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The scientific legacy of Juan A. Torres-Negrón[1]

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ABSTRACT

Juan A. Torres-Negrón (Juan Torres) studied ants, wasps, termites and other insect groups. I reviewed 34 of his publications and grouped them into six subjects: ecological theory, taxonomy, chemistry, ecology, synthesis, and commentaries. Juan Torres used empirical fieldwork, keen observations, and experimentation to advance the understanding of ant taxonomy and ecology in Puerto Rico. His taxonomic work involved the description of new species and genera of various insect groups, as well as revisions of taxonomic groups, and other observations of the ecology and behavior of rare taxa. Juan Torres also published several taxonomic keys in English and Spanish for various insect groups and localities. His work with ant communities advanced ecological niche theory and island biogeography highlighting the non-equilibrium and stochastic nature of ant community dynamics in Puerto Rico and adjacent islands. He also published synthesis summaries of the ants of Puerto Rico, Mona Island, and the Luquillo Mountains. His ecological studies of ants ranged from descriptions of biotic interactions among ants and with other animal species, to the quantification of the role of insects in wood decomposition and nutrient cycling. The research spanned from dry to wet forest and non-forest conditions in Puerto Rico and adjacent islands and cays.

Key words: ants, insects, hurricanes, biogeography, wood decomposition

RESUMEN

El legado científico de Juan A. Torres-Negrón

Juan A. Torres Negrón (Juan Torres) estudió hormigas, avispas, comejenes y otros grupos de insectos. Revisé 34 de sus publicaciones y

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las agrupé en seis temas: teoría ecológica, taxonomía, química, ecología, síntesis y comentarios. Juan Torres utilizó trabajo empírico de campo, sagaces observaciones y experimentación para avanzar el campo de la taxonomía y ecología de las hormigas en Puerto Rico. Su trabajo taxonómico resultó en la descripción de nuevas especies y géneros de insectos, revisiones taxonómicas, reportes de presencia de especies en la Isla y la documentación de nuevos aspectos ecológicos y del comportamiento de varios grupos taxonómicos. Además, publicó claves taxonómicas en inglés y español para varios grupos de insectos y distintas localidades. Sus trabajos con comunidades de hormigas ampliaron las teorías de ecología de nicho y la de biogeografía de islas enfatizando el estado de desequilibrio y la naturaleza estocástica de las comunidades de hormigas en Puerto Rico e islas adyacentes. Publicó resúmenes sobre la ecología y taxonomía de hormigas e insectos en Puerto Rico, Isla de Mona y las Montañas de Luquillo. Sus estudios ecológicos cubrieron una amplia gama de tópicos desde las interacciones bióticas entre grupos de hormigas y con otros grupos de plantas y animales, hasta la función de los insectos en la descomposición de la madera y el reciclaje de nutrientes en los bosques. Las investigaciones de Juan Torres incluyeron desde bosques secos a bosques muy húmedos, pastizales y sistemas agrícolas en el archipiélago de Puerto Rico.

Palabras clave: hormigas, insectos, huracanes, biogeografía, descomposición de madera

INTRODUCTION

I examined 34 articles published by Juan A. Torres with 34 co-authors (Appendix) to assess his scientific legacy. He was sole or senior author in 22 of those publications. The scientific legacy of Torres has influenced a wide range of geography from regional to global locations as evidenced by citations of his work by Chinese, Russian, and African scientists. For example, 15 articles in the Appendix were cited in 186 publications representing about 500 authors and co-authors. To facilitate the discussion of the publications, I grouped them into six topics (ecological theory, taxonomy, chemistry, ecology, synthesis, and commentaries), which I discuss below.

ECOLOGICAL THEORY

The Island Biogeography Theory of McArthur and Wilson (1967) predicted an equilibrium level in the number of species in islands as a result of a balance between species immigration rates and extinctions. Torres and Snelling (1997)[3] tested this theory by examining the temporal change in the number of ant species in Puerto Rico and 44 islands and cays in the vicinity of Puerto Rico. They found that the number of ant species on the islands increased due to low extinction rates and

[3]Citations for articles authored or co-authored by Juan Torres are in the Appendix. Other citations are in the Literature Cited.

greater immigration rates than extinctions. Data did not substantiate the presence of equilibrium as predicted by the McArthur and Wilson model, but suggested instead that the number of ant species on these islands was increasing. Torres and Snelling (1997) found that habitat diversity was the best predictor of ant species diversity. This work generated one of Juan Torres most cited papers and was scientifically significant because it was an empirical test of the island biogeography theory, which ruled ecological thinking since it was initially proposed. This study alone would have cemented the scientific legacy of Juan Torres, but he did much more beginning with his doctoral dissertation published in 1984 (Torres 1984 a, b).

Torres (1984a) examined ant species coexistence in grasslands, agricultural lands and forests. He found that diet, daily activities, food size and macrohabitat utilization contributed to, but were not necessary for species coexistence in agricultural lands. In forests, diet and litter utilization could facilitate species coexistence, while in grasslands, differences in diet and daily activity were the factors contributing to ant coexistence. However, there was overlap in niches in all three environments. Food limitation also contributed to structuring ant assemblages and led to interspecific aggression when food was concentrated. Microclimate and priority effects were also important in determining ant distributions. In some species, ant co-existence was dependent on stochastic events affecting their functioning.

Microclimate affected ant foraging and nesting places (Torres, 1984b). Increased temperature reduced colony activity and ant fighting activities. Shade reduced the number of ant colonies. There were more ant species in agricultural lands than in forests and grasslands because of a greater number of microhabitats. Contrary to expectations, greater structural complexity in forests did not translate into more ant species because the greater structure resulted in fewer microenvironments. Because ants don't build complex nests, they can quickly recover from disturbances to nests. They can also eat brood when starving, and workers, larvae and queens can tolerate long periods without food or water. Longevity gives ants stability.

In summary, Torres contributed to ecological theory through the comprehensive study of ant communities of many species in contrasting habitats. He used empirical data to document the natural history of ants and explain their abundance and diversity, and he conducted experiments to verify the role of environmental factors such as temperature or food availability and to understand aggressive behavior under different environmental conditions. These studies were interpreted in the context of accepted niche and biogeographical theory and served to demonstrate where they did or not apply to ants in the Caribbean.

TAXONOMY

Torres was not trained as an insect taxonomist, but his detailed ecological work required precise taxonomic identity for the species he studied. Therefore, he addressed taxonomic issues with success as evidenced in six taxonomic publications. Snelling and Torres (1998) discovered that *Camponotus ustus* specimens described originally from the US Virgin Islands and found to be common in Puerto Rico were in fact two new species, which they described as *C. kaura* and *C. taino*. Snelling and Torres also redescribed the original species *C. ustus* using more specimens including collections from Mona Island. In the process, they also reduced five species names to synonyms of the species, and an ant variety was elevated to the species level. English and Spanish keys were developed for separating the US Virgin Islands species from those of Puerto Rico.

Torres et al. (2000a) made observations on the ecology and behavior of the cryptic nocturnal ant *Anochetus kempfi*, describing for the first time the males and ergatoid queen. Similarly, Genaro and Torres (1999) redescribed the female, and described for the first time the male of *Pseudomethoca argyrocephala*, a species with marked sexual dimorphism. They also expanded information about its geographic distribution. Torres et al. (2000b) reported six new records for Puerto Rico of parasitoids of Aculeate Hymenoptera (stinging insects).

Snelling and Torres (2004) studied the spider wasps of Puerto Rico and the British Virgin Islands to clarify the taxonomy of the group (Hymenoptera Pompilidae) in the region. They found 16 species from Puerto Rico, including a new species (*Auplopus taino*), and by examining type specimens discovered a new genus not reported for Puerto Rico (*Episyron*). This study also involved new synonyms and movement of species from species to subspecies categories. English and Spanish keys plus illustrations were also included.

Bright and Torres (2006) reviewed the Scolytidae of Puerto Rico describing a new genus (*Allothenemus*), 14 new species, 21 new records for Puerto Rico, four new cases of synonymy, deletion of two species from the Puerto Rico record, and reporting new host records for the island. They found 71 species of Scolytidae in Puerto Rico and reported keys in English and Spanish for this group. Torres also published taxonomic keys in English and Spanish for other insect groups on Mona Island (Torres and Snelling 1992) and in the Luquillo Mountains (Torres, 1994b).

The legacy of taxonomic work of Juan Torres is impressive in light of the short time that he was active and the fact that the main thrust of his scientific effort was not taxonomical.

CHEMISTRY

Nine publications by Juan Torres focused on the chemistry of ants. This research explored the chemical compounds associated with ant parts and their potential relationship with ant taxonomy, mating behavior and defense from predators. For example, gland secretions from male mandibles of four species of *Camponotus* probably functioned as sex pheromones but proved of little use for taxonomic purposes (Torres et al., 2001a). A similar conclusion about the lack of taxonomic utility of extracts from *Megalomyrmex cyendyra* ants from Colombia and Ecuador was reported by Jones et al. (1999a). Caste-specific Tyramides extracted from Myrmicine ants also resulted in uncertain biological functions attributable to these compounds, although a role in ant-mating behavior could be inferred (Jones et al., 2010). Some of the chemical studies yielded records of new compounds reported for insects (such as phenylpyrrole in ants) or the third report of a pyrrole from ants (Jones et al., 1996a; Jones et al., 1999b).

Caste-specific alkaloid production in queen and workers of *Solenopsis maboya* and *S. torresi* could provide helpful criteria for taxonomic differentiation of complex taxa (Torres et al., 2001b). The same possibility was inferred for the use of 3-hexyl-5-methylindolizidine isomers from thief ants *Solenopsis* (*Diplorhoptrum*) sp. (Gorman et al., 1998). One of the most quoted articles of Juan Torres (Spande et al., 1999) was based on alkaloid venom extractions from *Solenopsis* (*Diplorhoptrum*) sp. collected in Puerto Rico and California (Jones et al., 1996b; Gorman et al., 1998). There were conspicuous differences in the alkaloids found in workers and queens. The alkaloids had been previously found in the skin of amphibians collected in various Latin American countries. They found that alkaloids normally used for ant defense against predators appeared to function as dietary sources for the frogs. The alkaloid was not metabolized by the frogs, but stored in their skin.

ECOLOGY

I subdivided the ecological legacy of the research conducted by Juan Torres into five insights about ant and insect ecology. First, he described quantitatively several important food web relationships involving ants. For example, Torres et al. (2000c) demonstrated that the blind snake *Typhlops platycephalus* fed on 13 of 30 available ant species in its immediate habitat and on two additional species that they could not find in the study location. The snake fed mostly on adult ants although it preferred brood in the laboratory. The diet also included termites, mites and sciarid fly larvae. They also found that not all consumed prey was digested by the snake.

Second, Torres (1989) surveyed the status of several fungus-growing ant species in Puerto Rico, and Torres et al. (1999) demonstrated the role of *Trachymyrmex jamaicensis* ants in the nutrient (N, P, K, Ca, Mg, Mn, Fe, Na, and C) cycling of forests. Ants altered the soil profile by moving subsoil to the surface. They also enriched the soil near the nest, particularly the refuse piles, where nutrient concentrations were high and seed germination was enhanced relative to control sites. Seedling survival, however, was lower in the refuse piles.

Third, Torres (1994a) conducted the most comprehensive study available on the role of insects in the wood decomposition of *Cyrilla racemiflora* in a montane forest above 600 m elevation in the Luquillo Mountains. He followed changes in wood density, nutrient content and invertebrate abundance through four decay classes for logs and also four decay classes for snags. Logs were enriched with nitrogen, lowering the C/N of decomposing wood. Locations with feces of the cerambycid *Parandra cribata* had higher nitrogen and phosphorus concentrations relative to surrounding wood. Wood cavities resulted from feeding activities of cerambycids, and these cavities benefited fungal growth and waterlogging. Torres found 138 invertebrate species contributing to wood decomposition, with species increasing as wood decomposition advanced. This level of invertebrate species richness is low compared to reports from other latitudes and Torres attributed the low species richness to insularity, elevation, high humidity and possibly, wood chemistry. Two species of termites and three species of ants were the most abundant invertebrates. Ants were more abundant in snags than in logs. Bark beetles and woodborers were absent in the wood of *C. racemiflora*, which contrasted with reports from decomposing wood of other species.

In another study, Torres and González (2005) found faster wood decomposition of *C. racemiflora* in dry forests than in wet forests. They attributed the faster decomposition in dry forests to higher diversity of invertebrate species and functional groups among invertebrates, particularly termites, and the slower wood decomposition in the wet forest to less biodiversity of invertebrates and waterlogging. Jones et al. (1995) found that termite abundance in dry forests was proportional to available dead wood in the forest. This study, a survey of termites on Mona Island, described the abundance of four dry wood termite species in relation to dead wood volume on the forest.

Fourth, Torres (1992a) made insightful observations on the response of Lepidoptera to hurricanes. An outbreak of 15 Lepidoptera species fed on 56 plant species belonging to 31 families, thus controlling their rapid growth after the hurricane. The most common larvae were *Spodoptera eridania*. At the peak of the outbreak, Torres observed the consumption of the preferred host plant and an increment in the parasitism of Lepidoptera by ichneumonids (Hymenoptera) and by tachinids (Diptera). These natural enemies of *S. eridania* were reported for the first time in Puerto Rico. Torres (1988) also documented and discussed the role of hurricanes in the dispersal of insects. He observed the arrival of thousands of individuals of *Schistocera gregari*a (locus) after hurricane Joan, an event that occurred in other islands of the Caribbean. The species failed to establish itself in Puerto Rico, probably because of mortality after a few weeks. Individuals were exhausted upon arriving on the island.

Fifth, in a study of ant nuptial flights in dry and moist environments, Torres et al. (2001) found that between 60 and 78 percent of over 30 species at the study locations engaged in nuptial flights, and do so often (average of four flights per night for all sites, time of day, and species combined), but those flights are generally dominated by a single sex, which raises issues about the reproductive strategies of the species involved. They found that flights were most common post sunset and pre-dawn with little activity between. Males flew on a greater number of nights and were more numerous. High winds inhibited flights as did heavy rain, but more flights occurred during the rainy season.

SYNTHESIS

The synthesis publications of Torres involving the Luquillo Mountains (Torres, 1994b), Mona Island (Torres and Snelling, 1992), and Puerto Rico (Torres and Medina-Gaud, 1998) contain insights into the natural history of insects, their ecology and taxonomy. Keys in English and Spanish for the Hymenoptera of Mona Island and the insects of the Luquillo Mountains are included in these publications. The syntheses contain abundant information about the importance of insects such as their role in hydrological phenomena (affecting water infiltration and soil aeration) or the geological implication of species distribution. For example, the presence of three species of the beetle *Entilliscaris* in Puerto Rico, plus a 38 percent endemism level in that group, suggests that the island is the oldest emergent landmass in the Greater Antilles. Torres and Medina-Gaud (1998) also tally the number of species of insects in Puerto Rico by order, totaling 5,373 species with 28 orders and 28 percent endemism.

When the Brazilian ant (*Solenopsis invicta*) was introduced into Puerto Rico, it created alarm and many calls for control were discussed at all levels of society, including the Puerto Rico Legislature. Torres (1990) published a synthesis of the knowledge available on the species, comparing the situation in Puerto Rico with that of mainland United States of America. He demythologized the species, proposed control methods that were consistent with the ecological situation of the species and specific to certain conditions, while allowing the ant to thrive in other locations and circumstances.

COMMENTARIES

Just as he used science to demythologize the introduced ant *Solenopsis invicta* (Torres, 1990), Juan Torres used some of his publications to clarify myths or popular beliefs that lacked a scientific foundation (Torres, 1992 b, c; 2000). His logic and use of scientific principle was impeccable and served well his objective of improving science education.

SUMMARY

Juan Torres was a naturalist, taxonomist and an ecologist who focused his scientific career on insects with an emphasis on ants. His research highlighted the non-equilibrium and stochastic nature of ant community dynamics in Puerto Rico and adjacent islands. He also published synthesis summaries of the ants or insects of Puerto Rico, Mona Island and the Luquillo Mountains. His ecological studies ranged from descriptions of biotic interactions among ants and with other animal species, to the quantification of the role of insects in wood decomposition and nutrient cycling. The research spanned from dry to wet forest and non-forest conditions in Puerto Rico and adjacent islands and cays. Juan Torres also published opportunistic natural history observations on the role of insects in the response of vegetation to hurricanes, and the role of hurricanes as insect dispersal agents. He collaborated with others in the study of venoms and pheromones in ants with an eye towards understanding ant behavior, mating and taxonomy. His synthesis publications and commentaries reflect a thorough review of available literature, the use of impeccable logic to explain natural phenomena and a strong didactic focus aimed at informing readers about the subtleties of ecological phenomena and the wonders of the insect world.

ACKNOWLEDGMENTS

Gisel Reyes assembled all the publications of Juan Torres, making them freely available electronically through Treesearch (Appendix), and searched the Internet for information on the level of citation of the publications. Evelyn Pagán, Miguel Canals, and Coral Torres contributed material and information on Juan Torres. This review was conducted in collaboration with the University of Puerto Rico. Ernesto Medina and Tamara Heartsill Scalley improved the manuscript with their comments.

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TAXONOMY

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CHEMISTRY

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[4]Compiled by Gisel Reyes, International Institute of Tropical Forestry. Links to Treesearch provide access to the publication.

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