

## RESEARCH ARTICLE

Journal of  
Biogeography

WILEY

# Do endemic mushrooms on oceanic islands and archipelagos support the theory of island biogeography?

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Email: [jstallma@purdue.edu](mailto:jstallma@purdue.edu)**Handling Editor:** Jacob Heilmann-Clausen**Abstract**

**Aim:** Terrestrial plant species on islands have a long history of study to determine how they evolved and what explains their levels of endemism, but studies on fungi are lacking. Here, we examine: (1) how percent endemism of non-lichenized class Agaricomycetes; hereafter, 'mushrooms' compares to angiosperms, ferns, bryophytes and lichens from oceanic islands/archipelagos; (2) whether endemic mushrooms evolved from an ancestor diversifying into multiple species after island colonization (cladogenesis) or over time evolved into a single endemic species unique from its ancestral mainland counterpart (anagenesis); and (3) if mushroom percent endemism and cladogenesis are correlated to geographic variables that help explain these phenomena in other species groups.

**Location:** Hawai'i, Galápagos, Canary Islands, Madeira, Azores, Cabo Verde, Christmas Island.

**Taxon:** Mushrooms, angiosperms, ferns, bryophytes, lichens.

**Methods:** Checklists of mushrooms and other species groups from seven oceanic islands/archipelagos were compared. Having multiple endemic congeners from a single island/archipelago was used to infer cladogenesis versus anagenesis in endemic mushrooms. Pearson's correlation coefficients were calculated between an island/archipelago's percent endemism and percent cladogenesis, and their distance to the nearest mainland, area, maximum elevation and latitude from the equator.

**Results:** Hawai'i has the highest mushroom endemism at 83%, of which 50% are potentially derived from cladogenesis. Considering mushrooms on all islands/archipelagos, speciation by cladogenesis leads to fewer endemic species (37%) than anagenesis (63%). We find positive and statistically significant relationships between distance to mainland and island area with percent endemism among mushrooms, and cladogenesis is positively and significantly correlated with island size and maximum elevation.

**Main conclusions:** Mushrooms show greater percent endemism on larger, more isolated islands/archipelagos. However, they display the lowest percent species derived from cladogenesis among the organismal groups examined. Both the lack of data and unreliability of data are impediments to studying fungal endemism on islands, making drawing decisive conclusions challenging.

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## KEYWORDS

Agaricales, fungi, macro-fungi (macrofungi), Magnoliophyta, Pteridophyta (pteridophyte), speciation

## 1 | INTRODUCTION

Since the seminal works of MacArthur and Wilson (1963, 1967) and Carlquist (1966), a tremendous amount of research has been focused on explaining the biodiversity patterns of terrestrial plants and animals on islands. MacArthur and Wilson (1963, 1967) proposed that island species richness could in large part be explained by geographic distance from the mainland and island size. Since the early development of the theory of island biogeography (TIBG), much attention has been paid to extending TIBG to more fully encompass the factors that determine biodiversity patterns on islands (e.g. Carlquist, 1974; Losos & Ricklefs, 2010; Whittaker et al., 2008), including patterns of island endemism (e.g. Cowie, 1995; Gillespie et al., 2020; Losos & Schluter, 2000). While these studies, among many others, have helped define the field of island biogeography, fewer studies have addressed these questions in microbial life, such as bacteria and fungi. Here, we examine the evolutionary patterns and determinants of endemism in the non-lichenized members of the fungal class Agaricomycetes (hereafter referred to as 'mushrooms')—a group of primarily mushroom-forming fungi (agarics, puffballs, conks, stinkhorns, crusts etc.) that have microscopic propagules (spores) and mostly cryptic life histories as microscopic hyphae in the substrate except when forming macroscopic structures for reproduction.

The Baas Becking Hypothesis posits that, 'everything is everywhere, but the environment selects', and recognizes little to no dispersal limitations for microbes such as bacteria and fungi (Baas Becking, 1934). The idea that 'endemism is not common among the fungi' (Park, 1968) was widely accepted by early mycologists studying the geographic distribution of fungi (Bisby, 1943). Mycologists studying Hawaiian fungi agreed, while allowing exceptions for higher endemism of fungi on unique substrates, such as endemic host plants (Baker & Goos, 1972). Therefore, most island biogeographers have focused on plant and animal groups (e.g. Gillespie et al., 2020), as fungi were not thought to show appreciable levels of endemism on islands that were worthy of detailed investigation, or no data existed from multiple locations for comparisons.

The Baas Becking paradigm started to change in the 1990s as mycologists began to understand that fungi, particularly macro-fungi, which form reproductive structures visible to humans, often have limited distributions (Lodge et al., 1995). The idea that microbes lack dispersal limitations and have extremely broad geographic ranges, in most cases, has now generally been rejected (Dickey et al., 2021; Fontaneto, 2011), although numerous exceptions exist for individual fungal species (e.g. *Lepiota subincarnata* as shown in Razaq et al., 2014 or *Rhodocollybia laulaha* as shown in Keirle et al., 2010). Restricted ranges among continental populations of saprotrophic and ectomycorrhizal (ECM) macro-fungi have been found based

on observational data (Andrew et al., 2018) and curated Sanger sequence meta-analyses (Bazzicalupo et al., 2019), and in ECM fungi based on high-throughput sequencing data at global scales (e.g. Tedersoo et al., 2012, 2014). The consensus that microbes have distinct and limited ranges has led to the expansion of microbial biogeography into microbial macroecology to develop and test models to understand and predict these geographic patterns (Xu et al., 2020), although basic descriptive biogeography of inventorying species and describing patterns is still needed (Hortal, 2011; Peay, 2014).

Until recently, fungal island biogeography studies used other systems as proxies (e.g. ECM tree stands as 'islands' in Peay et al., 2010), but true island systems have now been used to determine how distance to mainland and island size affect fungal community compositions (e.g. Li et al., 2020; Zheng et al., 2021) and to examine intra-archipelago diversity patterns (Tipton et al., 2021). In a recent review, Dickey et al. (2021) found that microorganisms as a whole followed the same community-level biogeographical patterns (species–area relationships, latitudinal diversity gradients and reduced alpha diversity with increasing distance from a mainland) as plants and animals 74% of the time, but noted that only two studies (Li et al., 2020; Tanesaka, 2012) have examined free-living fungi. Recently, Tedersoo et al. (2022) analysed endemism in soil fungi using a global dataset of fungal nuclear ribosomal internal transcribed spacer (nrITS) sequences that included 28 island ecoregions. Using a combination of five endemism indices, they did not find an increase in fungal endemism in their island ecoregions compared with continents, although approximately one half of these ecoregions contain continental islands (e.g. Taiwan, Great Britain). Additionally, how geographic variables may affect endemism on oceanic islands/archipelagos that have traditionally been studied in island biogeography, such as Hawai'i, were not discussed.

The Hawaiian Islands are the most isolated archipelago on Earth—over 3700km from the nearest land mass—and one of the most extensively studied, with a well-known geologic history and terrestrial biota. The terrestrial biota of oceanic archipelagos must colonize land via propagules or adults transported by highly mobile animals, such as birds, or by air or water transport, either through stochastic events or regular patterns in the jetstream or ocean currents (including rafting on other material). There are examples of fungi being transported long distances by all these modes (see Golan & Pringle, 2017 for review), including evidence of a diverse array of fungal spores in the air above Hawai'i Island (Tipton et al., 2019). While some Hawaiian species groups—such as angiosperms—have received extensive biogeographic study for over a century with known numbers of colonizing species leading to known numbers of both native and endemic species (e.g. Price & Wagner, 2018), mushrooms have received comparatively less attention until recent decades. From 1992 to 2007, knowledge of the mushrooms occurring



in the Hawaiian Islands grew from less than 100 species to over 600, with endemism estimates in the Agaricales (the largest order of mushroom-forming fungi in the Agaricomycetes, containing the majority of gilled species) and Agaricomycotina (the largest subphylum in the Basidiomycota comprising nearly all macro-fungi in the phylum) to be 88% and 80%, respectively (Hemmes & Desjardin, 2002; Mueller et al., 2006).

Although Hawai'i likely has one of the best-known tropical mycobiota, Mueller et al. (2006) estimate an additional 50 native species (29% of native macro-fungi) remain to be documented based on plant to macro-fungal ratios. While biogeographical explanations are only as strong as the completeness of taxonomic and geographic sampling (Knape et al., 2020; Mata et al., 2007) and this work continues for fungi (e.g. Hawksworth, 2001), data are now available to start addressing biogeographic hypotheses, as has been done historically for other species groups as species discovery continues.

Despite lacking complete information, biodiversity discovery of mushrooms over the last several decades has led to seven oceanic islands/archipelagos with available mushroom checklists including endemism estimates: Hawai'i, the Azores, Canary Islands, Cabo Verde, Christmas Island, Galápagos and Madeira & Selvagens. We are not aware of any prior comparative analyses of mushroom endemism percentages, cladogenesis (defined here as in situ species formation within islands/archipelagos by evolutionary branching events) or anagenesis (defined here as species formation by progressive evolutionary change within islands/archipelagos without evolutionary branching events), or exploration of geographic predictors of endemism percentage (but see Lodge et al., 1995; Melo & Cardoso, 2008).

To address these knowledge gaps, we updated a checklist of Hawaiian mushrooms, conservatively assigning species to native (i.e. endemic or indigenous to the archipelago), endemic (indigenous and only known from Hawai'i), non-native or unknown status (File S1). We tabulated similar data for the six other islands/archipelagos for which data were available from the literature, and made a list of all known endemic mushroom species from these islands/archipelagos (Table S3). Finally, we incorporated matching data on angiosperms, bryophytes, ferns and lichens into our analysis across all archipelagos for comparative analyses. These data allow us to: (1) compare endemism across these different organismal groups within and among islands and archipelagos, (2) estimate the relative contribution of speciation via cladogenesis versus anagenesis for mushroom species and (3) determine if distance from mainland, island size, maximum elevation and latitude from equator correlate to endemism and cladogenesis percentages.

We first hypothesized that endemism in mushrooms will be comparable to other highly dispersible organisms such as ferns and bryophytes. Second, we hypothesized that species formation via cladogenesis will be relatively rare, as has been shown for other highly dispersible organisms; again, ferns and bryophytes (Patiño et al., 2014). Finally, we hypothesized that both percent endemism and percent cladogenesis will be positively correlated with island/archipelago distance from nearest mainland, island/archipelago size and maximum elevation, and negatively correlated with latitude

from equator. These hypotheses are informed by what MacArthur and Wilson (1967) referred to as the 'radiation zone'—or an increase in species radiations (and therefore cladogenesis and total endemic species) as these variables (except for latitude) increase (MacArthur & Wilson, 1967; Whittaker et al., 2008). Lastly, latitudinal diversity gradients show larger species ranges (and therefore lower endemism) at high latitudes away from the equator (Hillebrand, 2004; Pianka, 1966), known as Rapoport's rule (Rapoport, 1975, 1982; Stevens, 1989), which has been supported in fungal studies as well (Tederloo et al., 2014), including those emphasizing macro-fungi (Geml et al., 2011; Pegler et al., 1980).

## 2 | MATERIALS AND METHODS

For Hawaiian mushrooms, data were partially derived from an unpublished list provided to Mueller et al. (2006) by Drs Dennis Desjardin and Don Hemmes for their analysis of global (and Hawaiian) macro-fungi. To create our checklist, we revisited every species in the primary literature to verify its occurrence in Hawai'i and add associated metadata, in addition to adding new species reported in Hawai'i since 2007. To be included, a reference needed to explicitly state the species occurred in Hawai'i. Species not formally named, but recorded with enough associated information (e.g. *Cystolepiota* sp. in Hemmes & Desjardin, 2002) were included. Records of species with incontrovertible DNA evidence and associated metadata such as photographs and location were included (e.g. *Psilocybe cyaneus*), but environmental sequencing studies were not considered. Mycobank (Crous et al., 2004) and IndexFungorum ([www.indexfungorum.org](http://www.indexfungorum.org)) were used to update fungal names and provide identification at higher ranks, and the primary literature was consulted in the case of disagreements.

To determine a species status as native, endemic or non-native, we followed statements in the literature when available, or inferred this information from its association with solely native and/or endemic vegetation or habitats (assigned native [i.e. indigenous] if considered to have reached Hawai'i without human-mediated dispersal, additionally assigned endemic if native and only found in Hawai'i) or assigned to be non-native if only found associated with non-native vegetation. We used a conservative approach, not assigning species to a specific category in ambiguous situations in which the species occurs in both, or mixed vegetation, unless additional evidence existed. The analysis was conducted at the species level without consideration for variation among forms, varieties or subspecies.

In searching for other oceanic islands with published lists or counts of mushrooms, angiosperms, lichens, bryophytes (mosses, liverworts and hornworts) and ferns with endemism estimates, we found six to include in our analysis: The Azores, Canary Islands, Cabo Verde, Christmas Island, Galápagos and Madeira & Selvagens. For data from the Canary Islands, we considered 'native secure' and 'native probable' to be native species, 'native possible' to be ambiguous (excluded from the analysis) and 'secure introduced', 'probably introduced' and 'invasive introduced' to constitute non-native species

from Tejera (2009) and Padrón and Pérez-Vargas (2009). Some species lists contained total species counts and endemic species counts, but lacked how many of the total species were native or introduced, making calculating an endemism percentage impossible. In these cases, we used the percent native species from the same group of organisms from the closest island/archipelago to calculate native versus non-native species numbers. This was done for bryophytes in the Galápagos (inferred 95% native based on Hawai'i), lichens in Hawai'i (inferred 99% native based on Galápagos) and Madeira (inferred 100% native based on the Canary Islands) and mushrooms in the Galápagos (inferred 13% native based on Hawai'i), Azores and Cabo Verde (both inferred 96% native based on the Canary Islands and Madeira). The limitations of this approach are addressed in the discussion.

To infer if an endemic species resulted from cladogenesis or anagenesis, we followed Stuessy et al. (2006) and Patiño et al. (2014) in which if a species had endemic congeners on an island or archipelago, this was considered possible cladogenesis, and recorded as such, whereas endemic species with no known endemic congeners were considered products of anagenesis. We note there are limits to this terminology and methodology. Dispersal of a species to an island followed by evolution into a single new species is described as anagenesis in this study and previously in Stuessy et al. (2006) and Patiño et al. (2014), although it may be viewed as cladogenesis in the broad sense when considering the lineage outside of the focal island/archipelago. Additionally, our data do not take extinction into account, which is poorly known for most tropical terrestrial organisms, including mushrooms, due to lack of study and/or poor preservation of organisms and their DNA (Hofreiter et al., 2015).

We used Pearson's correlation coefficient to determine if the island/archipelago characteristics of distance from mainland (km), area (km<sup>2</sup>), maximum elevation (m) and latitude from equator (in absolute degrees), correlated to mushroom endemism, average endemism across all organismal groups examined and inferred percent cladogenesis.

We searched NCBI's GenBank (Sayers et al., 2020) to determine if DNA sequence data were available for Hawaiian species at the universal fungal barcode, the nrITS (Schoch et al., 2012), and also whether any endemic species from other islands examined had this barcode available. Data cleaning and verification were completed in OPENREFINE 3.4.1 (Ham, 2013) and additional manipulation and analysis in R (R Core Team, 2021) including use of the packages 'taxize' (Chamberlain et al., 2020) and 'tidyverse' (Wickham et al., 2019).

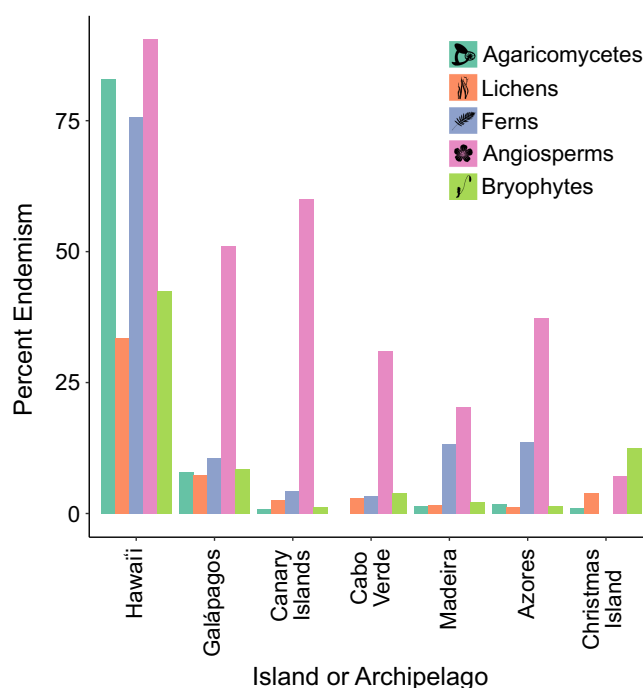
### 3 | RESULTS

We found 643 currently known mushroom species occur in Hawai'i (File S1 with data sources used to compile in Appendix S1). We updated 136 species names based on taxonomic and nomenclatural changes, added 67 species that were not previously recorded or had been reported since Mueller et al. (2006) and excluded 36 species on the previous list that could not be confirmed as occurring in the

Islands. These 36 excluded species were likely based on personal observations or collections of mycologists working in Hawai'i that were not formally recorded in the literature.

Of the 643 Hawaiian mushroom species, we assigned 236 to 'unknown' as their native or non-native status is not clear. Of the remaining 407 species, 354 (87%) species were assigned to non-native status and 53 to native (13%). Of the native species, 44 are considered endemic (83% endemism percent). On the six other islands and archipelagos examined, we found 1866 mushroom species, 1638 (88%) of which are native, only 21 of which are endemic, with endemism rates varying from 0% in Cabo Verde to 8% in the Galápagos (Figure 1; File S2 with data sources used to compile in Appendix S1). We also examined endemism percentages across organismal groups normalized by our geographic variables of interest. In general, this resulted in more even percentages of endemism across islands/archipelagos, although high outliers such as bryophytes on Christmas Island when considering island size and angiosperms in the Canary Islands when considering distance to mainland were present, likely due to Christmas Island's small area (137 km<sup>2</sup>) and the Canary Islands' proximity to the African mainland (~110 km; Figure S1).

We found 22 of 44 (50%) of the endemic Hawaiian mushroom species belonged to a genus with more than one endemic species in the archipelago, while this was two of nine (22%) in the Canary Islands, and no other endemic congeners were present in all other archipelagos. Table S1 lists genera with multiple endemic species

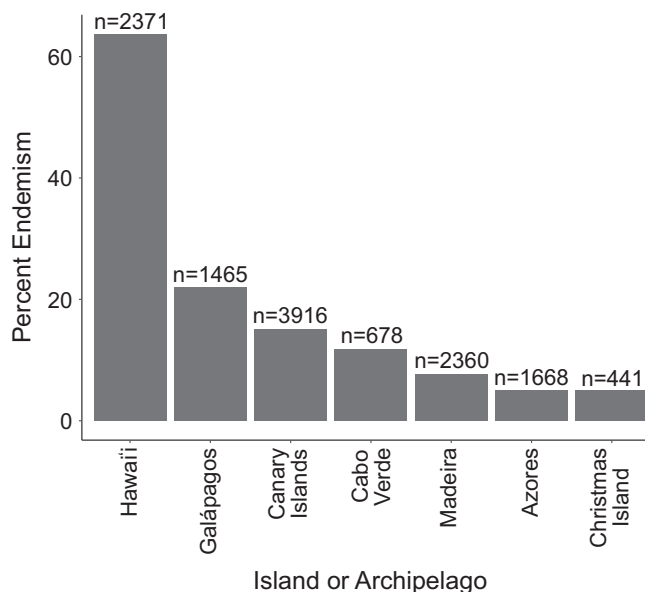


**FIGURE 1** Percent endemism by island or archipelago (Hawai'i, Galápagos, Canary Islands, Madeira, Azores, Cabo Verde, Christmas Island) for the five organismal groups examined in this study (mushrooms, angiosperms, ferns, bryophytes, lichens). The images *Laccaria* by Riccardo Percudani, *Cladonia* by Ramona Heim and *Polypodium glycyrrhiza*, *Geranium maculatum* and *Rosulabryum capillare* by Mason McNair are licensed under CC0 1.0 universal public domain dedication.



on the same island/archipelago, and Table S2 lists genera with multiple endemic species across more than one island/archipelago. Considering all mushrooms across all islands/archipelagos, 24 of 65 species (37%) have an endemic congener on the same island or archipelago and are considered products of cladogenesis.

For non-mushroom groups, we also found the highest percentages of endemism in Hawai'i. Angiosperms varied from 940 of 1039 (91%) endemic in Hawai'i to 15 of 207 (7%) on Christmas Island, bryophytes from 178 of 419 (43%) in Hawai'i to 6 of 502 (1%) in the Canary Islands, ferns from 109 of 144 (76%) in Hawai'i to 0 of 29 (0%) on Christmas Island, and lichens from 240 out of 716 (34%) endemic in Hawai'i to 10 of 788 (1%) in the Azores (Figure 1; see File S2). Considering a weighted average (controlling for sample size in each organismal group from each island/archipelago) of percent endemism across all organismal groups examined in this study, Hawai'i had the highest with 1511 of 2371 (63.7%) native species being endemic, while the lowest was Christmas Island with 22 of 441 (4.9%) native species being endemic (Figure 2; File S2). We also examined combined, weighted endemism percentages normalized by our geographic variables of interest. In general, this resulted in more even percentages of endemism across islands/archipelagos, although high outliers were present, such as the Galápagos Islands when considering latitude from equator, likely due to their equatorial location (Figure S2).



**FIGURE 2** Average percent endemism across all organismal groups examined (mushrooms, angiosperms, ferns, bryophytes, lichens) by island or archipelago (Hawai'i, Galápagos, Canary Islands, Madeira, Azores, Cabo Verde, Christmas Island). Endemism percentages were calculated from the sum of the total number of native species across all organismal groups within an island and/or archipelago divided by the sum of the total number of endemic species across all organismal groups within the same island or archipelago. The total number of native species considered across all organismal groups is provided for each island and/or archipelago.

Pearson's correlation coefficients for mushroom endemism percent, combined organismal group endemism percent and mushroom cladogenesis percent are shown in Figure 3a–l. Significant, positive and strong correlations were found between distance to mainland and mushroom endemism (Pearson's  $r = 0.92$ ,  $p < 0.004$ ) and combined group endemism ( $r = 0.81$ ,  $p = 0.027$ ), but not between distance to mainland and percent mushroom cladogenesis ( $r = 0.69$ ;  $p = 0.130$ ). Island/archipelago size and mushroom endemism ( $r = 0.87$ ,  $p = 0.011$ ), combined group endemism ( $r = 0.96$ ,  $p < 0.001$ ) and percent cladogenesis ( $r = 0.90$ ,  $p = 0.016$ ) were all significant, positive and strongly correlated. Correlations were not statistically significant in all cases considering maximum elevation (mushroom endemism  $r = 0.59$ ,  $p = 0.161$ ; combined endemism  $r = 0.66$ ,  $p = 0.105$ ) and latitude from equator (mushroom endemism  $r = -0.04$ ,  $p = 0.926$ ; combined endemism  $r = -0.16$ ,  $p = 0.739$ ; percent cladogenesis  $r = 0.08$ ,  $p = 0.874$ ) except for the correlation between percent mushroom cladogenesis and maximum elevation ( $r = 0.84$ ;  $p = 0.035$ ).

We found 76 of 643 (12%) Hawaiian mushroom species have an nrITS sequence available in GenBank; of these, 8 of 53 (15%) were native and 8 of 44 (18%) were endemic. Among endemic species from other island groups, 2 of 21 (10%) have an nrITS sequence available in GenBank (Table S3).

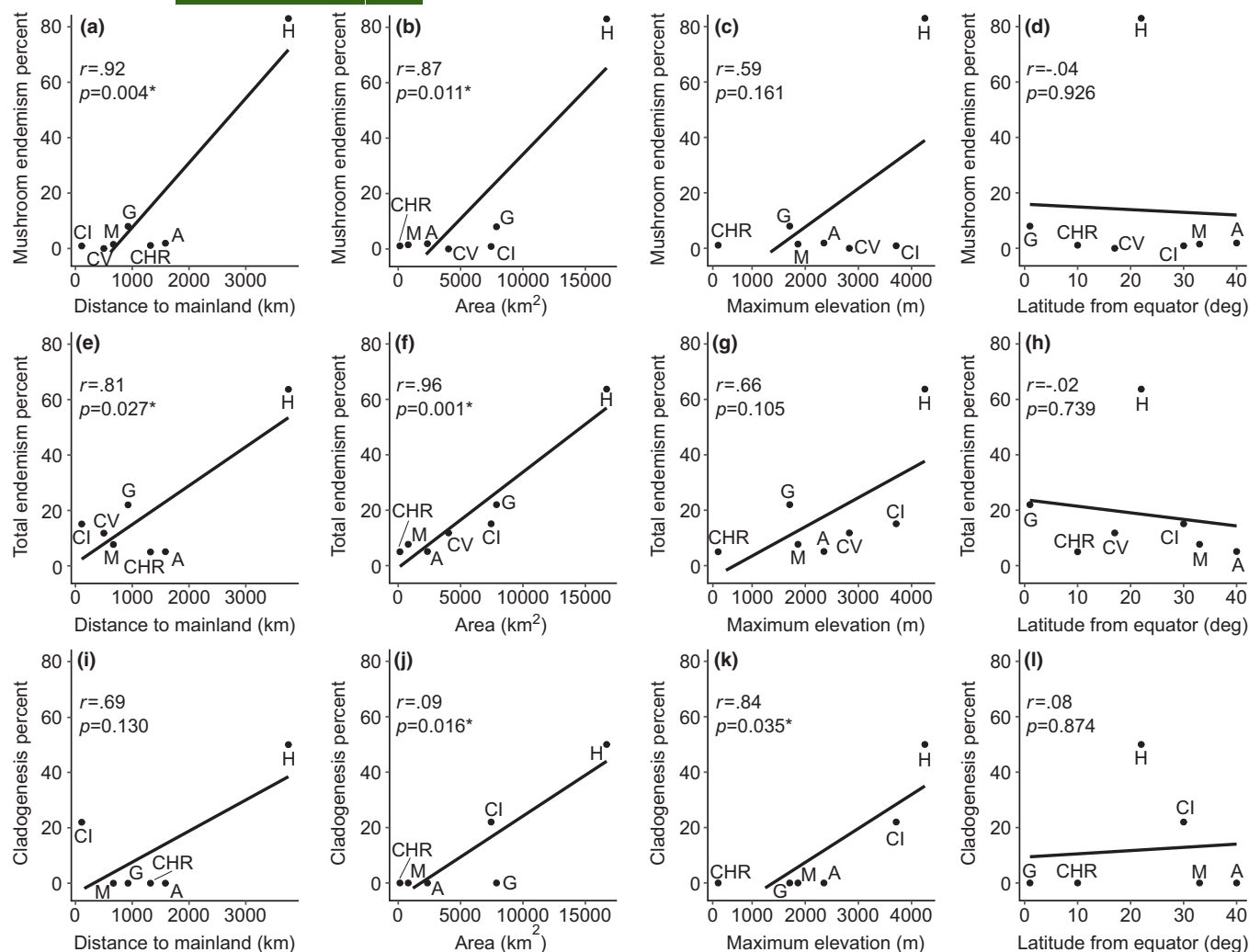
## 4 | DISCUSSION

In this study, we asked whether endemic mushrooms on oceanic islands/archipelagos follow similar biogeographic patterns to those observed in angiosperms, ferns, bryophytes and lichens. Although many limitations exist in the currently available data to form robust conclusions (discussed below), we provide a baseline analysis of comparative fungal island biogeography to initiate this line of inquiry.

Our first hypothesis that island endemism percentages in mushrooms will be comparable to ferns, bryophytes and lichens is partially supported; with support varying across islands/archipelagos. For example, in Hawai'i, mushroom percent endemism is the highest among these groups at 83%, similar to ferns at 76%, but substantially higher than that of lichens at 34% and bryophytes at 43%. In the Galápagos, our prediction is supported, but with overall quite low levels of endemism across all of these groups, with mushrooms at 8%, lichens at 7%, ferns at 11% and bryophytes at 9%. Elsewhere, such as the Canary Islands and Madeira, mushroom endemism is generally much lower than that for ferns, and generally lower than bryophytes and lichens (Figure 2). A limitation that our checklist-based study cannot account for is differing scientific effort across these organismal groups and islands/archipelagos. Varying effort and inclusion of molecular data may change our understanding of the identity and distribution of island organisms, and therefore our biogeographical conclusions, as shown in even presumably well-known groups such as angiosperms in the Azores (Schaefer et al., 2011).

Our second hypothesis that percent mushroom cladogenesis on islands/archipelagos will be relatively low, accounting for few





**FIGURE 3** Scatterplots with line of best fit for Pearson's correlation coefficients for the dependent variables mushroom species endemism percent (a–d), total endemism percent combined across mushrooms, angiosperms, ferns, bryophytes, and lichens (e–h), and cladogenesis percent (i–l) for the independent variables distance to mainland (a, e, i), island/archipelago area (b, f, j), maximum elevation (c, g, k) and latitude from equator (d, h, l) Pearson's correlation coefficient and p-values are shown in each plot. Island abbreviations are A for Azores, CHR for Christmas Island, CI for Canary Islands, CV for Cabo Verde, G for Galápagos, H for Hawai'i and M for Madeira.

endemic mushroom species is supported, with cladogenesis accounting for 37% (anagenesis 63%) of known endemic mushroom species across all islands/archipelagos. This is much lower than the 78% average found for cladogenesis in plants among 10 oceanic islands or archipelagos (those considered here except for Christmas Island and the Azores, instead including Tristan de Cunha, Juan Fernandez, Ogasawara, St. Helena and Ullung Island) by Stuessy et al. (2006). This is also lower than the 83% average found for cladogenesis in spermatophytes, 60% for ferns (pteridophytes) and 51% for bryophytes among oceanic islands and archipelagos (Tristan du Cunha, Juan Fernandez, St. Helena and those considered here except for Christmas Island) found by Patiño et al. (2014). We note that our study and the two plant-focused studies mentioned here await examination of congeneric species with molecular phylogenetic analyses for confirmation of cladogenetic events.

Finally, our hypotheses that (1) island mushroom percent endemism, (2) average percent endemism across all groups combined

and (3) percent cladogenesis will be positively correlated with distance from mainland, island size and maximum elevation, but negatively correlated with latitude from equator is generally supported for distance from mainland and island size, but not for maximum elevation or latitude. Pearson's correlation coefficients for mushroom endemism showed statistically significant, positive correlations with distance to mainland and with area, but no significant correlation with elevation or latitude from equator (Figure 2a–d). Similarly, Pearson's correlation coefficients for percent endemism averaged across all organismal groups also showed significant, positive correlations with distance to mainland and with area, but no significant correlation with elevation or latitude from equator (Figure 2e–h). Pearson's correlation coefficients for percent mushroom species derived from cladogenesis displayed significant and positive correlations with area and with elevation, but no significant correlation with distance to mainland or latitude from equator (Figure 2i–l). We also note that the directionality of all correlations



follow our predictions, except for cladogenesis which was not inversely correlated with increasing latitude from the equator.

#### 4.1 | Comparisons of endemism and cladogenesis percentages

The vast majority of native Hawaiian mushroom species, 44 of 55 (83%), are endemic, similar to prior estimates based on overlapping taxa across studies (88% for Agaricales in Hemmes & Desjardin, 2002 and 80% for Agaricomycotina in Mueller et al., 2006). Considering only Agaricales in our study, 26 of 34 (77%) are endemic. These estimates fall between that for Hawaiian angiosperms at 91% and ferns at 76%, and well above that for bryophytes at 43% and lichens at 34% (Figure 1). Hawaiian mushroom endemism is much higher than that of the next highest island or archipelago; the Galápagos at 8% (Figure 1). This pattern is followed across all organismal groups with Hawai'i having a higher percent endemism than the next highest island or archipelago by a difference of 31% in angiosperms (Hawai'i 91%, Canary Island's 60%), a difference of 30% in bryophytes (Hawai'i 43%, Christmas Island 13%), a difference of 62% in ferns (Hawai'i 76%, Azores 14%) and a difference of 27% in lichens (Hawai'i 34%, Galápagos 7%) (Figure 1). In the islands examined, angiosperms had higher percentages of endemism than all other taxa (except Christmas Island with a higher percentage of bryophytes), followed by ferns (with the exception of Hawai'i with a higher percentage of mushrooms and Christmas Island with angiosperms in second), whereas endemism percentages of lichens, bryophytes and mushrooms varied and did not follow clear patterns across islands/archipelagos.

High endemism percentages among Hawaiian organisms have been long known (e.g. Hillebrand, 1888), and as the most isolated archipelago by distance with a relatively large area and high maximum elevation, this is not surprising. Perhaps more surprising is that Hawaiian mushrooms have a higher endemism percentage than ferns, bryophytes and lichens, despite that cladogenesis—which inherently leads to more endemic species than anagenesis—has been demonstrated in Hawaiian ferns and lichens (Lücking et al., 2017; Schneider et al., 2005) but never conclusively in mushrooms. We note that endemism percentages of lichens will likely increase after examination with molecular data (e.g. *Sticta* spp. in Hawai'i as in Moncada et al., 2020) and a checklist incorporating these recent findings is not yet available.

Relatively few mushroom species across all islands and archipelagos potentially arose from cladogenesis (37%). This varied from 50% in Hawai'i to 22% in the Canary Islands to 0% in the rest of the locations examined. Cladogenesis is potentially overestimated because no detailed studies exist documenting in situ speciation of island mushrooms. Cladogenesis could also be underestimated because extinction events are unknown, and in some cases, a congeneric species may have gone extinct leaving only a single extant endemic species.

One mushroom family worthy of exploration for cladogenesis on islands/archipelagos is Hygrophoraceae, with eight endemic species in Hawai'i (Desjardin & Hemmes, 1997). Endemic Hygrophoraceae

species are also known from the Canary Islands and Azores (Table S1), and the genus *Hygrocybe* in the Greater Antilles also has a limited distribution, with more than 36% of 63 taxa confined to that region (Cantrell et al., 2001). Another potential cladogenetic event involves two unnamed, putatively endemic Hawaiian *Tomentella* spp. closely related by nrITS sequence data and associated with the same endemic Hawaiian host tree (Hayward & Hynson, 2014). Finally, potential speciation among ECM fungi was found in the Seychelles based on environmental sequence data (Tedersoo et al., 2007). The only study we are aware of specifically looking at potential cladogenesis in island mushrooms is Keirle et al. (2011). Using a single microsatellite locus and sampling 153 individuals of Hawaiian *R. laulaha*, no clear pattern of molecular evolution based on geography was found, although the single locus and uncertainty of *R. laulaha* as a native fungus left many questions unanswered. In contrast to mushrooms, cladogenesis in lichens on oceanic islands is well established, such as in Hawai'i (Lücking et al., 2017), the Canary Islands (Sérusiaux et al., 2011) and Galápagos (Tehler et al., 2009). Whether the reason cladogenesis is known from oceanic island lichens (a polyphyletic group of fungi, including Agaricomycetes species, sharing a symbiotic lifestyle with an alga or cyanobacterium) but not from mushrooms is due to a biological or other determinative difference or simply lack of study is unclear, although our results suggest the latter.

#### 4.2 | Limitations

Besides lacking knowledge of a lineage's full history, including possible extinction events, our study includes additional temporal bias towards the present in regard to geology. Island size and elevation are two explanatory variables that change throughout the lifecycle of a volcanic island/archipelago (e.g. Whittaker et al., 2008), and our analysis does not take historical changes of these variables into account. Additionally, fungal diversity on oceanic archipelagos and in the tropics in general is poorly understood, leading to small sample sizes and greater influence of outliers (Hawai'i, for example, in distance to mainland and size).

Determining a mushroom's status as native, endemic or non-native can also be difficult. This is demonstrated by *R. laulaha* (considered 'unknown' in our analysis), a fungus primarily associated with endemic Hawaiian vegetation and presumed to be a native, endemic species until its discovery in the neotropics (Keirle et al., 2010) prompted its current endemic status in Hawai'i to be uncertain. Ethnomycological knowledge has the potential to help determine native or non-native status of island mushrooms, but unfortunately this knowledge does not exist or has been lost in Hawai'i (Hemmes & Desjardin, 2002).

All organismal groups we examined contain cryptic or pseudo-cryptic species, and changes in endemism percentage can be expected, particularly in groups with comparatively few morphological features and relatively little molecular data, such as mushrooms and lichens. The same is true for cladogenesis percentage as more groups are examined with molecular phylogenetic assessments. Finally, with more detailed study on native or non-native status, the inferences



required between islands/archipelagos to determine percent native species may be improved or eliminated. However, until those data become available, in some cases, we need to use the percent native species from the closest island/archipelago to explore patterns of endemism. We examined how organismal groups with known percentages of native species compared to those with inferred percentages and found general agreement (File S2). For example, native angiosperms make up 42% of total Hawaiian species while in the Galápagos this is 36%; for ferns 83% of total Hawaiian species are native, while this is 90% for Galápagos species. For Macaronesia, total lichens in Madeira were inferred at 100% native and the Canary Islands, Azores and Cabo Verde all have 100% native species of lichens on these checklists. The Azores and Cabo Verde mushrooms were inferred at 96%, and both the Canary Islands and Madeira have native mushrooms making up 96% of the total species count. A similar pattern follows for bryophytes (all species 99 or 100% native). However, these inferences and low sample sizes in the number of islands/archipelagos examined and total number of putative endemic mushroom species lead us to interpret our results cautiously.

#### 4.3 | Future studies and nrITS sequence data

Incorporating environmental or Sanger sequence molecular data with associated natural history and ecological information is recognized as necessary to advance the field of fungal ecology (Dickey et al., 2021; Peay, 2014). Unfortunately, we find that nrITS sequences are lacking for 55 of 65 (85%) of the endemic island mushrooms considered in this study (Table S2). These data would help confirm identifications, allow for faster comparisons of geographic distributions through online databases such as GenBank, and improve examination of cladogenesis in island mushrooms. However, completeness of data is still a challenge for studies incorporating DNA data. Osmundson et al. (2022) found 58% of their macrofungal DNA sequences from Mo'orea had no match to sequences available in biorepositories at a 2% identity threshold, while this was 95% for ECM fungal DNA sequences in New Caledonia using a 2% identity threshold for *Cortinarius* and 3% for other genera (Carriconde et al., 2019). Both studies cautioned that this could be due to a lack of sequences from Pacific Islands and the tropics in general, and traditional morphological and ecological studies are needed to determine if species associated with these sequences have already been described from elsewhere but lack reference nrITS sequences.

Recently, global datasets of nrITS sequences obtained via the same methodology and bioinformatic pipelines (Tedersoo et al., 2021, 2022), or curated to allow comparisons (Větrovský et al., 2020) provide improved opportunities to study the biogeography of mushrooms. At this time, the Global Fungi (GF) dataset (Větrovský et al., 2020) contains samples from two of the seven islands considered in our analysis (Hawai'i, Christmas Island), while the Global Soil Mycobiome consortium (GSMc) augmented by other datasets (Tedersoo et al., 2022) contains four of the seven islands we considered (Hawai'i, Canary Islands, Madeira, Cabo Verde).

Using full-length nrITS sequences from soils and a 2% identity threshold for setting unique molecular operational taxonomic units (MOTUs), Tedersoo et al. (2022) examine endemism in global ecoregions by establishing five weighted indices, one of which is the proportion of endemic MOTUs divided by total MOTUs. Unfortunately, our work is not directly comparable as we calculate endemism on islands by dividing endemic species by all native (native plus endemic) species, as is standard in studies of island biogeography (e.g. Gillespie & Baldwin, 2010; Hillebrand, 1888; Price & Wagner, 2018). Although separating native from non-native species is always challenging and rarely definitive, even for mushroom-collection based studies, environmental soil samples provide less metadata, making the separation of native from non-native MOTUs not possible. We note that large numbers of non-native mushroom species may be present (e.g. 87% of Hawaiian mushrooms in our study), further challenging comparisons. Monteiro et al. (2022) recently found that islands do not necessarily have more non-native mushrooms than mainlands, but certain regions, including Oceania, have higher species richness of non-native mushroom species. Finally, datasets that include only soils may exclude large groups of mushrooms, including lignicolous species. For example, the putatively endemic, wood-inhabiting Hawaiian *Laetiporus* species (Lindner & Banik, 2008) does not have representative DNA sequences in the GSMc dataset (Tedersoo et al., 2021).

Environmental DNA studies incorporating all or part of the nrITS region complement collections-based studies on island mushrooms, each having advantages and disadvantages. Environmental DNA studies allow for quantification of sampling effort across islands and archipelagos and faster accumulation of data in comparison to incidental collecting and checklists. Additionally, using nrITS sequences to characterize organisms into MOTUs may lead to more accurate delimitation of species and allow examination of cladogenesis with phylogenetic methods. Yet, lacking morphological information and detailed study from individual collections precludes species discrimination from multiple lines of evidence and assignment of native or non-native status.

#### 5 | CONCLUSION

The predictions of TIBG (MacArthur & Wilson, 1963, 1967) were originally developed more than a half-century ago and have been extensively tested with both plant and animal species on islands (and 'island-like' systems) in the intervening decades (e.g. Losos & Ricklefs, 2010; and see Gillespie & Baldwin, 2010 therein for discussion of remote archipelagos). We now ask whether these same general principles also apply to island mushrooms, focusing on endemism. Baseline findings from checklists support the predictions of TIBG that endemism percentage is positively correlated to island/archipelago distance from mainland and island/archipelago size for mushrooms. Additionally, cladogenesis of mushroom species appears to be positively correlated with island/archipelago size and maximum elevation, although this awaits confirmation with molecular phylogenetic assessments.

No clear pattern exists in fungal endemism percentages compared to the other organismal groups examined; although they



remain below angiosperms in all cases, and are often similar to percentages for ferns, lichens and bryophytes. Levels of endemism in all organismal groups examined, including mushrooms, is much higher in Hawai'i than other islands/archipelagos, but reevaluation with molecular data may increase these percentages in all locations, particularly among organismal groups with many cryptic species. Both unrecognized extinction and recent human disturbance, along with limitations in the availability and reliability of data, make studies of comparative oceanic fungal biogeography challenging. However, we look forward to continued species discovery, increased availability of molecular data and descriptive biogeography on mushrooms occurring on oceanic islands and archipelagos to continue expanding this nascent field.

## ACKNOWLEDGEMENTS

We thank Don Hemmes for sharing his and Dennis Desjardin's list of Hawaiian mushrooms. We also thank Amy Durham and Benjamin Lillibridge for helping with data collection. Finally, we thank Don Hemmes and Nicole Hynson for providing feedback on an early draft of this manuscript, and two anonymous reviewers whose comments helped improve the paper. No permits were needed to carry out this work.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DataDryad at doi:10.5061/dryad.rxdwbrvc9.

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## BIOSKETCH

Jeff is interested in the taxonomy, systematics, and biogeography of macro-fungi, with an emphasis on the Hawaiian Islands. Kyra is interested in the macroecology of tropical fungi and conservation of tropical forest biodiversity. Matt is primarily interested in the ecology of speciation and extinction across multiple taxonomic groups.

**Author contributions:** Jeffery K. Stallman and Matthew L. Knope designed the research, Jeffery K. Stallman and Kyra Robinson completed the research and analyzed the data, and Jeffery K. Stallman and Matthew L. Knope wrote the paper.

## SUPPORTING INFORMATION

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

**How to cite this article:** Stallman, J. K., Robinson, K., & Knope, M. L. (2022). Do endemic mushrooms on oceanic islands and archipelagos support the theory of island biogeography? *Journal of Biogeography*, 00, 1–11. <https://doi.org/10.1111/jbi.14517>