Hawai'i's Toxic Plants: Species Richness and Species–Area Relationships[1]

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Abstract: The Hawaiian Islands have long been seen as relatively devoid of native toxic plant species, a result of the paucity of herbivorous predators in this biogeographically isolated archipelago. This assertion has been subjective, without quantitative comparison to floras that evolved in the presence of such predators. We test this assertion by comparing the richness of toxic species in the native flora of the main Hawaiian Islands to that in the naturalized flora of these islands. That test shows the assertion to be correct: the relative abundance of toxic plant species in the naturalized Hawaiian flora is nearly ten times greater than the relative abundance of those species in the Hawaiian native flora. Of the approximately 150 toxic plant species now found in these islands, 92% are naturalized. The species richness of both native and naturalized Hawaiian plant species correlates positively with island size, as does the richness of toxic native and toxic naturalized plant species. These results, and the lack of significant residuals in species–area relationships across the main Hawaiian Islands, suggest that the relative youth of Hawai'i Island is not needed to account for native plant species richness on this island.

Keywords: Hawaiian Islands, island biogeography, toxic plants, species–area relationships, extinct birds, moa-nalos

In the absence of predators, plants that colonize islands are routinely predicted to lose the anti-predator defenses that marked their founding, continental, populations (e.g., Bowen and VanVuren 1997, Blumstein et al. 2004, Lahti et al. 2009, Burns 2014, 2019, Hess 2016, Leopold and Hess 2017, Salladay and Ramirez 2018, Cubas et al. 2019). Although there are significant exceptions (e.g., Funk and Throop 2010, Hoan et al. 2014, Meredith et al. 2019, see the reviews in Lahti et al. 2009, Burns 2019), much evidence supports this prediction for both structural and chemical defenses (e.g., Vourc'h et al. 2001, Salladay and Ramirez 2018, Cubas et al. 2019).

The toxic native plants of Hawai'i have long been seen as an example of the loss of such chemical defenses from founding populations of better-defended ancestors derived from elsewhere. "The Hawaiian flora is exceptionally poor in poisonous plants," Carlquist (1970:173) observed, because of the lack of "evolutionary pressure for plants to produce poisonous substances." Three decades later, Ziegler (2002) made the same point, observing that the Hawaiian flora contains "less than a half a dozen genera" of plants that "are known or alleged to have some degree of toxicity, at least to vertebrates" (2002:197). The likely reason for this was as clear to Ziegler (2002) as it was to Carlquist (1970): the "ancestral characteristic of poisonous qualities was apparently lost . . . because it was of little or no selective advantage due to the scarcity of not only former herbivorous vertebrates but also

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former continental invertebrate predators" (2002:198).

Ziegler (2002) was careful to observe that former herbivorous vertebrates were scarce, rather than absent, because he knew something that Carlquist did not know: that there had once been a far more diverse variety of herbivorous ducks and geese in the Hawaiian Islands. All of these birds became extinct sometime between the initial arrival of Polynesians some 750 years ago (Rieth et al. 2011, Wilmshurst et al. 2011) and the arrival of Europeans in 1778 (Olson and James 1991, James and Burney 1997, Sorenson et al. 1999, Paxinos et al. 2002, Iwaniuk et al. 2009, Olson 2013, Witmer et al. 2017). Indeed, Givnish et al. (1994) argued that the thorn-like prickles in Hawaiian *Cyanea* (Campanulaceae) might have served as a structural defense against predation by some of these birds, an argument that has also been applied to *Argemone glauca* (Papaveraceae; Barton 2014). Nonetheless, and as Ziegler also knew, the level of predation exerted by these avian herbivores was likely to have been far less than that encountered by the continental ancestors of Hawaiian native plants.

The assertions by Carlquist (1970) and Ziegler (2002) that the native Hawaiian flora has only a small number of chemically defended ("toxic") plant species were subjective. Neither author attempted to determine precisely how small this number might be, or to compare that number to floras that had presumably evolved under greater selective pressure from herbivores. In this paper, we attempt to accomplish both of those goals. We derive a more complete list of the toxic plant species contained within the native flora of the main Hawaiian Islands. In addition, we derive a list of the toxic plant species within the naturalized flora of those islands. Comparing the two lists provides an objective test of the assertion that the native flora of the main Hawaiian Islands is comparatively depauperate in toxic species.

Having compiled an inventory of the toxic plant species within the native and naturalized flora of the main Hawaiian Island, we use that compilation to address a broader issue. In his important analysis of the distribution of Hawaiian native plants across a wider set of the Hawaiian Islands than we examine here, Price (2004, Price and Wagner 2011) argued that the flora of Hawai'i Island has fewer species than would be expected from its large size and suggested that it is the relative youth of this island that explains that shortfall. We use analyses of the species–area relationships of the toxic native and naturalized plant species across the main Hawaiian Islands, and of the full run of native and naturalized plant species across these islands, to assess whether the flora of Hawai'i Island is, in fact, depauperate in native plant species and whether it is necessary to call on recent Hawaiian geological history to explain aspects of the quantitative plant biogeography of this region.

METHODS

Our focus is on the main Hawaiian Islands as geographically defined by Imada (2012, 2019): Hawai'i, Ka'ula, Kaho'olawe, Kaua'i, Lāna'i, Lehua, Maui, Moloka'i, Ni'ihau, and O'ahu (Figure 1). These are the same islands that were at the heart of the discussions of Hawai'i's poisonous plants by Carlquist (1970) and Ziegler (2002). We compiled our catalogue of the native and naturalized toxic plants of these islands in two stages. First, we collated the species listed in the three substantial treatments of those plants that are available: Arnold (1944), Baldwin (1979), and Scott and Thomas (2000). All three define a toxic plant as a plant dangerous, or potentially dangerous, to people.

Although we recognize it as a possibility, we assume throughout that the current toxicity of native plants has not been induced (*sensu* Tollrian and Harvell 1999) by the impact of the introduction of vertebrate herbivores to the Hawaiian Islands, either by Polynesians (Kirch 1982, 2017) or by later human arrivals (Leopold and Hess 2017, Burns 2019, Duffy and Lepczyk 2021).

Second, we compiled a list of all poisonous plants known from the main Hawaiian Islands that are included in Wagstaff (2008), a global compendium of plants known to be toxic. This compendium uses a definition of toxicity

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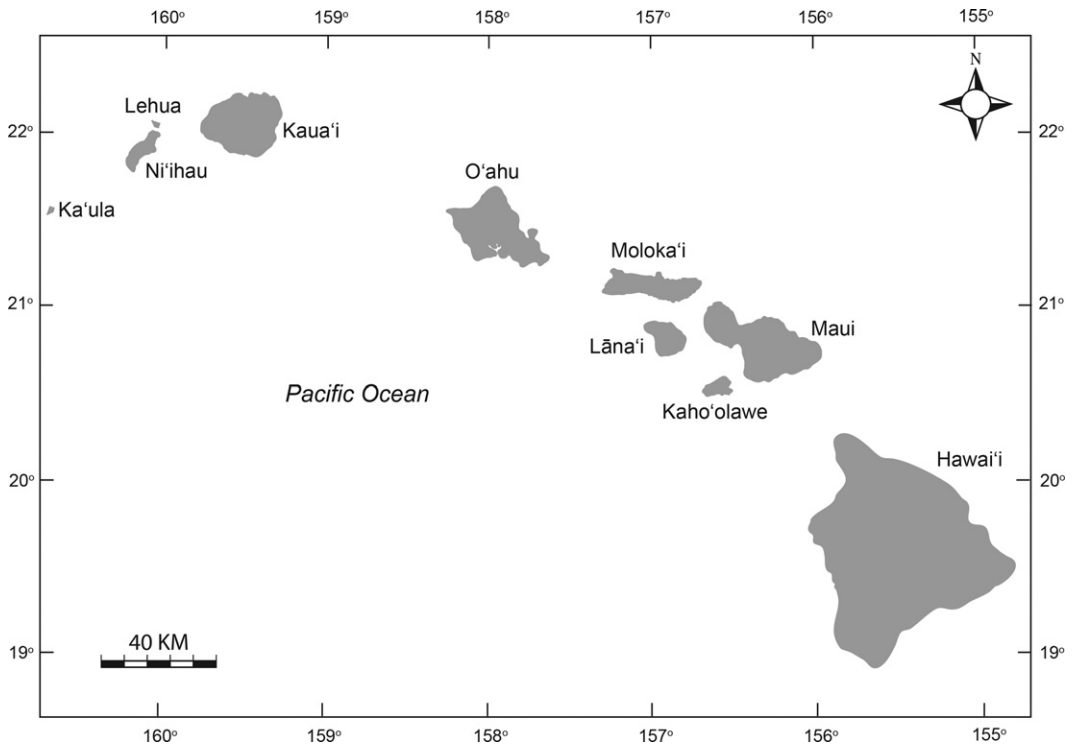


FIGURE 1. The main Hawaiian Islands, as defined by Imada (2012, 2019).

that might seem broader than that used by Arnold (1944), Baldwin (1979), and Scott and Thomas (2000), who focused on plants toxic to humans. Wagstaff (2008:xi) included all those plants “which, by means of toxic substances it contains, produces adverse effects in humans or economic animals such as livestock, laboratory animals, pets, wild animals, birds, fish, and bees.” The three works devoted to the toxic plants of Hawai‘i, however, also included plants thought to be toxic to non-human vertebrates, so the difference in approach is not as great as it might appear.

None of these compendia of toxic plants is complete. For instance, *Sapindus saponaria* (Sapindaceae) is indigenous to Hawai‘i (Imada 2012) and identified as toxic by Little and Skolmen (1989) and others (e.g., Ide 2001), but does not appear in Arnold (1944), Baldwin (1979), Scott and Thomas (2000), or Wagstaff (2008). Because of such complexities, the compilation of the toxic plant species of Hawai‘i presented here must be seen as a non-exhaustive list of such species.

Arnold (1944), Baldwin (1979), and Scott and Thomas (2000) were primarily concerned with the toxicity of plant species found in Hawai‘i and not with the origin of those species. One of our prime interests, however, is in comparing the toxicity of the native and naturalized plants of Hawai‘i. Our list of those species is drawn from Imada (2012) for the endemic and indigenous (“native”) plants of Hawai‘i, and from Imada (2019) for Hawaiian naturalized species. In building these lists, we excluded those species whose status is uncertain—for instance, our lists do not include species that may or may not be naturalized or that may or may not be indigenous.

Supplemental online Appendix 1 provides the results of these efforts. Throughout, botanical nomenclature follows Imada (2012, 2019).

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The Wikstroemia Problem

The genus *Wikstroemia* (Thymelaeaceae) includes approximately 70 species of plants found in southeastern Asia, Australia, and the Pacific Islands (Mabberley 2017). Twelve of those species, all endemic, have been described for the Hawaiian Islands (Wagner et al. 1990, Imada 2012). Since at least the mid-nineteenth century, western naturalists have recognized that at least some of these species contain toxins traditionally used by Native Hawaiians to poison fish (e.g., Andrews 1865, Hillebrand 1888).

The most detailed description of this usage was provided by Stokes (1921), who emphasized the roles played by three plant taxa as fish poisons—the Polynesian introductions *Lagenaria siceraria* (Cucurbitaceae) and *Tephrosia purpurea* (Fabaceae), and the endemic *Wikstroemia* ('ākia in Hawaiian). Stokes observed that older Native Hawaiians distinguished between bitter and non-bitter forms of 'ākia, and that only the bitter form is toxic. He was unable to identify the species of *Wikstroemia* that were used in this context and observed that Native Hawaiians were also unable to do so. He did, however, provide experimental evidence showing that "imported small rainbow fish" (Stokes 1921:229) were killed by both *Wikstroemia elongata* and *W. foetida*. The former species is now treated as synonymous with *W. oahuensis*, while Hawaiian subspecies of *W. foetida* have been synonymized with either *W. oahuensis* or *W. uva-ursi* (Wagner et al. 1990; nativeplants.hawaii.edu). Stokes also provided anecdotal evidence that mixtures of infusions derived from *T. purpurea* and *Wikstroemia* and added to kava (*Piper methysticum*: Piperaceae) served as a human poison.

Degener (1930:224) repeated the information provided by Stokes (1921) and expanded on the toxic nature of 'ākia. This plant, he observed, is "extremely poisonous" if eaten, and that its roots and bark were combined with parts of other plants to form a drink that was used for suicide or to execute criminals. Following those who had come before him, he did not identify the species of *Wikstroemia* used for this purpose.

Arnold (1944) was extremely skeptical about the toxicity of this plant. He had, he noted, eaten 'ākia berries to no ill effect and had rubbed the sap, leaves, and bark on his skin, again with no ill effect. Guinea pigs (*Cavia porcellus*: Caviidae) fed extracts from the plant remained "perfectly well" (1944:58). It is possible, he concluded, that 'ākia is not poisonous at all. Indeed, in a partial replication of Stokes's (1921) fish experiment, Tabrah and Eveleth (1966) attempted to poison tilapia (*Tilapia* sp.: Cichlidae) with an 'ākia infusion, with no significant adverse effects on the fish. Baldwin (1979) reported that he had known people who had eaten 'ākia with no negative results but also reported that unpublished experiments had shown that extracts from the plant were toxic to mice.

With the exception of the experiment reported by Stokes (1921), none of these authors referred to particular species of *Wikstroemia*. Most other writers have followed suit, observing that 'ākia was used as a fish poison without specifying which species of the plant were so used (e.g., Neal 1965, Tabrah and Eveleth 1966, Handy et al. 1972, Lamb 1981, Wagner et al. 1990, Abbott 1992, Culliney and Koebele 1999, Ziegler 2002). There is probably a good reason for this. As Mayer (1991*a*,*b*, 1992) has observed, Hawaiian *Wikstroemia* is extremely variable, many of the species are interfertile, and, as a result, "it may be inappropriate to try to force the entities constituting this group into species" (1991*b*:702).

Nonetheless, the approach we take here requires species counts even if the validity of some of those species may be questioned and the toxicity of the separate endemic populations that comprise Hawaiian *Wikstroemia* is unknown. Those who have been bold enough to name those specific species of 'ākia that are toxic—and, in particular, were used as fish poisons—have targeted two taxa: *W. oahuensis* (e.g., Rock 1913, Stokes 1921, Carlquist 1970), and *W. uva-ursi* (Acevedo-Rodríguez 1990). Accordingly, we have incorporated those two species into our toxic species list.

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TABLE 1

Numbers of Species of Toxic and Non-toxic Plant Species in the Hawaiian Flora, Including Those Mentioned Only in Wagstaff (2008)

	Native Species	Naturalized Species
Toxic	8 END + 8 IND = 16	333 NAT + 12 POL= 345
Non-toxic	1197	1121
Totals	1213	1466
Proportion toxic	16/1213 = .0132	345/1466 = 0.2353

END = endemic; IND = indigenous (native but not endemic); POL = introduced by Polynesian voyagers prior to the European arrival and subsequently naturalized; NAT = naturalized after European arrival. Native species counts tabulated from Imada (2012); naturalized species counts from Imada (2019).

NUMBERS OF TOXIC SPECIES IN THE NATIVE AND NATURALIZED HAWAIIAN FLORA

We take two approaches to determining the number of toxic species in the native and naturalized Hawaiian flora. We begin with the full list of those species, including those mentioned only by Wagstaff (2008). That list includes 16 species of toxic native plants within 14 families and 345 species of toxic naturalized plants scattered across 79 families (see Supplemental online Appendix 1). In that full list, toxic species are approximately 18 times more common in Hawai'i's naturalized flora (23.5% of that flora) than in its native counterpart (1.3%; see Table 1). The difference is impressively significant ($\chi^2 = 280.94$, $P < 0.001$).

These numbers, however, may misrepresent the differences in the relative abundances of Hawai'i's native and naturalized toxic plant species. This is because plants can alter their chemical defenses with remarkable speed when colonizing novel territory (Ridenour et al. 2008, Sardans et al. 2010). We simply do not know whether species discussed in Wagstaff (2008) but not addressed by Arnold (1944), Baldwin (1979), or Scott and Thomas (2000) have lost, retained, or even increased their toxicity since becoming naturalized here.

Excluding toxic species discussed only in Wagstaff (2008) provides a list of 12 species of native toxic Hawaiian plants within 10 genera (Table 2) and 138 naturalized toxic species within 48 genera (Supplemental online Appendix 1). The magnitude of proportional difference in the toxicity of the two floras remains substantial. Toxic species are approximately ten times more common in the naturalized Hawaiian flora (9.4%) than in the native one (about 1%; see Table 3). This difference is again highly significant ($\chi^2 = 89.12$, $P < 0.001$).

Carlquist (1970:173) noted only two species of native Hawaiian poisonous plants: *Cocculus orbiculatus* (Menispermaceae) and *Wikstroemia oahuensis*. As we have noted, Ziegler (2002:197) put the number of plant genera containing toxic species as fewer than six. Our list is longer—12 species within 10 genera—but this does not change the general validity of the arguments made by Carlquist (1970) and Ziegler (2002). The modern flora

TABLE 2

The Native Toxic Plant Species of Hawai'i, Excluding Species Listed Only in Wagstaff (2008)

Species	Family	Status
Argemone glauca	Papaveraceae	END
Erythrina sandwicensis	Fabaceae	END
Hesperocnide sandwicensis	Urticaceae	END
Melicope anisata	Rutaceae	END
Phytolacca sandwicensis	Phytolaccaceae	END
Wikstroemia oahuensis	Thymelaeaceae	END
Wikstroemia uva-ursi	Thymelaeaceae	END
Cassytha filiformis	Lauraceae	IND
Cocculus orbiculatus	Menispermaceae	IND
Ipomoea pes-caprae	Convolvulaceae	IND
Mucuna gigantea	Fabaceae	IND
Mucuna sloanei	Fabaceae	IND

See Table 1 for abbreviations.

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TABLE 3

Numbers of Toxic and Non-Toxic Plant Species in the Hawaiian Flora, Excluding Those Mentioned Only in Wagstaff (2008)

	Native Species	Naturalized Species
Toxic	7 END + 5 IND = 12	131 NAT + 7 POL = 138
Non-toxic	1201	1328
Totals	1213	1466
Proportion toxic	12/1213 = .0099	138/1466 = 0.0941

See Table 1 for abbreviations. Native species counts tabulated from Imada (2012); naturalized species counts from Imada (2019).

of Hawai'i is far more toxic than was the flora encountered here when Polynesians first arrived some 750 years ago, with nearly all of that increase occurring after Cook's arrival. Of the approximately 150 species of toxic Hawaiian plants, 92% (138) are naturalized.

The presence of three potentially toxic species of ferns in the native flora of Hawai'i is worth noting: *Huperzia serrata* (Lycopodiaceae), *Nephrolepis exaltata* (Nephrolepidaceae), and *Pteridium aquilinum* (Dennstaedtiaceae). These species are mentioned only by Wagstaff (2008), though the toxicity of *P. aquilinum*—bracken fern—is frequently discussed in Hawaiian contexts (e.g., Neal 1965, http://nativeplants.hawaii.edu/plant/view/Pteridium_aquilinum_decompositum).

Well into the Holocene, a subset of the main Hawaiian Islands supported three genera, and four species, of large, flightless waterfowl (Anatidae) collectively known as moa-nalos (Olson and James 1991, James and Burney 1997, Sorenson et al. 1999). As a group, these birds filled the ecological role of giant tortoises. One of these species, *Thambetochen chauliodous*, is known from Lāna'i, Maui, and Moloka'i, islands that were joined into a single landmass, Maui Nui, during the Last Glacial Maximum (Kaho'olawe was part of this complex earlier in the Pleistocene; see Carson and Clague 1995, Funk and Wagner 1995, Price 2004, Price and Elliott-Fisk 2004, Medeiros and Gillespie 2011, Clague and Sherrod 2014). Close relatives are known from Kaua'i and O'ahu. We know, from data provided by coprolites, that *Thambetochen chauliodous* included ferns in its diet (James and Burney 1997). All three fern species are currently found on islands that once supported the moa-nalos and their close relatives (Imada 2012) and if all are, in fact, toxic, that toxicity might be explained by predation pressure by moa-nalos, much as the presence of avian herbivores may help explain the structural defenses of Hawaiian *Cyanea* and *Argemone glauca*, discussed earlier.

SPECIES–AREA RELATIONSHIPS

Price (2002, 2004) analyzed the species–area relationship of Hawaiian native plants across a wider range of islands than we have examined here: 18 islands ranging from Kure Atoll in the northwest to Hawai'i Island in the southeast and including all the islands we have examined with the exception of Lehua.

Using logarithmically transformed data, Price (2004) found a strong linear relationship between island area and native species richness ($r = +0.94$, $P < 0.001$). He observed that within the high islands represented in his analysis, those with elevations above 500 m above sea level (Price and Wagner 2011:450), the largest negative residuals were for Ni'ihau, Kaho'olawe, and Hawai'i. The first two of these islands, he observed, have been badly degraded by human activities, while Hawai'i Island is geologically youngest (Price 2004). He also pointed out that "despite containing more area than all other islands combined, Hawai'i's species number is most comparable with that of Moloka'i, which is less than one-fifteenth of its area" (Price 2004:494).

Price (2002, 2004) did not assess whether any of the residuals in his species–area relationship were significantly different from

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TABLE 4

The Total Number of Species per Island

	KL	LE	NI	K	O	MO	L	M	KA	H
Native	15	20	85	626	582	479	354	617	57	509
Naturalized	11	31	88	696	940	503	397	895	146	900
Area (km^2)	0.6[a]	1.15[b]	176[c]	1,431[c]	1,548[c]	675[c]	365[c]	1,999[c]	117[d]	10,433[c]

KL = Ka'ula; LE = Lehua; NI = Ni'ihau; K = Kaua'i; O = O'ahu; MO = Moloka'i; L = Lāna'i; M = Maui; KA = Kaho'olawe; H = Hawai'i. Island area sources: a: Price (2004); b: State of Hawaii Lehua Island Ecosystem Restoration Project (2018); c: State of Hawaii Economic Data Book (2014); d: CRAMP Study Sites (n.d.).

their predicted values, but it is easy to show that they are not. Because the species richness data he provides for Ka'ula is incorrect (Price 2002: Table B1, 2004: Appendix 1), we extracted the correct value (15) from Price (2004: Figure 5). Using that value precisely replicates his regression plot and regression equation for this relationship ($Y = +1.131 + 0.444[X]$), though it does provide a slightly higher correlation coefficient ($r = +0.97$, $P < 0.001$). There are no significant outliers in this data set, although Gardner Pinnacles comes close (−1.94 standard deviations [sd]). Hawai'i falls at 1.72 sd beneath the regression line ($P = 0.09$).

How, we ask, do these results compare to the distributions of the native and naturalized plants of the main Hawaiian Islands and, among them, to the native and naturalized toxic plants of these islands? For reasons discussed earlier, our treatment of toxic plants in what follows excludes those mentioned only in Wagstaff (2008). Counts of native and naturalized plants were tallied from Imada (2012, 2019). The distributions of native and naturalized toxic plant species are provided in Supplemental online Appendix 2; the total number of plant species by island, and the island areas used in our analyses, are presented in Table 4.

As is the case for the larger set of Hawaiian Islands examined by Price (2004), the number of native plant species of the 10 main Hawaiian Islands analyzed here is positively and significantly correlated with island area ($r = +0.94$, $P < 0.001$; see Figure 2). Our results also duplicate those of Price (2004) in that the largest negative standardized residuals are for Ni'ihau (sd = −1.18), Kaho'olawe (sd = −1.58), and Hawai'i Island (sd = −1.16). Also as in Price's larger dataset, none of these values differs significantly from its predicted value. The number of nontoxic and toxic native Hawaiian plant species is also significantly correlated across those islands ($r = +0.97$, $P < 0.001$; see Figure 3). As a result, it is not surprising that the number of native Hawaiian toxic plant species scales significantly to island size across these islands ($r = +0.96$, $P < 0.001$; see Figure 4).

Multiple analyses have established that the number of native and exotic plant species in both island and mainland settings are routinely positively correlated at large geographic scales (see, for instance, Davies et al. 2005, Sandel and Corbin 2010, Bartomeus et al. 2012, Burns 2016, Baiser and Li 2018, Rojas-Sandoval et al. 2020). This is also the case for the Hawaiian Islands examined here ($r = +0.95$, $P < 0.001$; see Figure 5). Given this relationship, it is also not surprising that the number of naturalized plant species across these islands is significantly correlated with island area ($r = +0.96$, $P < 0.001$; see Figure 6). In fact, the slopes and intercepts of the species–area relationships for the native and naturalized plants of the main Hawaiian Islands (Figures 2 and 6) are virtually identical and there are no significant residuals in either relationship (for important discussions of such relationships and comparisons with other settings, see Burns 2015, Li et al. 2018, Guo et al. 2020).

Finally, since the number of toxic native and toxic naturalized plant species is significantly correlated across these islands ($r = +0.96$, $P < 0.001$; see Figure 7), it follows that the number of toxic naturalized plant species

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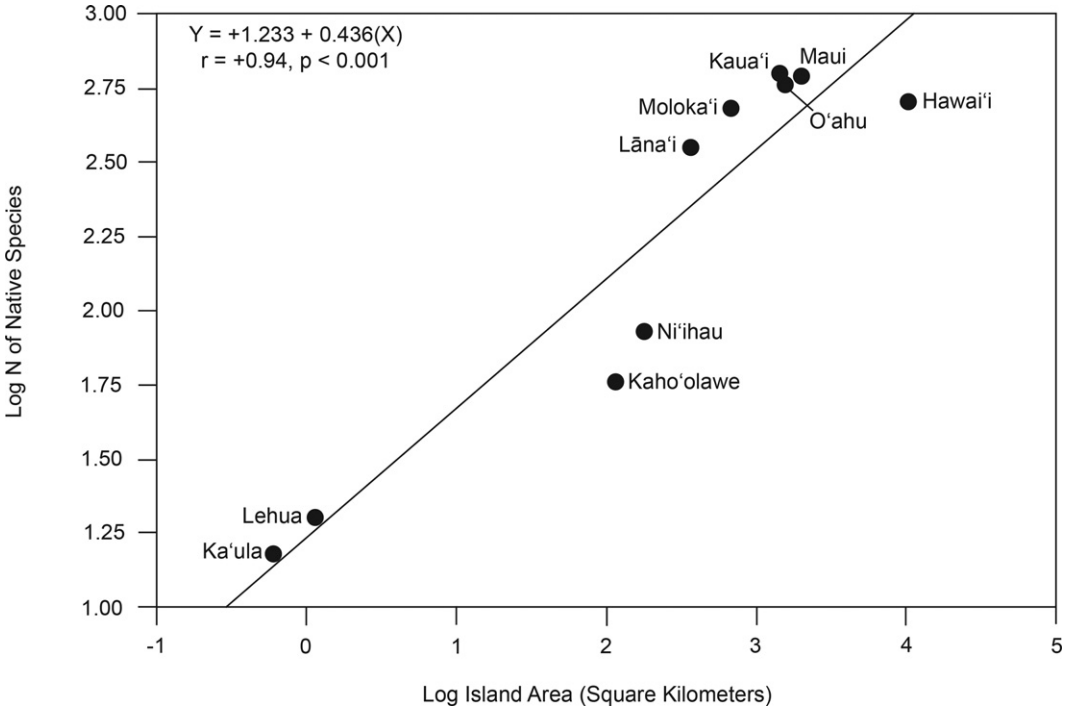


FIGURE 2. The relationship between island area and the number of native plant species for the main Hawaiian Islands (species counts derived from Imada 2012).

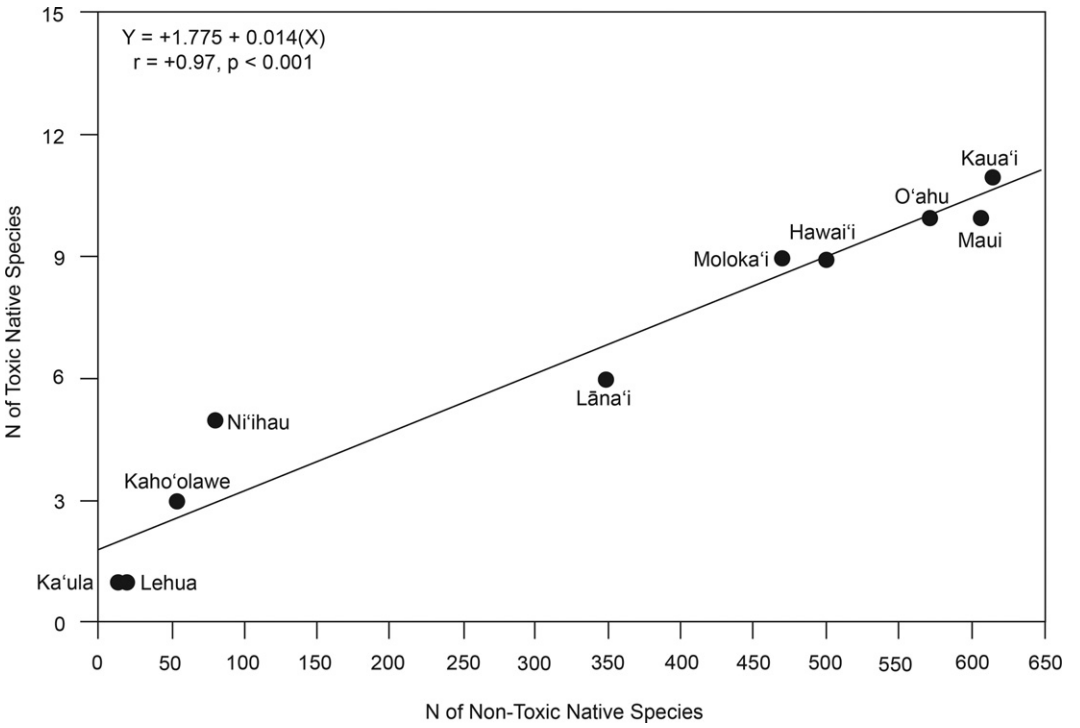


FIGURE 3. The relationship between the number of non-toxic and toxic native plant species across the main Hawaiian Islands.

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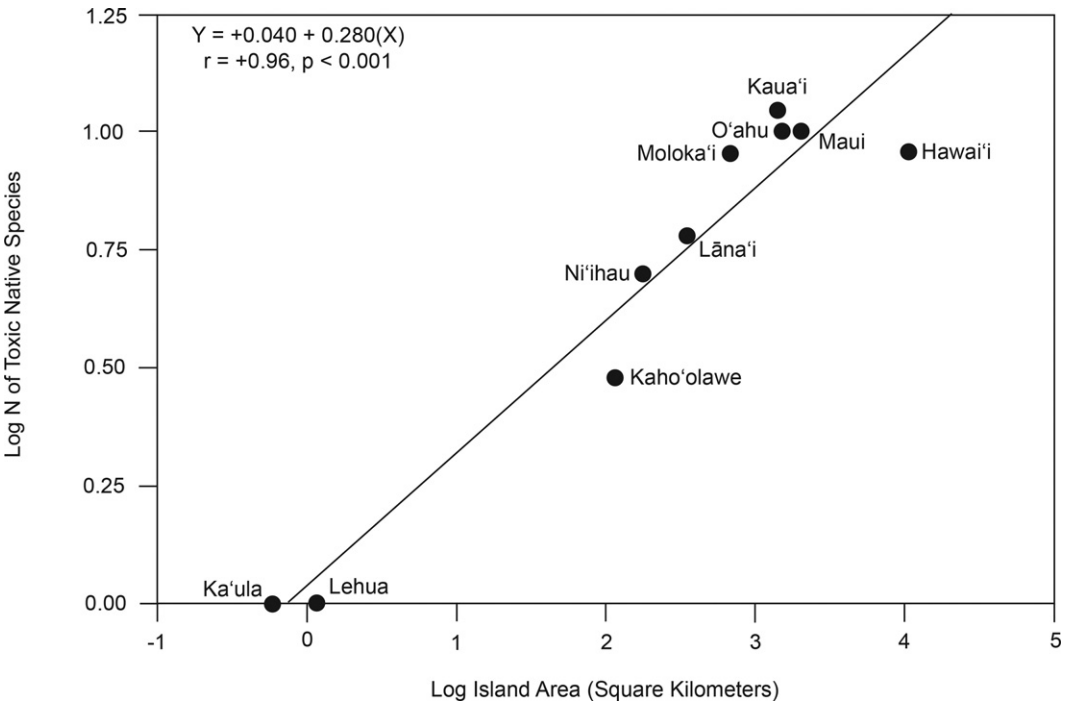


FIGURE 4. The relationship between island area and the number of toxic native plant species for the main Hawaiian Islands.

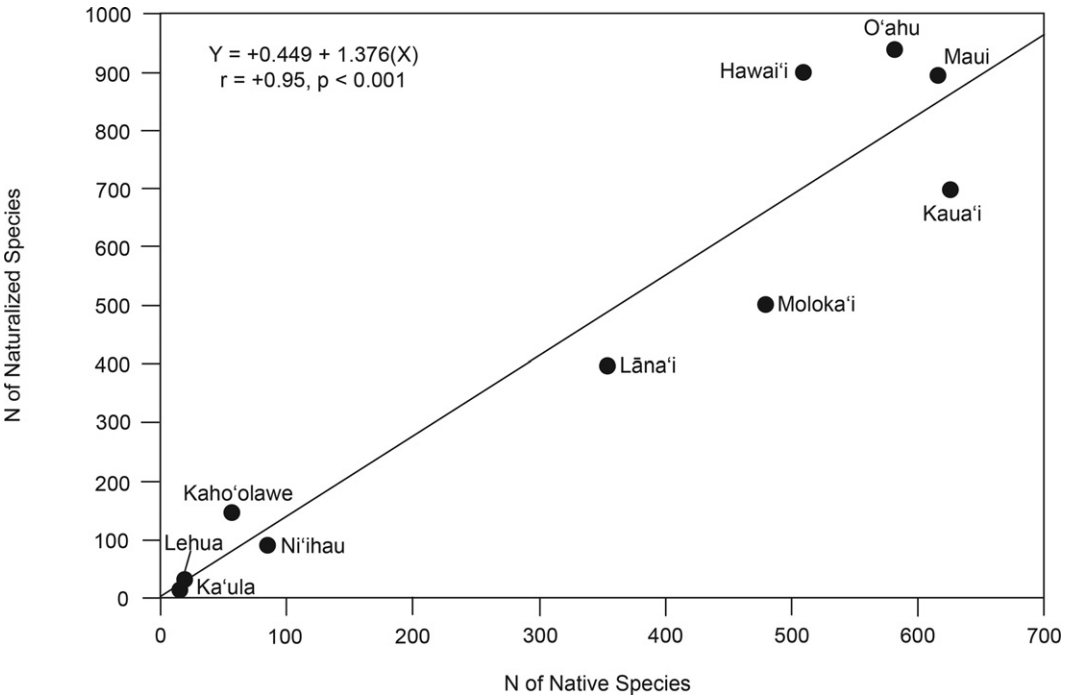


FIGURE 5. The relationship between the number of native and naturalized plant species across the main Hawaiian Islands.

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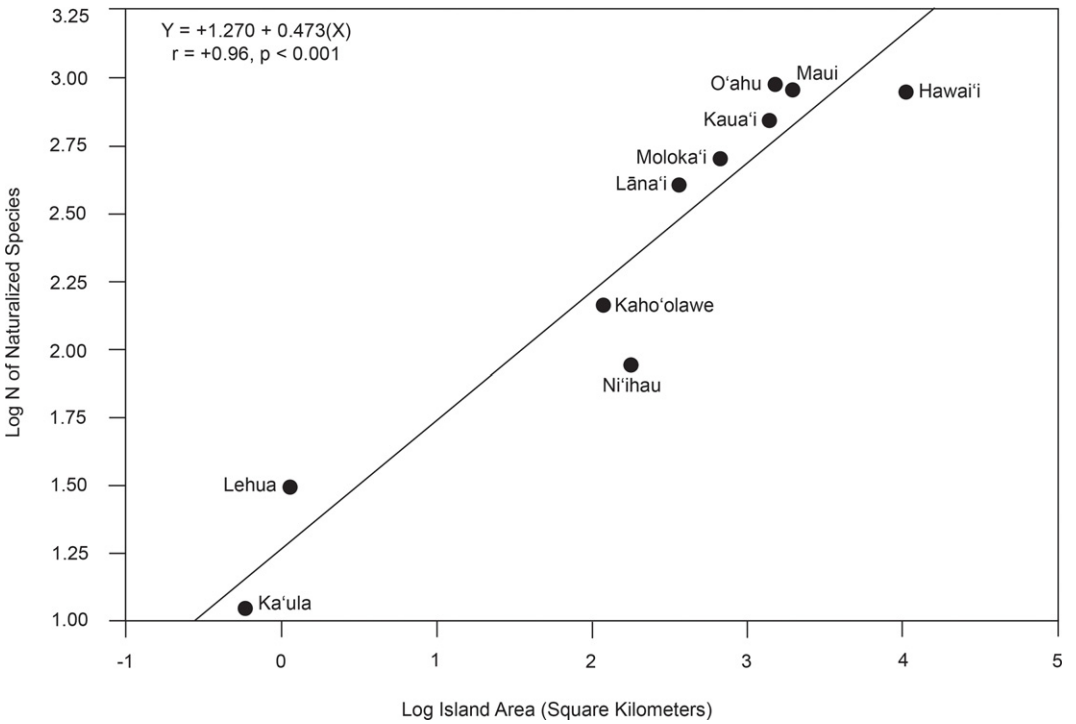


FIGURE 6. The relationship between island area and the number of naturalized plant species for the main Hawaiian Islands (species counts derived from Imada 2019).

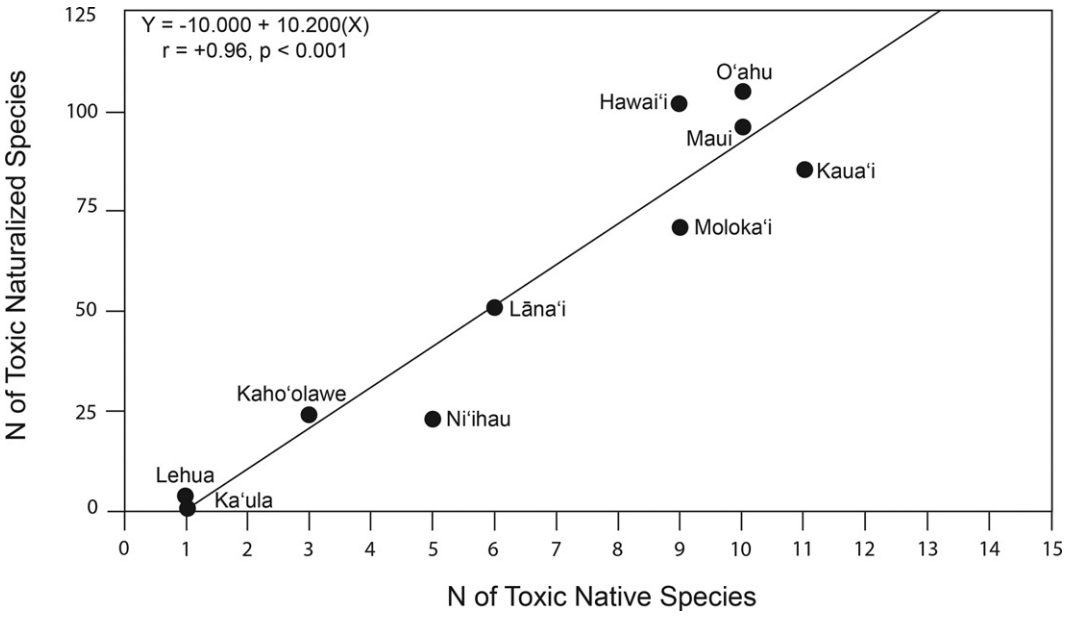


FIGURE 7. The relationship between the number of toxic native and toxic naturalized plant species across the main Hawaiian Islands.

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also scales significantly to island area across the main Hawaiian Islands ($r = +0.97$, $P < 0.001$; see Figure 8).

As we have noted, Price (2004) associated the negative residuals shown by Ni'ihau and Kaho'olawe in his larger dataset to their ecologically degraded nature, and that of Hawai'i Island to its relative youth. Hawai'i Island is by far the youngest of the Hawaiian Islands, some 30 million years younger than Kure Atoll, the northwesternmost of those islands, and roughly one million years younger than the islands that formed Maui Nui during the Last Glacial Maximum. Price and Wagner (2011) suggested that the native flora of Hawai'i Island contains fewer species than predicted by the general species–area relationship across the Hawaiian Islands because the island gained much of its native flora by dispersal from older islands, a suggestion akin to the "giant habitat conveyor belt" of Funk and Wagner (1995:380). They hypothesized that insufficient time has passed for Hawai'i to accrue or develop large numbers of endemic species.

Our results show that the toxic native plant species of the main Hawaiian Islands have much the same numerical distribution across those islands as their non-toxic native counterparts. We have also shown that the numerical distributions of the naturalized plant species of these islands, both toxic and non-toxic, mirror the distributions shown by their native counterparts. While the native plants of Hawai'i Island have accumulated over the past 600,000 years or so, the main accumulation of naturalized species did not begin until after the arrival of James Cook in 1778. Something other than the recent emergence of Hawai'i Island must be the cause of the similarity in these biogeographic patterns. Given the lack of significant residuals in the species–area relationships we have

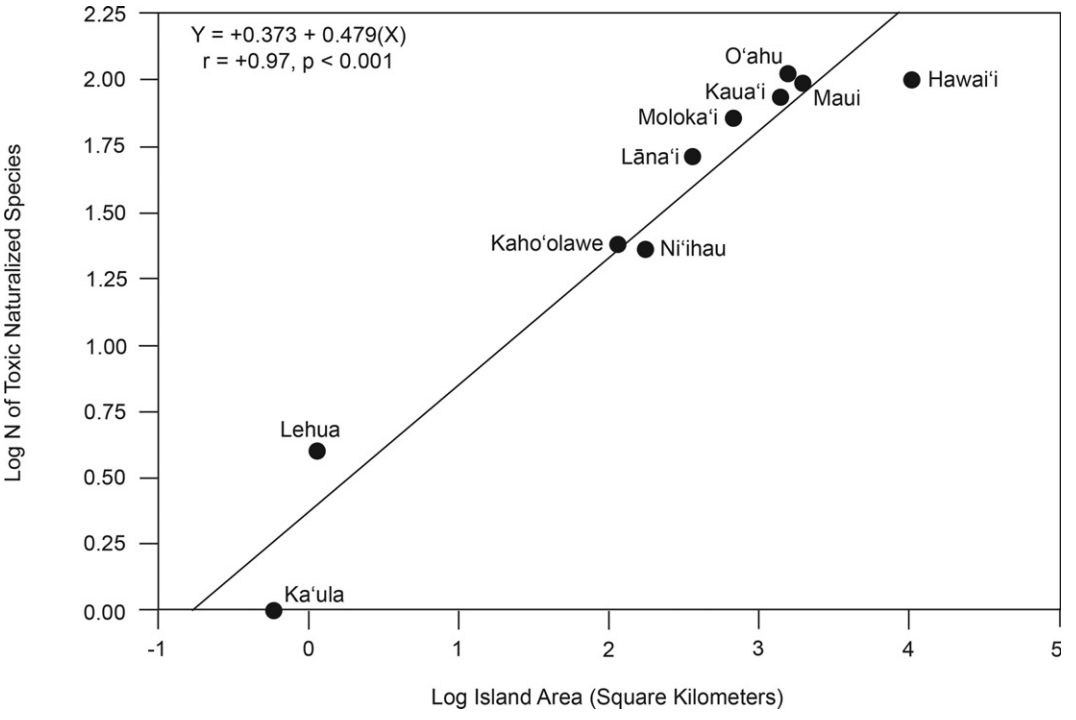


FIGURE 8. The relationship between island area and the number of toxic naturalized plant species for the main Hawaiian Islands.

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discussed here, including that provided by Price (2004), island area, and variables associated with it, would seem to be the obvious factor.

RESULTS AND CONCLUSIONS

In asserting that the native Hawaiian flora is depauperate in toxic plant species, neither Carlquist (1970) nor Ziegler (2002) provided specific comparisons to other floras. We have provided one such comparison here, asking whether the number of toxic plant species in the native Hawaiian flora is depauperate relative to the number of such species in the naturalized Hawaiian flora. The answer is that it is: about 1% of the species in the native Hawaiian flora are toxic, compared to about 9.4% in the naturalized Hawaiian flora. That difference is even greater—1.3% versus 23.5%—if naturalized species known to be toxic elsewhere but not listed as such in Arnold (1944), Baldwin (1979), and Scott and Thomas (2000) are included in the analysis. In this sense, our results strongly support the positions taken by Carlquist (1970) and Ziegler (2002).

For the native plants of the main Hawaiian Islands (Figure 1), our results show a strong positive species–area relationship for native plant species (Figure 2), replicating the results reported by Price (2004) for a broader set of Hawaiian Islands. Our results also show strong positive species–area relationships for naturalized plant species (Figure 6), toxic native plant species (Figure 4), and toxic naturalized plant species (Figure 8). Price and Wagner (2011) suggested that it is the youth of Hawai'i Island that accounts for the relatively small number of native plants species that it supports. However, our results question this hypothesis for two reasons. First, in neither the analyses conducted by Price (2002, 2004) nor those presented here does Hawai'i Island emerge as a significant negative outlier. Second, the vast majority of naturalized plants of the Hawaiian Islands were introduced during the last 250 years or so but show precisely the same biogeographic pattern as that shown by native plants.

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