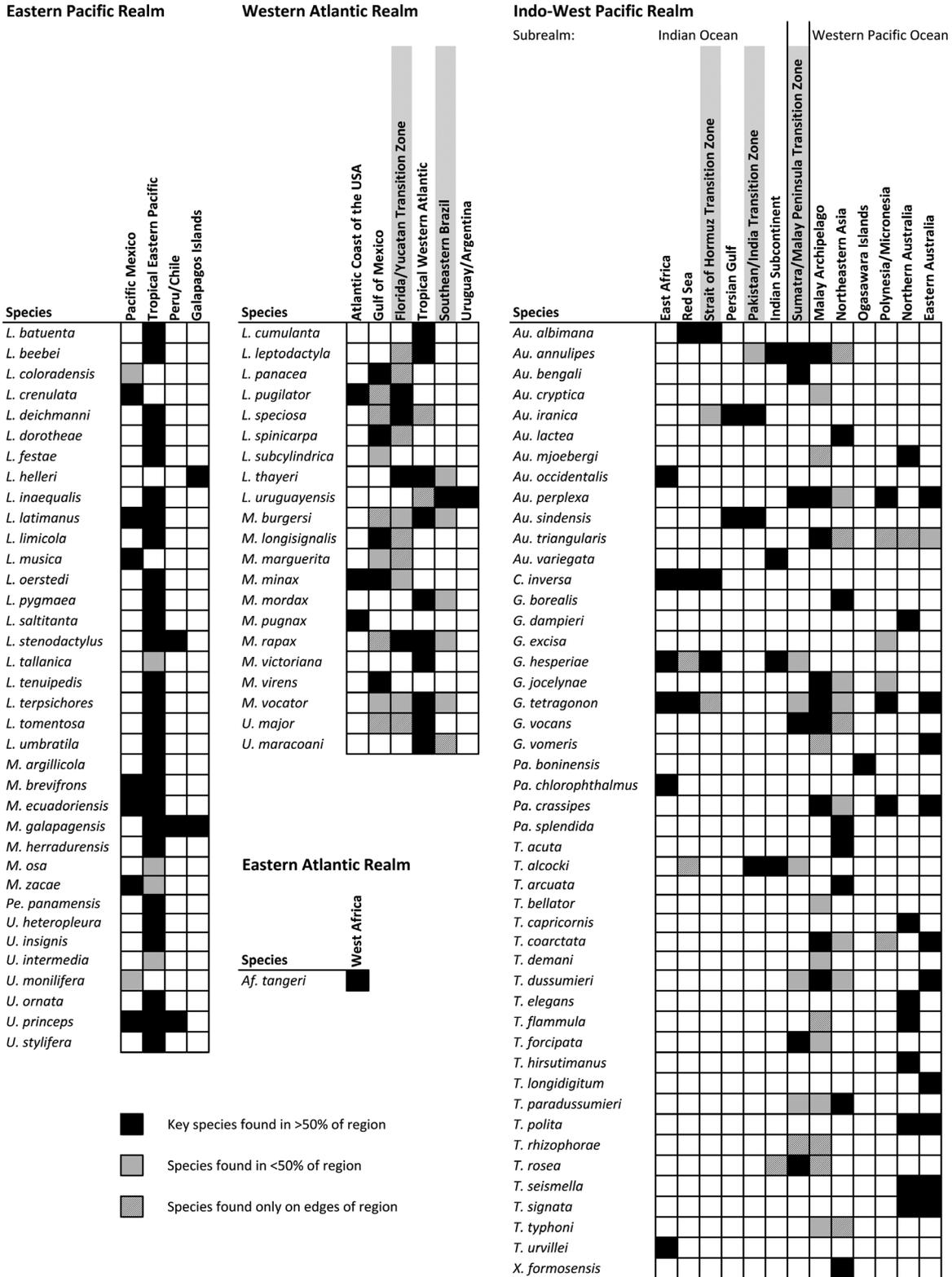
Eastern Pacific Realm

Columns: Pacific Mexico, Tropical Eastern Pacific, Peru/Chile, Galapagos Islands

Species:
L. batuenta, L. beebei, L. coloradensis, L. crenulata, L. deichmanni, L. dorotheae, L. festae, L. helleri, L. inaequalis, L. latimanus, L. limicola, L. musica, L. oerstedi, L. pygmaea, L. saltitanta, L. stenodactylus, L. tallanica, L. tenuipedis, L. terpsichores, L. tomentosa, L. umbratila, M. argillicola, M. brevifrons, M. ecuadoriensis, M. galapagensis, M. herradurensis, M. osa, M. zacae, Pe. panamensis, U. heteropleura, U. insignis, U. intermedia, U. monilifera, U. ornata, U. princeps, U. stylifera

Western Atlantic Realm

Columns: Atlantic Coast of the USA, Gulf of Mexico, Florida/Yucatan Transition Zone, Tropical Western Atlantic, Southeastern Brazil, Uruguay/Argentina

Species:
L. cumulanta, L. leptodactyla, L. panacea, L. pugilator, L. speciosa, L. spinicarpa, L. subcylindrica, L. thayeri, L. uruguayensis, M. burgersi, M. longisignalis, M. marguerita, M. minax, M. mordax, M. pugnax, M. rapax, M. victoriana, M. virens, M. vocator, U. major, U. maracoani

Eastern Atlantic Realm

Column: West Africa

Species:
Af. tangeri

Indo-West Pacific Realm

Subrealm: Indian Ocean | Western Pacific Ocean

Columns: East Africa, Red Sea, Strait of Hormuz Transition Zone, Persian Gulf, Pakistan/India Transition Zone, Indian Subcontinent, Sumatra/Malay Peninsula Transition Zone, Malay Archipelago, Northeastern Asia, Ogasawara Islands, Polynesia/Micronesia, Northern Australia, Eastern Australia

Species:
Au. albimana, Au. annulipes, Au. bengali, Au. cryptica, Au. iranica, Au. lactea, Au. mjoebergi, Au. occidentalis, Au. perplexa, Au. sindensis, Au. triangularis, Au. variegata, C. inversa, G. borealis, G. dampieri, G. excisa, G. hesperiae, G. jocelynae, G. tetragonon, G. vocans, G. vomeris, Pa. boninensis, Pa. chlorophthalmus, Pa. crassipes, Pa. splendida, T. acuta, T. alcocki, T. arcuata, T. bellator, T. capricornis, T. coarctata, T. demani, T. dussumieri, T. elegans, T. flammula, T. forcipata, T. hirsutimanus, T. longidigitum, T. paradussumieri, T. polita, T. rhizophorae, T. rosea, T. seismella, T. signata, T. typhoni, T. urvillei, X. formosensis

Legend:
- Key species found in >50% of region
- Species found in <50% of region
- Species found only on edges of region

Figure 3. Summary of fiddler crab regionalization with species sorted into realms and provinces.

southward across most of the west coast of Africa to Angola (Fig. 4). The province includes nearby islands such as São Tomé and Príncipe, Cape Verde archipelago, and the Canary Islands. The province does not extend into the Mediterranean, where fiddler crabs are absent, perhaps due its moderately high salinity which is at the upper end of their tolerance in general (Crane, 1975), and above that of *A. tangeri* specifically (Spivak & Cuesta, 2009).

Western Atlantic Realm

The Western Atlantic realm contains 21 species, including members of *Uca*, *Minuca*, and *Leptuca*. This region can be divided into four provinces and two transitional zones (Fig. 5). These four provinces are similar to the zones described for this region by Crane (1975).

Atlantic Coast of USA Province. The province contains three well-studied species, *Minuca pugnax*, *M. minax* (Le Conte, 1855), and *Leptuca pugilator* (Bosc, 1802), and extends along almost the entire Atlantic coast of the United States from Massachusetts to eastern Florida. At the northern end, *M. pugnax* extends into New Hampshire (Johnson, 2014), slightly further northward than the other two species, whereas all three species have somewhat different southern extents, with *M. pugnax* extending to the east coast of Florida; *L. pugilator* wrapping around Florida to Alabama or Mississippi; and *M. minax* with a disjunct distribution on the east and west coasts of Florida (but not southern Florida) extending along the northern Gulf of Mexico to Texas.

Gulf of Mexico Province. This province begins about the panhandle of Florida, USA, and encircles the Gulf of Mexico to Veracruz, Mexico. This region contains six essentially endemic species: *Leptuca panacea* (Novak & Salmon, 1974), *L. spinicarpa* (Rathbun, 1900), *L. subcylindrical* (Stimpson, 1859), *Minuca longisignalis* (Salmon & Atsaides, 1968), *M. marguerita* (Thurman, 1981), and *M. virens* (Salmon & Atsaides, 1968). *Minuca minax* and *M. vocator* (primarily members of neighboring subregions to the east and south, respectively) are found throughout large parts of the Gulf subregion as well. A few additional species extend into the edges of the Gulf province from neighboring regions, including: *Leptuca pugilator*, *Minuca burgersi* (Holthuis, 1967), *M. rapax* (Smith, 1870), and *Uca major* (Herbst, 1782). Crane (1975) regarded this province as only including the US states bordering the Gulf, but modern range data clearly suggest that it include the entire western coast of the Gulf, including the Mexican states of Tamaulipas and Veracruz. Recent biogeographic studies of the fiddler crabs in the region include Hopkins & Thurman (2010) and Thurman *et al.* (2018).

Florida/Yucatán Transition Zone. The state of Florida, USA represents a transitional zone between three distinct provinces: the temperate Atlantic Coast province to the north, the semi-tropical Gulf of Mexico province to the west, and the Tropical Western Atlantic province to the south. Members of all three provinces intermix

in Florida, leading to a faunal assemblage that is unique to the state and otherwise not representative of any of the surrounding provinces. A similar transition zone is found on the opposite side of the mouth of the Gulf of Mexico, ranging from the Yucatán Peninsula west into the state of Tabasco. One species, *Leptuca speciosa* (Ives, 1891), is primarily restricted to this transitional zone, with additional observations only from western Cuba (directly between the two peninsulas and arguably part of the zone) and the Bahamas to the east of Florida.

Tropical Western Atlantic Province. The islands of the Caribbean, including the greater and lesser Antilles, as well as the Atlantic coasts of Central and South America all makes up one large province consisting of 10 species: *Leptuca cumulanta* (Crane, 1943), *L. leptodactyla* (Rathbun, in Rankin, 1898), *L. thayeri*, *Minuca burgersi*, *M. mordax* (Smith, 1870), *M. rapax*, *M. victoriana* (von Hagen, 1987), *M. vocator*, *Uca major*, and *U. maracoani*. *Leptuca speciosa* may be present along the northern margin of the province, whereas *L. uruguayensis* may be present along the southern margin. The province extends to southern Brazil, ending about Rio de Janeiro and Santos (São Paulo state). This southern limit marks the boundary between two local biomes: tropical mountains and sedimentary plains to the north and subtropical mountainous Gondwana Shield to the south (Thurman *et al.*, 2013).

The province could be divided into subprovinces, although none of the possibilities are particularly satisfactory. Four of the major species in this province (*L. thayeri*, *M. burgersi*, *M. rapax*, and *M. vocator*) are generally found throughout most of the province. The other six major species have a variety of distributional patterns (Table 1) that could lead to continental *versus* island, Central *versus* South America, and even northern South America *versus* eastern South America subdivisions. As many as four potential subprovinces can be envisioned: Caribbean Islands, Central American Atlantic Coast, Northern South American Coast, and Eastern South American Coast, although these could be combined into larger-grained units as well.

The division between northern and eastern South America was studied by Thurman *et al.* (2013), with the point of separation around the Ponta do Calcanhar, Rio Grande do Norte, Brazil, the location at the northeastern corner of the continent where the Central South Equatorial Current that flows from Africa to South America splits into the North Brazil and South Brazil currents. Thurman *et al.* (2013) did not find any restriction to population gene flow across this potential barrier.

Southeastern Brazil Transition Zone. The tropical species that extend southward to around Rio de Janeiro and Santos quickly begin to disappear southward into more subtropical and temperate biomes (Thurman *et al.*, 2013). This is approximately where one first encounters the only South American temperate species, *Leptuca uruguayensis*, making the stretch of Brazilian coastline from approximately Santos to Cabo de Santa Marta, Santa Catarina, a transition zone between the tropical and temperate provinces of the southwestern Atlantic.

Uruguay/Argentina Province. This small temperate province starts in southern Brazil about Cabo de Santa Marta and extends south across Uruguay into northern Argentina. It contains one species, *Leptuca uruguayensis*. The province represents approximately 60% of the range of this species, most of the rest being in the transitional zone to the north. Truchet *et al.* (2019) reported new southernmost records of this species, possibly representing another example of poleward expansion as ocean temperatures rise.

Eastern Pacific Realm

The Eastern Pacific realm contains 36 species of the genera *Uca*, *Minuca*, *Leptuca*, and *Petruca*. Most of the species have ranges falling
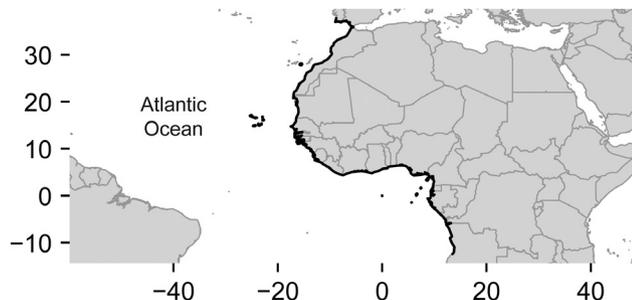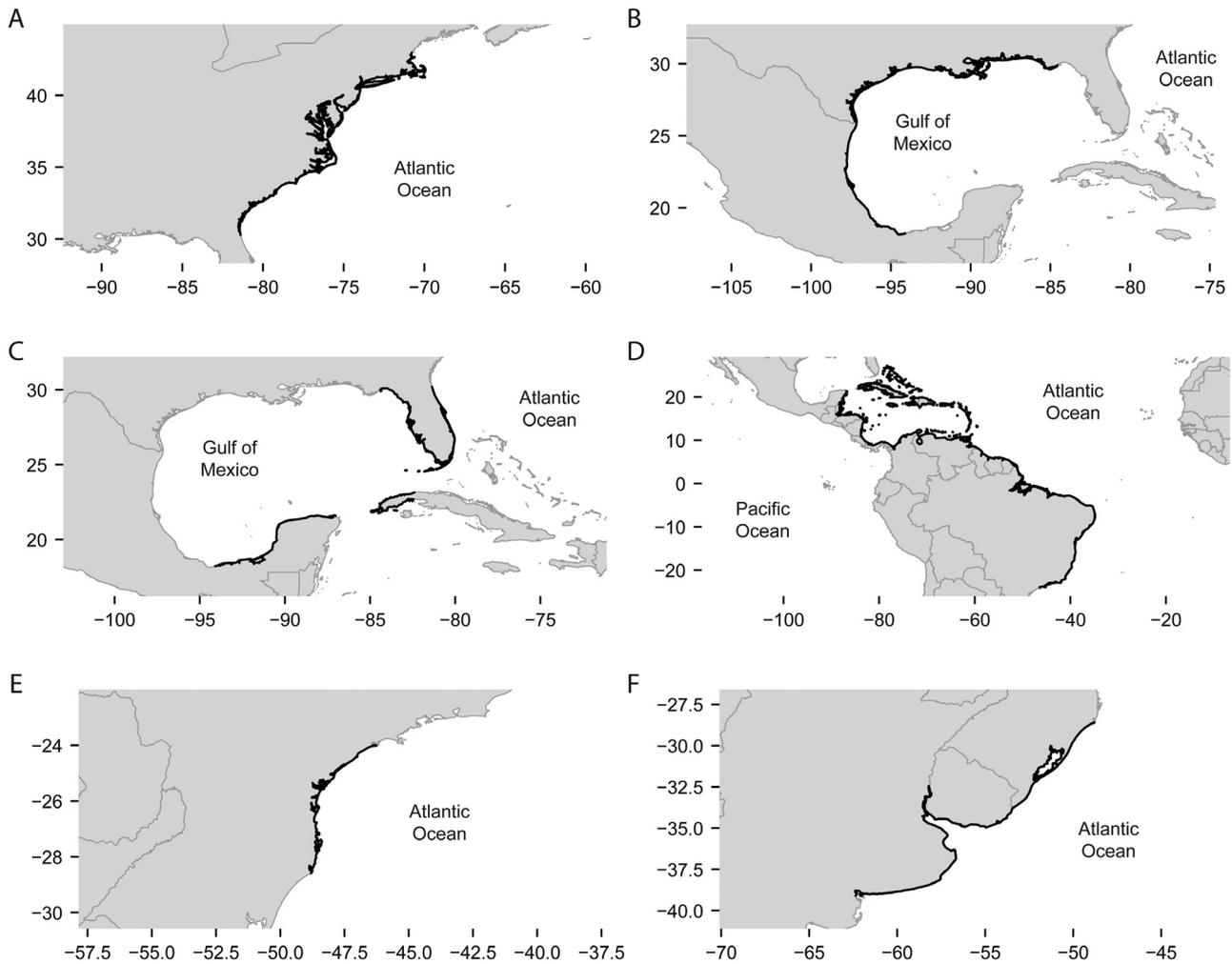

Figure 4. Provinces of the Eastern Atlantic Ocean Realm: West Africa.

Figure 5. Provinces of the Western Atlantic Ocean Realm: Atlantic Coast of the USA (**A**), Gulf of Mexico (**B**), Florida/Yucatán Transition Zone (**C**), Tropical Western Atlantic (**D**), Southeastern Brazil (**E**), and Uruguay/Argentina (**F**).

Table 1. General distribution of six species of fiddler crabs in the Tropical Western Atlantic province; four additional species are found in all four subareas. X, major presence throughout area; ~, minor presence.

Species	Caribbean Islands	Central America	Northern South America	Eastern South America
Leptuca cumulanta	~		X	~
L. leptodactyla	X	~	X	X
Minuca mordax		X	X	X
M. victoriana				X
Uca major	X		X	
U. maracoani			X	X

into one of four general patterns: 1) species endemic to the Gulf of California, Mexico; 2) species found across the Pacific coast of Mexico (including the Gulf of California) but not extending further south; 3) species extending from at least the southern Gulf of California into South America; and 4) species found predominantly between El Salvador and northern Perú. These species combine to create one island province and two to three semi-distinct continental provinces similar to the three zones described by Crane (1975), two of which have the potential for further internal division (Fig. 6).

Pacific Mexico Province. The northernmost of the eastern Pacific regions extends from southern California, USA through Baja

California and the Gulf of California (Sea of Cortez), Mexico and south to Oaxaca in southern Mexico. It contains eight primary species, two of which, *Uca monilifera* Rathbun, 1915 and *Leptuca coloradensis* (Rathbun, 1893), are endemic to the northern part of the Gulf; another two, *L. crenulata* and *L. musica* (Rathbun, 1915) ranging beyond the Gulf but still constrained southward within Mexico (with *L. crenulata* extending northward into the southern part of California, USA). Five additional species, *Leptuca latimanus* (Rathbun, 1893), *Minuca brevifrons* (Stimpson, 1860), *M. ecuadoriensis*, *M. zacae* (Crane, 1941), and *Uca princeps*, are common in at least part of this region but extend well southward, most to South America.

One could arguably divide this province into two to three subprovinces: 1) a northern subprovince, including the Pacific
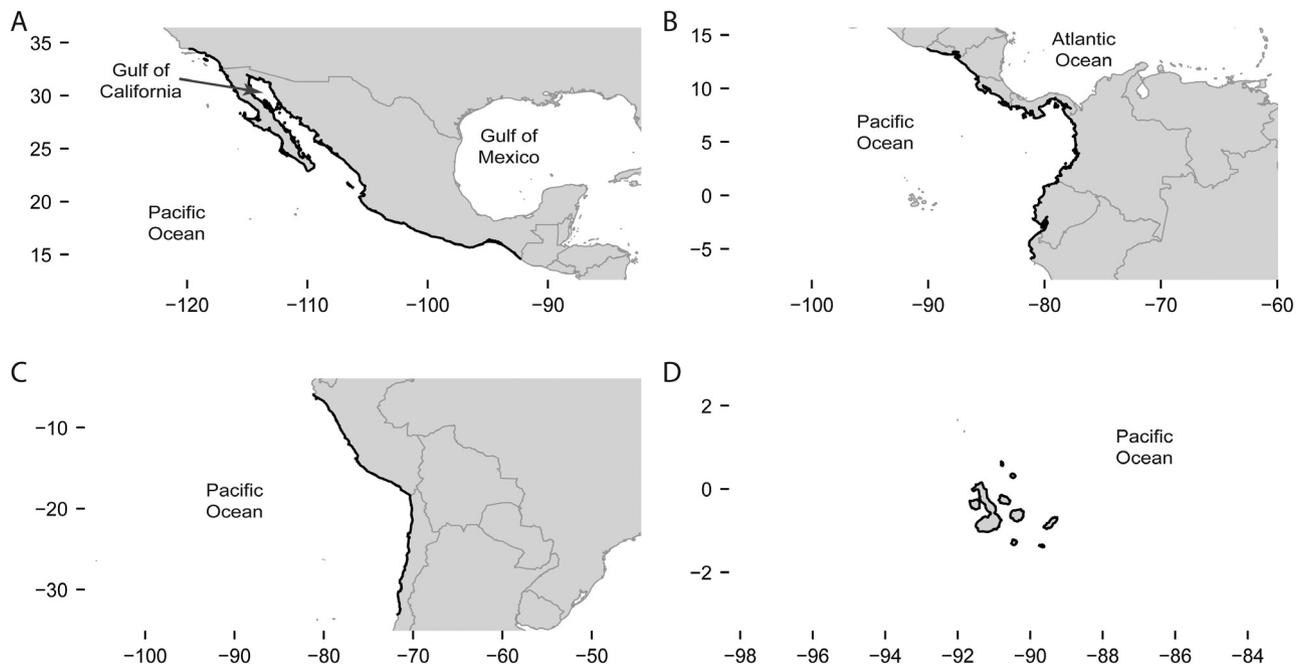
Figure 6. Provinces of the Eastern Pacific Ocean Realm: Pacific Mexico (**A**), Tropical Eastern Pacific (**B**), Perú/Chile (**C**); Galápagos Islands (**D**).

coast of Baja California state, Mexico and southern California, USA containing two species: *L crenulata* and *U. princeps* (their distribution in the US was more recently discussed by Rosenberg, 2018); 2) a northern Gulf of California subprovince containing four species (*L. crenulata, L. coloradensis, U. monilifera,* and *U. princeps*); and 3) a western Mexico subprovince including the Pacific coast of Mexico south of the Gulf of California, the southern part of the Gulf, and the Pacific coast of the Baja California Sur state, Mexico, containing all of the province's species other than the two northern Gulf endemics.

There likely should be a transition zone between the southern edge of this province and the northern edge of the Tropical Eastern Pacific province, likely located in southern Mexico, Guatemala, and/or El Salvador, but surveys of these coasts have been rare enough to make clear delineation currently impossible.

Tropical Eastern Pacific Province. Twenty-four species are thought to have roughly similar ranges starting from approximately El Salvador to Nicaragua in the north through at least Panamá in the south, with most extending at least to the Gulf of Guayaquil in northern Perú: *Leptuca batuenta* (Crane, 1941), *L. beebei* (Crane, 1941), *L. deichmanni* (Rathbun, 1935), *L. dorotheae* (von Hagen, 1968), *L. festae* (Nobili, 1901, see Nobili, 1901b), *L. inaequalis* (Rathbun, 1935), *L. limicola* (Crane, 1941), *L. oerstedi* (Rathbun, 1904), *L. pygmaea* (Crane, 1941), *L. saltitanta* (Crane, 1941), *L. stenodactylus, L. tenuidpedis* (Crane, 1941), *L. terpsichores, L. tomentosa* (Crane, 1941), *L. umbratila, Minuca argillicola* (Crane, 1941), *M. galapagensis* (Rathbun, 1902), *M. herradurensis* (Bott, 1954), *Petruca panamensis* (Stimpson, 1859), *Uca heteropleura* (Smith, 1870), *U. insignis, U. intermedia* von Prahl & Toro, 1985, *U. ornata* (Smith, 1870), and *U. stylifera* (H. Milne Edwards, 1852). Two additional species fall within this province, but with substantially more limited ranges: *Minuca osa* (only known from the Golfo Dulce, Costa Rica) and *Leptuca tallanica* (von Hagen, 1968) (restricted to southern Ecuador and northern Perú). Five additional species (*Leptuca latimanus, Minuca brevifrons, M. ecuadoriensis, M. zacae* and *Uca princeps*) extend from Mexico through most of this province as well, bringing the total number of species in the region to 31.

The province can roughly be divided into three subprovinces: 1) a northern subprovince consisting of the Pacific coasts of El Salvador, Honduras, and Nicaragua; 2) a central subprovince consisting of the Pacific coasts of Costa Rica and Panamá, and 3) a southern subprovince consisting of the Pacific coast of Colombia, along with Ecuador and northern Perú (Gulf of Guayaquil to Sechura). The central subprovince is the core of the region, with 30 of the 31 species present (*Leptuca tallanica* is only found in southern Ecuador and northern Perú), with most found across the entire subprovince. The northern and southern subprovinces each contain about 24 of the 31 species, with different missing subsets. Missing from the north are *L. dorotheae, L. pygmaea, L. tallanica, M. argillicola, M. galapagensis, M. osa,* and *U. intermedia*; missing from the south are *L. deichmanni, L. limicola, L. oerstedi, Minuca brevifrons, M. herradurensis, M. osa,* and *M. zacae.*

Perú/Chile Province. Most of the Tropical Eastern Pacific species have ranges that end in northern Perú between the Gulf of Guayaquil and Sechura, with only three species (*L. stenodactylus, M. galapagensis,* and *U. princeps*) extending further south through the remainder of the Peruvian coast and into northern Chile. Compared to the area immediately north, this region is particularly impoverished with respect to fiddler crabs, with few suitable habitats and relatively cool temperatures due to the Humboldt Current (Crane, 1975). Lacking the unique element that contributes to some of the other subtropical/temperate provinces (such as the temperate endemic *L. uruguayensis* found on the southern Atlantic coast), there is no transition zone between this and the Tropical Eastern Pacific province so the Perú/Chile province might alternatively be considered an extremely southern subprovince of its tropical northern neighbor.

Galápagos Islands Province. The eastern Pacific Ocean largely lacks the large offshore island chains and oceanic islands found in the western Atlantic and Indian oceans, and the central and western parts of the Pacific Ocean. Fiddler crabs are either absent from central Pacific islands (such as the Hawaiian Islands) or clearly part of the IWP fauna (as in French Polynesia). The notable exception are the Galápagos Islands, which contain two species: *Leptuca helleri* (Rathbun, 1902) (endemic to the islands, but see below) and *Minuca galapagensis* (also found in the Pacific Coastal region, although a strong candidate for a population genetic and taxonomic

study to determine if the island and continental populations actually belong to the same species). The two Galápagos species never appear to be locally sympatric, being found on different islands or on different parts of the same island, with only one known instance of them being found as close as adjacent coves of the same bay (Garth, 1946).

Moscoso (2012, 2013) reported *L. helleri* in catalog lists from Puerto Pizarro, northern Perú. I have been unable to confirm or otherwise obtain more information about these observations and do not know if it is an error or that it represents an expansion of the otherwise Galápagos endemic to the continent.

Indo-West Pacific Realm

This large region includes both the entirety of the Indian Ocean as well as the central and western Pacific Ocean. The realm contains 47 species of *Austruca, Cranuca, Gelasimus, Paraleptuca, Tubuca,* and *Xeruca,* all of which constitute the tribe Gelasimini, exclusively of IWP species (Rosenberg, 2019). A number of species previously thought to be widespread across this realm have been subsequently split into multiple species with reduced geographic range (Naderloo *et al.,* 2010; Shih *et al.,* 2010a, 2012, 2013; Naderloo *et al.,* 2016; Shih *et al.,* 2018, 2019). The Indian Ocean species are almost completely distinct from those of the western and central Pacific Ocean, excluding the transitional overlap zone in western Indonesia and the Malay peninsula. Only *Gelasimus tetragonon*

(Herbst, 1790) is widely spread across both oceans, although *Austruca annulipes* (H. Milne Edwards, 1837) still has a large degree of overlap as well. It can be suggested that the Indian Ocean and the central and western Pacific Ocean should be viewed as subrealms of the IWP. This realm also shows the sharpest divergence between the provinces described below and the divisions suggested by Crane (1975).

Indian Ocean Subrealm

The subrealm contains 12 species and can be divided into four provinces and two transition zones (Fig. 7). The eastern edge of the Indian Ocean is a major transitional area, separating the Indian Ocean and western Pacific faunas. The Maldives are currently not included in any province as the identification of its species is somewhat uncertain. This regionalization contrasts with Crane (1975), who divided the Indian Ocean into two divisions, one from eastern Africa to western India, and one from eastern India across the Malay Peninsula to northern Borneo.

East Africa Province. The province extends from the southeastern coast of South Africa through the southern part of Somalia together with the islands of the western Indian Ocean, including Madagascar, Réunion, Mauritius, Mayotte, and the Seychelles. The province contains three endemic species, *Austruca occidentalis, Paraleptuca chlorophthalmus* (H. Milne Edwards, 1837), and *Tubuca*
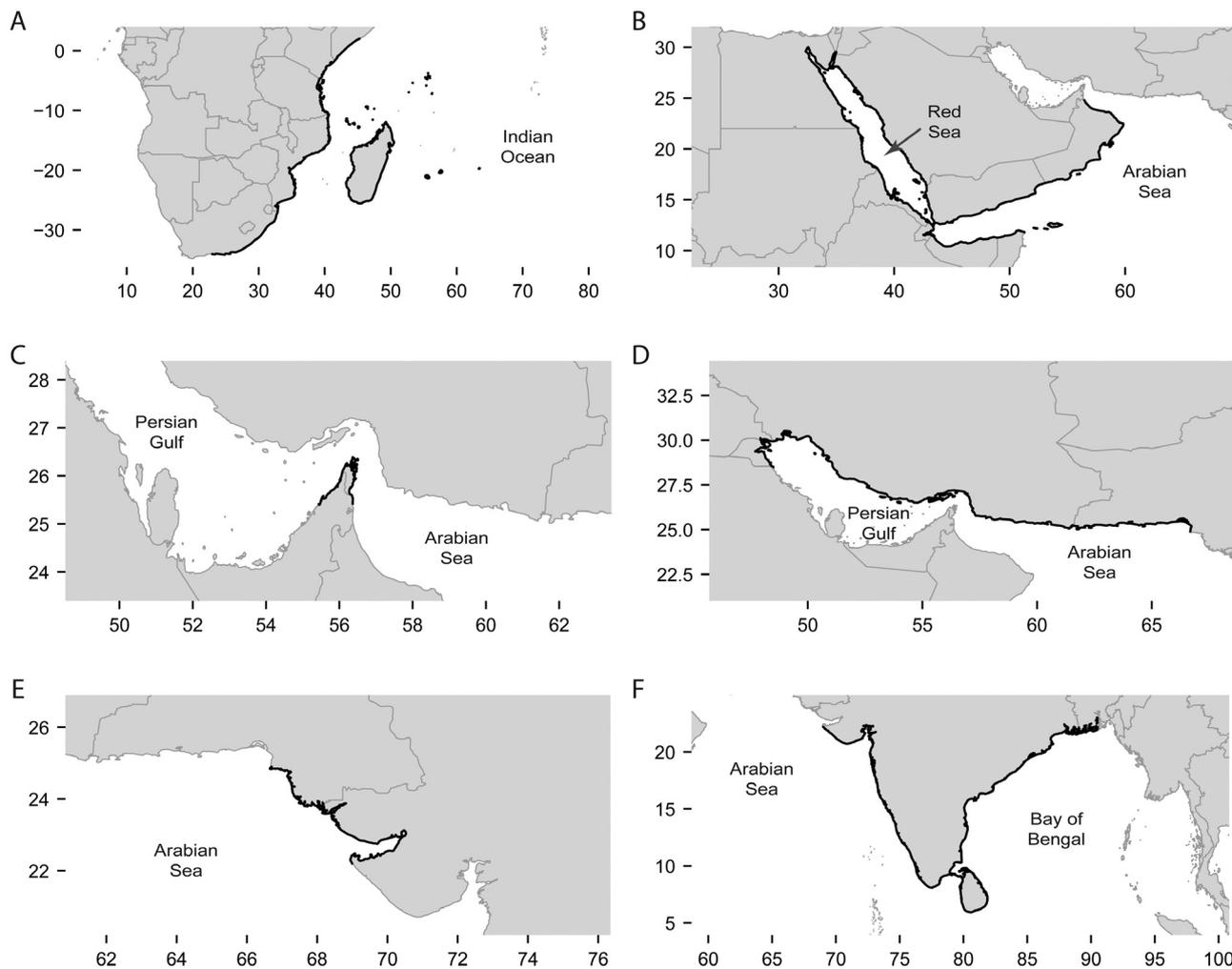
Figure 7. Provinces of the Indian Ocean Subrealm: East Africa (**A**), Red Sea (**B**), Strait of Hormuz Transition Zone (**C**), Persian Gulf (**D**), Pakistan/India Transition Zone (**E**). and Indian Subcontinent (**F**).

urvillei (H. Milne Edwards, 1852), as well as three species that extend into other provinces, *Cranuca inversa* (Hoffmann, 1874), *Gelasimus hesperiae* (Crane, 1975), and *G. tetragonon*.

Red Sea Province. The Red Sea Province includes not only the Red Sea, but most likely the Gulf of Aden, the island of Socotra, and possibly the southeastern coast of Oman. The province contains three species: *Austruca albimana* (Kossmann, 1877), *Cranuca inversa*, and *Gelasimus tetragonon*, with *G. hesperiae* and *Tubuca alcocki* Shih, Chan & Ng, 2018 (Shih *et al.*, 2018) occasionally found along the fringe of the province. The province is largely defined by the presence of *Austruca albimana*, which otherwise is only found on the edges of the neighboring transition zone.

Strait of Hormuz Transition Zone. The Strait of Hormuz, the waterway connecting the Persian Gulf to the Arabian Sea, also serves as the meeting point for fiddler crabs from the Red Sea Province to the south and the Persian Gulf Province to the west and north. This zone includes the coastline along the southern edge of the strait, starting from the Musandam Peninsula of Oman and running southwest across the United Arab Emirates, and Qeshm Island on the north side of the strait off the coast of Iran. Species in the zone include *Austruca albimana*, *A. iranica* (Pretzmann, 1971), *A. sindensis* (Alcock, 1900), *Cranuca inversa*, *Gelasimus hesperiae*, and *G. tetragonon*.

Persian Gulf Province. This province runs across the northern coasts of the Persian Gulf and the Gulf of Oman between Kuwait to the west and western Pakistan to the east. Two species, *Austruca iranica* and *A. sindensis*, inhabit the province. Fiddler crabs are not found on the southern coast of the Persian Gulf (Saudi Arabia, Bahrain, and Qatar) due to unusually high salinity (Apel & Türkay, 1999; Naderloo, 2017) (see above).

Pakistan/India Transition Zone. A small transition zone exists in eastern Pakistan and northwestern India, representing the boundary between the Persian Gulf and Indian Subcontinent Provinces.

Indian Subcontinent Province. The province includes continental India as well as Bangladesh and Sri Lanka. It might also include the Andaman and Nicobar Islands, whose unclear species assemblage makes it hard to place in either this province or the neighboring transition zone. Four species are found in the province: *Austruca annulipes*, *A. variegata*, *Gelasimus hesperiae*, and *Tubuca alcocki*. An additional species, *T. rosea* (Tweedie, 1937), has a range that extends to Bangladesh and northeastern India. *Austruca variegata* is only found on the eastern coast of India, opening up the possibility of eastern (Arabian Sea) and western (Bay of Bengal) subprovinces.

Sumatra and Malay Peninsula Transition Zone. The tropical lands and water separating the Indian and Pacific Oceans contain a complex mix of species from both subrealms (Fig. 8). This transition zone includes the western Malay Peninsula (southern Myanmar,

Figure 8. Sumatra/Malay Peninsula Transition Zone.

southern Thailand, continental Malaysia, and Singapore) and the island of Sumatra. It likely includes the Andaman and Nicobar Islands (which otherwise would be part of the Indian Subcontinent Province), and may also include the eastern side of the Malay Peninsula, including some or all of the coast of the Gulf of Thailand (which otherwise would represent a southern extension of the Northeast Asian Province). It likely does not extend further eastward to Borneo or Java.

One of the complicating features of this zone is that it represents a likely sympatric zone for many difficult-to-distinguish species (which are otherwise allopatric from neighboring regions), leading to many records with unresolved taxonomic issues. For example, the species name *vocans* has been commonly used in the identification of fiddler crabs in this zone, but may refer to either *Gelasimus vocans* (Linnaeus, 1758) or *G. hesperiae*. Similar issues exist with a variety of species of *Austruca* and *Tubuca*.

Two species are predominantly found only in this zone: *Austruca bengali* and *Tubuca rosea*, with the former entirely restricted to the zone and the latter with isolated populations in neighboring provinces.
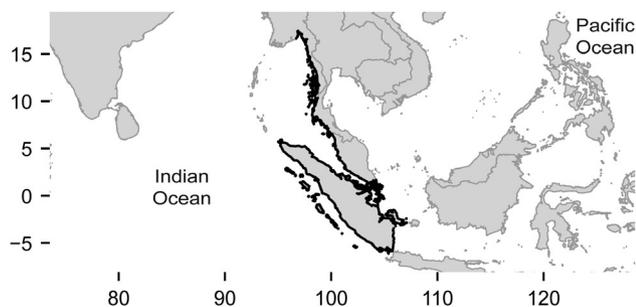
Western Pacific Ocean Subrealm

The Western Pacific Ocean subrealm (which includes both the western and central Pacific Ocean) easily has the most complex physiography for fiddler crabs. This is the only region that can be viewed functionally as having two-dimensional coastlines because of the dense island groups of (primarily) Indonesia and the Philippines allow for admixture and spread from Japan to Australia (north to south) and eastern Asia to New Guinea and beyond (west to east) (Fig. 9). In contrast, the islands of the Caribbean have neither the number, density, extent, or arrangement (outside of the northern cluster of larger islands, most of the Antilles form a rather linear, if curved chain) to have such an effect beyond relatively local scales. This subrealm contains 36 species, substantially more than the 12 of the neighboring Indian Ocean subrealm. Many of the provinces below are similar to those described by Crane (1975), although the precise bounds are often somewhat different.
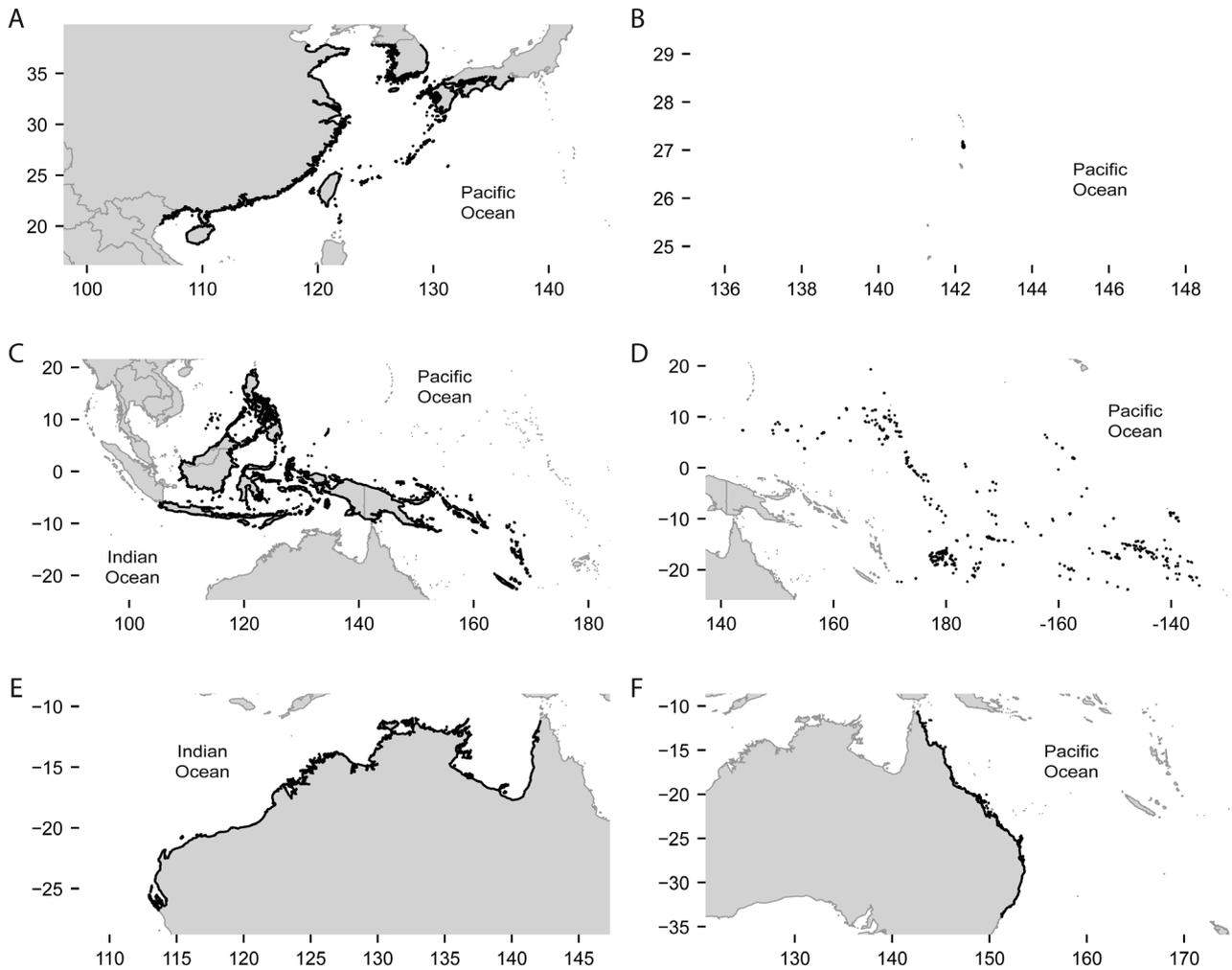
Northeastern Asia Province. This province includes Vietnam, eastern China, and the southern half of the Korean peninsula (the northern extent of IWP fiddler crabs is approximately at 37–38° latitude, so the northern coastlines of these countries are outside of the province), as well as Japan (including the Ryukyu Islands) and Taiwan. The province has five dominant species: *Austruca lactea* (De Haan, 1835), *Gelasimus borealis* (Crane, 1975), *Paraleptuca splendida* (Stimpson, 1858), *Tubuca arcuata* (De Haan, 1835), and *T. paradussumieri* (Bott, 1973), the first four being essentially endemic to the province. The province can be further subdivided into two subprovinces: a continental subprovince (Vietnam, China, and Korea), and an island subprovince (Taiwan and Japan).

The continental subprovince includes one additional species, *Tubuca acuta* (Stimpson, 1858), which is endemic to the continent. It is possible that this subprovince (and the province as a whole) continues southward through the rest of Vietnam and into Cambodia and even northeastern Thailand, but as mentioned earlier, species surveys from those regions are absent or uncertain.

The island subprovince, which might alternatively be viewed as a transition zone, contains one endemic species *Xeruca formosensis* (Rathbun, 1921), found only on Taiwan and neighboring small islands, and seven additional species also found in the neighboring Malay Archipelago province: *Austruca perplexa* (H. Milne Edwards, 1852), *Austruca triangularis* (A. Milne-Edwards, 1873), *Gelasimus jocelynae* (Shih, Naruse & Ng, 2010; see Shih *et al.*, 2010a), *Gelasimus tetragonon*, *Paraleptuca crassipes* (White, 1847), *Tubuca coarctata* (H. Milne Edwards, 1852), *T. dussumieri* (H. Milne Edwards, 1852), and *T. typhoni* (Crane, 1975). *Austruca annulipes* and *Gelasimus vocans*

Figure 9. Provinces of the Western Pacific Ocean Subrealm: Malay Archipelago (**A**), northeastern Asia (**B**), Ogasawara Islands (**C**), Polynesia/Micronesia (**D**), northern Australia (**E**), and eastern Australia (**F**).

may rarely be found in this subprovince as well. The subprovince borders the Malay Archipelago Province to the east and somewhat merges into the Sumatra and Malay Peninsula Transitional Zone to the south.

Ogasawara Islands Province. This tiny province (or perhaps proto-province) consists of the isolated Ogasawara Islands southeast of the main Japanese islands. Only an endemic species is found on the islands, *Paraleptuca boninensis.*

Malay Archipelago Province. This island province is predominantly made up of Indonesia (excluding Sumatra, part of the Malay Peninsula Transition Zone) and the Philippines, but also includes nations sharing islands with Indonesia (e.g., the islands of Borneo, New Guinea, and Timor), as well as Palau and most of Melanesia (Solomon Islands, Vanuatu, and New Caledonia). This is likely the most structurally complicated province, not only because of its two-dimensional structure, but also because it sits in the center of the other five provinces of the Western Pacific subrealm, with potential species mixing on almost every margin, not even including where this province merges into the Indian Ocean and its fauna along its southwestern margin. The core of the province would best be described as the central islands that run from Sulawesi and the Banda Arc of Indonesia in the south, through Luzon in the Philippines in the north. Islands on the western (Borneo), southern (e.g., Java, Bali, Nusa Tenggara, Timor), and eastern (New Guinea

and beyond) fringes are more likely to have species that overlap with those from the neighboring regions. Major species in the province include: *Austruca annulipes, A. cryptica* (Naderloo, Türkay & Chen, 2010; see Naderloo *et al.*, 2010), *A. perplexa, A. triangularis, Gelasimus jocelynae, G. tetragonon, G. vocans, Paraleptuca crassipes, Tubuca bellator* (White, 1847), *T. coaractata, T. demani* (Ortmann, 1897), *T. dussumieri, T. forcipata* (Adams & White, 1848), *T. paradussumieri, T. rhizophorae* (Tweedie, 1950), and *T. typhoni.* Additional species found on the fringes are included in Figure 3. Attempts to further divide this province into subprovinces are hindered not only by its complicated physiography, but by taxonomic uncertainty surrounding many species identifications and the potential for sympatry of closely related and difficult-to-distinguish species.

Polynesia and Micronesia Province. The province consists of most of the isolated islands of the central and western Pacific Ocean, including most of Polynesia (Cook Islands, French Polynesia, Samoa, Tonga, Tuvalu, and Wallis and Futuna; but excluding the Hawaiian Islands, New Zealand, Eastern Island, and Pitcairn Islands, none of which have fiddler crabs), Micronesia (Kiribati, Mariana Islands, Marshall Islands, Wake Island, Federated States of Micronesia, Caroline Islands, Guam), Fiji (representing the eastern most part of Melanesia), and Palmyra Atoll. The primary species in this province are *Austruca perplexa, Gelasimus excisa* (Nobili, 1906), *G. tetragonon*, and *Paraleptuca crassipes. Gelasimus excisa* is endemic to a geographic cluster of islands including Tonga, Tuvalu,

Samoa, Wallis and Futuna, and Fiji. The other three primary species are all long-range, predominantly island specialists, with *G. tetragonon* the only species to span essentially the entire breadth of the Indian Ocean and Western Pacific subrealms. Additional species found on the western margins of this subregion (particularly as one moves closer to the larger islands of Indonesia, Papua New Guinea, and the Philippines) include *A. triangularis, G. jocelynae,* and *Tubuca coarctata.*

Australia Superprovince

Although clearly part of the greater Western Pacific subrealm, Australia almost deserves an entire unit of its own, thus designated the only superprovince in this treatment. It has two distinct provinces, containing nine and eleven species, respectively, with only three species overlapping both provinces. More importantly, of the 17 species found in Australia, eight are endemic to the continent, with another three mostly restricted to the continent.

Northern Australia Province. This Australian province includes Western Australia, the Northern Territory, and the north coast of Queensland west of the of Cape York Peninsula/Torres Strait. This zoogeographical region was discussed by Crane (1975) and von Hagen & Jones (1989), who referred to it as the Dampierian division/province after the terminology of Hedley (1904). The province contains nine species: four endemic to the province: *Gelasimus dampieri* (Crane, 1975), *Tubuca capricornis* (Crane, 1975), *T. elegans* (George & Jones, 1982), and *T. hirsutimanus* (George & Jones, 1982); three endemic to Australia: *T. polita* (Crane, 1975), *T. seismella* (Crane, 1975), and *T. signata* (Hess, 1865); and two primarily found in this province but also observed in southern Indonesia: *Austruca mjoebergi* (Rathbun, 1924) and *T. flammula.* Although never found on the mainland, *A. triangularis* has been observed on Melville Island just off the coast near Darwin, Northern Territory.

Eastern Australia Province. This Australian subregion includes Queensland east of the Cape York Peninsula/Torres Strait and the northern part of New South Wales. This province was discussed by Crane (1975) and von Hagen & Jones (1989), who referred to it as the Solanderian division/province after the terminology of Hedley (1904), a terminology not followed here as, strictly speaking, Solanderian only refers to the Queensland portion of the province. The species in this subregion include one endemic to the subregion: *Tubuca longidigitum* (Kingsley, 1880); three endemic to Australia: *T. polita, T. seismella,* and *T. signata; Gelasimus vomeris* (McNeill, 1920) (mostly confined to Australia, but also found in New Caledonia and possibly New Guinea), and six additional species also found well beyond Australia: *Austruca perplexa, A. triangularis, G. tetragonon, Paraleptuca crassipes, T. coarctata,* and *T. dussumieri.* Unlike the largely distinct species assemblage of the Northern Australia subregion, this subregion shows substantial overlap with the island regions to the north and east. Crane (1975) included New Caledonia as part of this subregion (likely due to the presence of *G. vomeris*), although it is here considered more of a transitional edge between Eastern Australia and the Malay Archipelago provinces.

This central domain of this subregion is eastern Queensland. Only a few of the species extend southward into the more temperate New South Wales (to about Sydney). Like the Pacific coast of South America, this southern extension might be viewed as a temperate subprovince but lacks the unique characteristics that would lead one to view it as an independent unit.

DISCUSSION

The regions and results described herein are only as good as the underlying data and, as with any organism, there are several reasons why these range data may contain inaccuracies. One

obvious problem is the potential inaccuracy of species identifications. Records for a given location may use a variety of different names for the same species or fail to recognize similar species as separate entities. While efforts have been followed to correct for this (e.g., Rosenberg, 2014), these corrections are often based on underlying assumptions about species distributions that may simply be wrong. Not only does this lead to more vague definitions of boundaries between neighboring provinces and transitional zones, but a handful of locations known to contain fiddler crabs were left out of specific provinces when the species assemblages were clearly ambiguous. For example, the literature on the Andaman and Nicobar Islands includes (both directly and indirectly) at least twenty different specific names (used in about three times as many binomial and trinomial combinations and spellings) for the fiddler crabs present on these islands (Heller, 1865; Kingsley, 1880; Alcock, 1900; Pesta, 1911, 1913; McNeill, 1920; Sankarankutty, 1961; Tikader & Das, 1985; Tikader *et al.,* 1986; Das & Dev Roy, 1989; Bairagi, 1995; Dev Roy & Das, 2000; Das, 2001; Dev Roy & Nandi, 2012). Our current best estimate of the species located on the islands is five: *Austruca annulipes, Gelasimus tetragonon, G. vocans, Tubuca alcocki,* and *T. paradussumieri.* If these five are correct, the islands would be included as part of the transition zone between the Indian and Pacific oceans. It would be entirely reasonable, however, to suspect that the species being referred to as *G. vocans* is actually *G. hesperiae,* while the two *Tubuca* identified on the islands might both belong to *T. alcocki.* If both of these assumptions were to be the case, these islands would instead be viewed as part of the Indian Subcontinent province.

Another underlying assumption of these data and the regionalization treatment as a whole is that species ranges remain static over time. The only records available for many areas are decades (or even a century or more) out of date. Even if these records were completely accurate at the time of reporting (assuming easily and accurately transferable taxonomic concepts), there is no guarantee they still represent the current species ranges. We can be reasonably certain that the ranges of some species have likely changed over roughly the three centuries elapsed since some of the reports; at least four examples of recent range expansion into previously unoccupied areas have been documented in just the past decade (Johnson, 2014; Peer *et al.,* 2015; Peer *et al.,* 2018; Rosenberg, 2018; Truchet *et al.,* 2019), and this does not consider habitat loss (or recovery) in many coastal wetlands around the world. Similarly, even if the regionalization treatment presented here is perfectly accurate today, there is no guarantee it will still be so at any future date, particularly as ocean temperatures and currents are affected by changes in global climate (Sadowski *et al.,* 2018). This work thus represents a snapshot in time for future comparison and contrast, rather than a finished, static product.

A third general issue with the underlying data is that species ranges are generally presented in a binary presence/absence framework, perhaps with seasonal modifications for migratory animals. While certainly the simplest way to conceive a geographical range, a binary system fails to accurately represent the fluidity and uncertainty of ranges, particularly on marginal areas. Relatively few species have ranges with true static edges that can be tied to a clearly defined environmental barrier. Rather than strict presence/ absence, species ranges would more accurately be described via spatial probability density functions that illustrate the likelihood of finding a species in a particular area (see Royle *et al.,* 2012; Fleming & Calabrese, 2017). This would also allow for greater accuracy in depicting patchy distributions of high or low likelihood of local occurrence within the centers of overall ranges.

This study does not reveal anything that had not already been reported with respect to ranges of individual species, but it does highlight some of the species with more unusual ranges. *Afruca tangeri* has often been considered unusual given its large latitudinal range (~50°) across the west coast of Africa (Crane, 1975), but over a dozen species have similar, if not larger latitudinal extents.

What makes *A. tangeri* particularly noteworthy is that it is strictly allopatric over that entire range.

Of high interest is the species with the largest longitudinal range of fiddler crabs, *Gelasimus tetragonon*. This species has long been recognized as among a handful with unusually large ranges, but one of the outcomes of taxonomic revision over the previous four decades has been the fractionation of most of these "long-ranging" species into separate species. Although "*Uca vocans*" *sensu* Crane, 1975 and "*Uca lactea*" *sensu* Crane, 1975 both contained recognized subspecies (six and four, respectively), the recognition of these now as seven and eight distinct species (the subgenera *Gelasimus* (*Gelasimus*) and *Austruca* (*Austruca*), respectively) drastically changes and limits the overall distribution of individual species. Only *G. tetragonon* remains unchanged across its entire range, with limited genetic comparison (Shih *et al.*, 2016b) revealing little divergence among distant geographic locations (Madagascar, Taiwan, and French Polynesia), particularly relative to other cryptic species that have been discovered in recent years (Shih *et al.*, 2009, 2019; Naderloo *et al.*, 2016). The longitudinal range of *G. tetragonon* covers almost 193°, between two-thirds to double that of the next two closest species: *Paraleptuca crassipes* and *Austruca perplexa*. All three species have only in common a wide distribution throughout the islands of the western and central Pacific Ocean. *G. tetragonon* is unusual in persisting across the entire Indian Ocean as well. Although occasionally found in patches along continental coasts, all three species appear to be something of island specialists. What allows *G. tetragonon* to maintain genetic cohesion over so long wide a range, whereas other species living on the same islands do not, remains unknown. As geneflow in fiddler crabs is basically mediated by larval dispersal (Wieman *et al.*, 2014; Peer *et al.*, 2018), some unusual aspect of either the life history, behavior, or morphology is likely the cause. Perhaps *G. tetragonon* has an unusually long larval developmental period; most studied species of fiddler crabs have larval periods of two to four weeks (Rabalais & Cameron, 1983). Perhaps the larvae are prone to moving into deeper water with stronger currents. An alternative hypothesis is that the apparent range is an artifact of limited genetic markers used in previous studies and broader genetic surveys will reveal cryptic species with greater genetic divergence than currently reported.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

Supplementary material maps. Geographical distribution of the 105 species of fiddler crabs.

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