

Dewlap color variation in *Anolis sagrei* is maintained between habitats within islands of the West Indies

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Abstract

Animal signals evolve in an ecological context. Moreover, locally adapting animal sexual signals can be especially important for initiating or reinforcing reproductive isolation during the early stages of speciation. Dewlap color in *Anolis* lizards can be highly variable between populations in relation to both biotic and abiotic adaptive drivers, albeit at relatively large geographical scales. Here, we investigated local adaptation of the dewlap across habitat-types at a small spatial scale, as this may give an indication of how conditions for the early stages of speciation may be met. We explored variation in dewlap coloration in one widespread species, *Anolis sagrei*, across three characteristic habitats spanning the Bahamas and the Cayman Islands. Using reflectance spectrometry as well as supervised machine learning, we found some consistent differences in spectral properties of the dewlap between habitats within small islands. Passive divergence in dewlap phenotype associated with isolation-by-distance did not explain our results. Instead, the observed patterns in dewlap coloration are more consistent with an adaptive explanation in these *A. sagrei* populations, as one would otherwise expect differences within islands to be erased by gene flow at such small geographical scales. Although these habitat-specific dewlap differences vary in magnitude and direction across islands, and islands themselves differ substantially, we found a suite of consistent archipelago-wide differences between habitat types, suggesting parallel responses to similar selective pressures. While at present, populations from these different habitats probably experience too much gene flow to follow distinct evolutionary lineages, should additional barriers arise between habitat-specific populations, the observed disruptive selection on dewlap coloration may facilitate ecological speciation.

Keywords — *Anolis*, reflectance, local adaptation, sexual signal, supervised machine learning

Introduction

The staggering diversity of animal communication signals has long been of interest to evolutionary biologists. Animals use chemical, mechanical, electromagnetic, and visual signals to communicate in a wide variety of contexts, including competition for mates, species recognition, aposematism, cooperation, etc. (?). A primary evolutionary factor shaping communication signals is the sensory system and behavior of their recipient(s) (the sensory drive hypothesis; ???). Over the past decades, scientists have established that signals evolve in an ecological context and are dependent on environmental conditions (???). Just as different habitats may favor different combinations of eco-morphological traits to maximize performance and fitness (?), they may also shape different forms of a signal, so as to maximize its transmission and detection (e.g. ?), or reduce its detection by unintended recipients such as predators (????). This selective pressure may drive the local adaptation of communication signals.

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	coastal	coppice	mangrove
Abaco	41	24	21
Bimini	38	14	15
Cayman Brac	15	18	17
Eleuthera	22	25	9
Little Cayman	17	12	16
Long Island	26	14	13
North Andros	9	9	10
Ragged Island	18	15	17
South Andros	10	9	12

One potential barrier to the maintenance of localized signal divergence is the homogenizing effect of gene flow. Population genetics theory suggests that gene flow may counteract local adaptation between localities and prevent divergence altogether, especially at small spatial scales, because of the inflow of maladapted alleles or because of the breaking of linkage between coevolving loci (????). This has been confirmed empirically in systems such as stick-insects (?) and sticklebacks (?). Yet, examples of microgeographic adaptation, i.e. adaptation at smaller scales than the range of dispersal, exist, highlighting a high potential of some organisms to respond to selection in the face of gene flow (see ? and references therein). Examples include small scale adaptation in fragmented areas in Australian fruit flies (?), or local adaptation to predation pressure in North American salamanders (?). Therefore, despite evidence that local adaptation may be particularly difficult at small spatial scales where gene flow tends to cause adjoining populations to remain genetically homogeneous, the potential adaptive response of species traits, in particular communication signals, to localized differences in habitats remains relatively unknown (?).

Lizards of the neotropical genus *Anolis* are a model system for studying the eco-evolutionary dynamics of local adaptation and natural selection (?). A particularly conspicuous trait of anoles is their dewlap; an extensible flap of skin that is typically sexually dimorphic and used as a communication signal in courtship (???), competition (???) as well as in predator deterrence (???). Dewlap characteristics vary widely among the approximately 400 species of the genus (?). Inter-specific variation in dewlap coloration is implicated in species recognition (???????), and possibly involved in speciation (???).

Within species, studies have shown a link between variation in dewlap coloration and differences in habitats or climatic conditions (?????????). Some studies suggest that those differences may be adaptive, and that dewlaps may have evolved to maximize detectability given local light conditions (???). Other studies testing this hypothesis, however, found no pattern (???).

Previous studies investigating variation in anole dewlaps compared populations at relatively large geographical scales, e.g. between islands (??) or within large islands such as Puerto Rico (??) or Hispaniola (??). These large scales should reduce gene flow (????). That said, examples do exist of divergence in dewlap coloration at smaller scales or between populations with high degrees of gene flow (????).

The species *Anolis sagrei* is widespread across islands of the West Indies (?). It is a model organism in studies of local adaptation (????), biological invasion (?) and sexual selection (?????). Between-island variation in the mainly orange-red color of its dewlap was shown to be better explained by climatic variables (?) than biotic factors such as sexual selection or predation pressure (?). How intra-island differences in habitat may contribute to the diversity of dewlap coloration, however, remains unexplored, and may reveal new insights into the scale of local adaptation despite gene flow.

The island bank systems of the Bahamas and Cayman Islands comprise relatively small islands, with no major geographic barriers within islands limiting dispersal for this promiscuous species (?). These islands all share three characteristic native West Indian habitat-types – beach scrub bush, closed-canopy primary coppice forest, and mangrove forest – that are often spatially inter-

mingled. These habitats contrast in environmental parameters including vegetation community, light irradiance, humidity and temperature (??). Each of these islands has been colonized independently by *A. sagrei* (???, van de Schoot et al. unpubl.), such that these archipelagos constitute an ideal suite of natural replicates to explore within-island dewlap diversity across multiple islands.

Here, we analyzed the color characteristics *A. sagrei* dewlaps within nine islands in the Bahamas and Cayman Islands, combining reflectance spectrometry and supervised machine learning. Our sampling design included sites in close proximity (the median distance between two sites within an island was 11.2km). We tested the hypothesis that the spatial scale was too small for phenotypic divergence to build up. If this was not the case, we predicted that if light conditions in the environment indeed drive color evolution, dewlaps should be most similar between beach scrub and mangrove forest, which both have high levels of light irradiance, contrary to the darker, closed-canopy coppice forest. Similar, if detectability is maximized given the local conditions, we expected darker and more contrasting dewlaps in high irradiance habitats. Finally, if habitat characteristics are strong determinants of dewlap color variation, similar patterns should be observed across multiple islands (?). We found strong support for fine-scale, within-island differences in coloration between lizards inhabiting the three habitat-types in several color space dimensions, suggesting a potentially strong effect of divergent selection. However, the divergence patterns we observed did not match our expectations and were highly variable between islands. We found no evidence of isolation-by-distance as an explanation for the observed differences. Our results are nevertheless consistent with small-scale adaptive maintenance of signal polymorphism despite presumed considerable opportunity for gene flow.

Methods

Data collection

We sampled 466 lizards from seven islands in the Bahamas Archipelago – Abaco, North Andros, South Andros, South Bimini, Eleuthera, Long Island, Ragged Island – and two in the Cayman Islands – Cayman Brac and Little Cayman (Figure 1). These islands and island banks were chosen to span the West Indian range of *Anolis sagrei*. Three habitats were sampled on each island based on characterizations by ? and ?. Each habitat is clearly distinguishable by their dominant vegetation type — xeric coastal scrub (open, relatively dry habitat consisting of low vegetation or isolated trees), primary coppice forest (closed-canopy forest) and mangrove forest (wet coastal habitat with trees growing in brackish water and high light penetration). Sample sizes are given in Table ?? . Our sampling design enabled us to test for differences between habitats at a coarse and fine geographical scale. The median distance between two localities within an island was 11.18km, with some islands being sampled at smaller or larger scales (Figure S1, Table S1). 80.3% of all pairwise distances within islands were below 50km. Additionally, there are no major barriers to dispersal (such as mountains) on any of the islands that we sampled.

Reflectance measurements

We measured reflectance between 300 and 700nm wavelength, a range that encompasses the colors visible to most lizards and vertebrates in general (?). Measurements were taken with an Ocean Optics USB4000 spectrometer, a pulsed Xenon light source (PX-2, Ocean Optics, Largo, FL, USA) and a reflectance probe protected by a black anodized aluminum sheath. Measurements were taken with a 45-degree inclination to prevent specular reflection (?). The device was regularly standardized with a Spectralon white standard (Labsphere, North Sutton, NH, USA). Reflectance was measured at the center of the dewlap.

Analysis

All analyses in this study were performed in R 3.6.1 (?).

Dimensionality reduction

Reflectance curves were smoothened using the R package pavo (?) as well as custom R functions (where are those?) to results into one reflectance value at each nanometer in wavelength from 300

to 700nm. Because neighboring wavelengths are highly collinear in reflectance, we reduced the dimensionality of the data using principal component analysis (PCA), as per ???. We performed PCA on each island separately and systematically retained the first four principal components (PC), which together always explained more than 88.8% of the variance across islands (Table S2). PC1 explained between 40 and 56% of the variance across islands; PC2 explained 17.4–27.9%; PC3 12.7–17.6% and PC4 4.3–10.5%. The first four PCs explained similar proportions of variance when calculated for all islands together (Table S2). PCs need not represent the same wavelengths across islands because they are fitted on different datasets. Nevertheless, PC1 was very collinear with brightness for all islands (Table ??). PC2 correlated highly with the red and ultraviolet ends of the spectrum, which were inversely correlated with each other (Fig. 3A). Higher PCs corresponded to various combinations of wavelengths. Because PC1 correlated uniformly with all wavelengths across the spectrum we considered PC2 onwards to capture the chromatic dimensions of color space, i.e. the relative contributions of the wavelengths regardless of brightness.

Machine learning

Our data violated the multivariate analysis of variance (MANOVA) assumption of homogeneity of covariance matrices across groups for all islands but Ragged Island (Box’s M-test, ??, implemented in the R package heplots, ?, Table S5). We also detected within-habitat deviations from multivariate normality, primarily on Abaco, Bimini and Eleuthera (Henze-Zirkler’s test, ?, implemented in the R package MVN, ?, Table S3). For these reasons and to reduce the chances of false discovery, we conducted multivariate group comparisons using support vector machines (SVMs), a model-free, nonparametric supervised machine learning technique.

Machine learning for group comparison has become more popular in ecology and evolution in the recent years (e.g. ?). In particular, SVMs are designed to find the best possible nonlinear boundaries between labelled groups of points in multidimensional spaces, without assumptions about the distribution of the data (???). This makes them well suited to field biological data, which often violate the assumptions of classical linear modeling (?) and can be, as in the case of coloration, inherently highly multivariate (?). The significance and robustness of a classification is assessed by training a machine to recognize differences between groups on part of the data, and using that fitted machine to predict the group-labels of data points from a testing set that were not included in the training, based solely on their multivariate coordinates. This cross-validation procedure results in a proportion of correctly classified points, or generalization accuracy score, which can be compared to that expected under random guessing using a binomial test.

In this study, we performed SVM classifications on each island separately. We used a standard five-fold cross-validation procedure, where the data were randomly split into five bins of approximately equal sizes, and each bin was in turn taken as the testing set while the rest was used as a training set, thus resulting in five trained machines per cross-validation. We replicated this procedure 100 times for each island to account for stochastic outcomes. We performed binomial tests to evaluate the significance of the deviations in observed mean generalization accuracy per island to null expectations under random guessing. Each training data set was downsampled to the size of its least represented habitat to ensure balanced training samples. We ensured that each habitat was represented by at least five data points in the training set. All classification analyses were repeated using the more classical linear discriminant analysis (LDA), a supervised machine learning technique finding linear boundaries that maximize the differences between groups, albeit assuming multivariate normality and homogeneity of covariance matrices (?). We used the R package rminer (??) for SVMs, and MASS (citation) for LDAs. We used rminer’s default heuristic search option to automatically tune the Gaussian kernel parameter σ and the complexity parameter C for the SVMs.

Univariate analyses

For each island where significant differences in multivariate dewlap coloration were detected between habitats, we used multiple univariate analyses of variance (ANOVA) to identify which variables were responsible for the observed differences. We constructed our ANOVA models in two steps, as per ?. In a first step, we accounted for heterogeneity of variances across groups by systematically comparing the goodness-of-fit of an ANOVA model estimated with ordinary least

squares (OLS) with that of a model estimated with generalized least squares (GLS), which allowed one estimate of residual variance per habitat (using the R package nlme, ??). Both models were fitted with restricted maximum likelihood (REML). Goodness-of-fit was estimated using Akaike's Information Criterion corrected for small sample sizes (AICc, from the R package MuMIn, ?), and the estimation method yielding the lowest AICc was retained. In a second step, we re-fitted the retained model with maximum likelihood (ML) to test for the effect of habitat-type using likelihood ratio tests (LRT) between a model including a habitat-term and a null model lacking it. Significant *post hoc* contrasts were assessed using Tukey's Honest Significant Difference (HSD) test whenever the OLS-model was the best fit, and pairwise Wilcoxon tests whenever there was evidence for heterogeneity of variances, and the GLS-model was the best fit.

We further tested the robustness of our results to non-normality. For each habitat-island combination where multivariate non-normality was detected (Table S3), we assessed the univariate normality of each variable (Shapiro-Wilk's test, Table S4) and backed our ANOVA results with nonparametric Kruskal-Wallis tests every time significant deviations were detected.

Spatial autocorrelation

We tested for within-island spatial autocorrelation between the geographical distances among sampling sites and their euclidean distances in multivariate color space (mean PC1 to PC4 per site, Table S1), regardless of habitat-type. Because often only a few sites were sampled per island, we could not get meaningful results from tests using sites as units of observation. Instead, we designed a permutation test where we randomly reshuffled individual lizards across sites within islands 1,000 times each, and systematically recalculated Pearson's correlation coefficient between geographic distances (computed as geodesic distances using the R package geosphere, ?) and phenotypic distances. We used the resulting null distributions of correlation coefficients to assess the significance of the observed spatial autocorrelation for each island (Table S8).

Results

We tested for variation in *A. sagrei* dewlap coloration between populations living in three characteristic habitat types across nine islands that span the West Indian range of the brown anole (Fig 1, S1). We found that most of the variation in coloration partitioned between islands (semi-parametric MANOVA, modified ANOVA-type statistic (MATS) = 2009.6, $P < 0.001$, Fig. S2, explained variance $\eta^2 = 44.3\%$, MANOVA approximation). Nonetheless, we did find evidence for differences in dewlap coloration between habitat-types, and those were mostly island-specific (habitat-by-island interaction term, MATS = 384.4, $P < 0.001$, explained variance $\eta^2 = 11.4\%$), leaving a small but significant portion of the variation explained by an archipelago-wide habitat effect (MATS = 42.5, $P = .001$, $\eta^2 = 4.8\%$).

The small archipelago-wide effect of habitat-type was detected for PC1, PC2 and PC3 (mixed ANOVA with island as a random effect, Table S11), but this effect was too small for post hoc tests to find which habitats differed. Because we identified deviations from univariate normality for each group (Table S13, but no deviations from homoskedasticity, Table ??), we repeated the analysis with a Kruskal-Wallis test

SVM classifiers correctly assigned individuals to their habitat of origin based solely upon dewlap coloration on five islands: Abaco, Bimini, Cayman Brac, Little Cayman, and Long island (Fig. 2). An LDA approach yielded similar success rates (Fig. S3), suggesting robust differences between these populations. Of the five islands, Little Cayman was the best discriminated with a mean SVM generalization success of 73.4% (Table S6). The results of the classification analyses on PCA data were very similar to results from SVMs and LDAs trained on reflectance values at 50nm-spaced wavelengths from 300 to 700nm (Fig. S4 and S5).

Differentiation in dewlap coloration occurred in multiple dimensions of color space. Moreover, the differences in dewlaps between habitats were not always consistent between islands, thus, we will discuss the habitat-specific variation in dewlap coloration for each island where significant differences were detected in turn (Fig. 3, Table ??). Figure 3A provides a key to map principal

244 component scores to the underlying wavelengths. Throughout, all reported significant differences
245 in analyses of variance (ANOVA, Table ??) where significant deviations from normality were de-
246 tected (Table S4) were also significant in nonparametric Kruskal-Wallis tests (Table S7).

247
248 On Abaco, dewlaps did not differ in PC1, which represents brightness. Mangrove lizards had
249 significantly lower PC2 scores, corresponding to higher ultraviolet reflectance and lower red re-
250 flectance. Coastal beach scrub lizards had lower scores on PC3, corresponding to lower ultraviolet
251 reflectance and higher blue reflectance.

252
253 On Bimini, coastal beach scrub lizards had significantly brighter dewlaps than lizards from
254 mangroves (PC1), but mangrove lizards had higher PC2 scores than beach scrub lizards, indicat-
255 ing higher violet and blue reflectance, and lower red reflectance. Lizards from primary coppice had
256 higher PC3 scores overall, which correlated very positively with ultraviolet reflectance.

257
258 On Cayman Brac, coppice-lizard dewlaps were significantly less bright than lizards from the
259 other habitats. Coastal beach scrub lizards had dewlaps that scored low on PC2, corresponding
260 to lower violet-blue and more red, while the mangrove lizards exhibited the opposite: relatively
261 higher levels of violet-blue and less red. In PC3 space we found that dewlaps from lizards in the
262 coastal habitat had high ultraviolet reflectance, coppice lizards had intermediate levels, and man-
263 grove lizards had relatively low levels.

264
265 On Little Cayman, the dewlaps of coppice lizards were significantly darker (PC1) than coastal-
266 lizards. Mangrove lizards had less ultraviolet and redder dewlaps (PC2). The dewlaps of the
267 coastal beach scrub lizards had higher levels of red and ultraviolet reflectance and less blue re-
268 flectance than the dewlaps of the other habitat-populations (PC3).

269
270 On Long Island, lizards from the coppice habitat had darker dewlaps than lizards from the
271 other habitats (PC1, Kruskal-Wallis test accounting for the presence of one outlier with very high
272 brightness, Fig. 3A, Table S7). Coastal lizards had relatively more ultraviolet and less blue-
273 green reflectance in their dewlaps (PC3). These coastal-habitat lizards also scored lower on PC4,
274 corresponding to slightly more violet and green-yellow dewlaps, and less blue dewlaps, than the
275 mangrove lizards on the island.

276
277 Sensitivity analyses on classifiers suggested an overall higher relative importance for PC2 and
278 PC3 in determining between-group differences on Abaco, both in SVM and LDA classifiers (Fig.
279 ??, ??), consistent with our ANOVA results (Fig. 3B). There was no strong signal of differences
280 in relative importance among principal components on the other islands. Sensitivity analyses of
281 SVMs trained on reflectance scores rather than principal components revealed, however, a con-
282 sistently higher importance of ultraviolet reflectance in between-group differences on all islands
283 (Fig. ??). This pattern was not recovered for LDAs trained on reflectance scores (Fig. ??).
284 Another way to get insights into the importance of variables is to perform a single LDA on the
285 significant islands and see what variables correlate with the LDs (on PCA and on reflectance data).

286
287 We did not find significant spatial autocorrelation between the sampling sites on the islands
288 where we detected a significant habitat effect. We did, however, detect a significant positive sig-
289 nal of autocorrelation on Eleuthera ($P = 0.02$, Table S8), suggesting possible color differentiation
290 through isolation-by-distance on this island.

291
292 In contrast, differences in dewlap coloration between habitats were often detected in close ge-
293 ographical proximity. For example, Bimini, Cayman Brac and Little Cayman were among the
294 smallest islands in our study (Fig. S1). Besides, for pairs of habitats where significant differences
295 in dewlap coloration were detected along some principal components, comparisons of the actual
296 sampling sites indicate that the most detectable differences involve sites that are mostly 5-10km
297 apart, with significant differences in PC3 detected between the beach scrub and coppice habitat
298 at little more than 100m distance from each other on Bimini (Fig. ??, Table S9).

299
300 Patterns of differentiation were inconsistent across the five most significant islands. No pattern
301 of variation was shared by all five islands, along any dimension. Some patterns did seem more

common however, such as darker dewlaps among coppice lizards (Cayman Brac, Little Cayman, and Long Island, Fig. 3) or the intermediate position of coppice lizards in chromatic color space (Cayman Brac and Long Island). In other cases, patterns of differentiation were reversed from one island to another, with more ultraviolet reflecting dewlaps in mangroves than in coastal habitat on Abaco and Cayman Brac, but the opposite on Little Cayman and Long Island. Overall, it seemed that patterns of heterogeneity of variance were often driven by higher variances in coloration within beach scrub lizards (Fig. 3, Table ??). Yet other patterns were idiosyncratic, such as the combination of higher red and ultraviolet reflectance in coastal lizards on Little Cayman, where the rule seemed to be a negative correlation between ultraviolet and red reflectance across every other island.

That said, archipelago-wide differences in dewlap coloration between habitats were detected by a set of SVMs trained on data pooled from the whole archipelago, regardless of island identity, both for PCA data and reflectance scores (Fig. ??, ??). This pattern seemed to be driven by mangrove lizards being correctly reassigned more often than predicted by chance. Sensitivity analyses on these machines suggest a relatively small role of long wavelengths (red reflectance) in driving this pattern (Fig. ??), but did not reveal strong differences between the PCs in relative importance (Fig. ??). Archipelago-wide differences were not detected by LDA classifiers at all (Fig. ??, ??), nor by a MANOVA (Wilk's $\lambda = 0.98$, $df = 2$, $F(8, 920) = 1.17$, $P = 0.316$) or a semi-parametric MANOVA-equivalent (R package MANOVA.RM, citation, Wald-type statistic ($df = 8$) = 12.58, parametric bootstrap with 1,000 iterations, $P = 0.131$, Fig. ??).

Discussion

Dewlap coloration differs between habitat-types We found that male dewlap coloration in *A. sagrei* significantly varied between habitat-types (beach scrub bush, primary coppice forest and mangrove forest) on five islands of the West Indies: Abaco, Bimini, Cayman Brac, Little Cayman and Long Island. However, the habitat-specific variation in dewlaps was not consistent between these islands. Although those results are consistent with adaptation at a very local scale, other evolutionary drivers could be at work, including phenotypic plasticity, random drift, or historical contingency including multiple colonization events. We reject this last explanation because all of the island populations in this study are strictly monophyletic, implying a single colonization event per island (van de Schoot, unpublished thesis; ?). While random drift cannot be completely ruled out, we see little evidence for a role of phenotypic isolation-by-distance (spatial autocorrelation) in explaining the differences we report. While we found a significant signal of isolation-by-distance on Eleuthera, we did not detect differences in dewlap coloration between habitats on this island.

A role of phenotypic plasticity is unlikely Phenotypic plasticity could explain differences in coloration between habitat populations because of diet differences. The yellow, orange and red coloration in anoline dewlaps are produced by pterins and carotenoids (???????). Animals lack the ability to synthesize carotenoids, and those must therefore be found in the diet, while pterins are synthesized from nucleotides (???). Experimental manipulation of dietary carotenoid content showed no effect on dewlap coloration in *A. sagrei* (?) nor in *A. distichus* (?), another species with an orange-based dewlap. Plasticity due to differences in development (e.g. egg rearing conditions) is unlikely because dewlap coloration develops at sexual maturity (?). ? further found a high degree of heritability of dewlap coloration in *A. sagrei*. These studies suggest that dewlap coloration is not a plastic trait, although transgenerational plastic effects cannot be completely ruled out by these one or two-generation common garden experiments (?). That leaves an adaptive explanation, where dewlap color could be under differential natural and/or sexual selection in these different habitats.

Divergence is maintained in the face of gene flow The small spatial scale (the median distance between island sample sites was 11.2km + mention the minimum distance at which we found differences) and the lack of geographic barriers within islands, together with the high mobility *A. sagrei* individuals (?), imply ample opportunity for extensive gene flow between the populations in this study. In agreement with this, populations from different habitats were found to not be monophyletic based on <insert marker name here> (van de Schoot et al. unpublished thesis). While

gene flow is expected to erase any differences acquired by drift without selection maintaining such polymorphism (?), these divergent patterns remain, which may support an adaptive explanation. Maintenance of dewlap color divergence despite gene flow has been found in *A. distichus* in Hispaniola (??) and proposed as a mechanism of reproductive isolation in the early stages of speciation (???). ? found that dewlap color polymorphism was maintained in the absence of genetic structure between populations of *A. apletophthalmus* from Panama. ? found that divergence in dewlap coloration matched habitat-type better than mitochondrial lineage in *A. roquet* on Martinique, and a convergent pattern was found in *A. trinitatis* on the featureless island of St Vincent (?). Divergence in body coloration, but not dewlap coloration, was also reported in *A. conspersus* on another small island, Grand Cayman (?). Those results suggest a high adaptive potential of the anoline dewlap.

Sexual selection could be at play Substantial levels of promiscuity in *A. sagrei* suggest ample opportunity for female mate choice and sexual selection (?). A number of studies suggest that characteristics of the dewlap are indicators of male quality and may therefore act as a cue in mate choice, according to the "good genes" model of sexual selection (?). ? found lower orange reflectance in dewlaps with heavily parasitized *A. brevirostris*, suggesting a trade-off in carotenoid use between the immune response and pigment deposition. ? found that lower UV and orange-red reflectance predict contest-winning success between males. ? further found that more yellow and red dewlaps (relative to UV) predict better body condition, and that higher yellow and UV reflectance at the margin of the dewlap predict higher hematocrit (the concentration of red blood cells), indicating a better health. Other aspects of the dewlap may be important for sexual selection, for example, dewlap size correlates with bite force (?) and sexual size dimorphism (a proxy for sexual selection; ?). Even though display frequency increases in the presence of females (?), there seems to be no link between dewlap display frequency and mating success (??) or individual quality (?). Our report of inconsistent divergence between islands, however, is at odds with the good-genes model of sexual selection, which would predict the evolution of dewlap coloration in the same direction across the archipelago. This is consistent with ?, who found no link between the average island-dewlap coloration and sexual size dimorphism in *A. sagrei* across the West Indies. If sexual selection is at play in our system, it more likely involves divergent female preferences that are not linked to male quality but rather to components of the environment, and may well be arbitrary (Fisherian sexual selection; ?).

Dewlap coloration could be locally adapted Presently, we do not know the adaptive drivers of dewlap color divergence observed in this study. Some degree of parallel evolution is usually a good indicator for an adaptive process (?), and convergent patterns of dewlap color evolution in similar environments across islands and species have been documented (??). Here, we found evidence for a few consistencies in within-island divergence across the nine islands studied (show some archipelago-wide results?); dewlap brightness was lower in the primary coppice habitat on three islands, and the primary coppice habitat was intermediate in coloration between mangrove and beach scrub on two islands. Those patterns could reflect adaptation to components of the habitat (?). However, it is not clear what those components of the habitat might be. Previous studies have found that dewlap coloration maximizes detectability given the light conditions in the local habitat, primarily through UV contrast – with UV-brighter dewlaps in UV-dark, mesic habitats and UV-darker dewlaps in UV-bright, xeric habitats – in *A. cristatellus* and *A. cooki* on Puerto Rico (??). We found no such pattern in *A. sagrei*, where instead, we found the darkest dewlaps in the darkest, mesic habitat – primary coppice forest – on three islands, and dewlaps often differed the most between beach scrub and mangrove forest, two xeric habitats with similar, high irradiance levels (??). The inconsistent and idiosyncratic patterns we observed suggest that dewlap color variation between habitats cannot be predicted by habitat identity alone. Studies of Jamaican and Hispaniolan anoles similarly found between-habitat differences in dewlap coloration but no evidence for higher detectability (??). Habitats on different islands may also differ in other aspects than light conditions such as densities of predators or other anole species, which have been shown to affect among-island dewlap diversity (??). In particular, ? recently showed that dewlaps with spotted patterns occurred more often in *A. sagrei* on islands with more coexisting species of anoles.

Implications in the context of speciation Local adaptation can be a precursor to ecological speciation, a process that may have given rise to the adaptive radiation of *Anolis* lizards (??). Ecologically-mediated divergence of a sexual signal may be a potent path to the evolution of reproductive isolation through divergent sexual selection (??). Evidence suggests that dewlap coloration could take this role in anoles (????), or at least that it is frequently involved in species recognition (????????). Although this signal is not detected at the phylogenetic scale of the whole genus (???), sexual signals are often evolutionarily very labile (?), and the anole dewlap in particular is capable of rapid macroevolution; for example, *A. conspersus* on Grand Cayman evolved a UV-blue dewlap from an ancestral orange dewlap in 2 to 3 million years (?). We present evidence of multiple cases of potentially adaptive maintenance of habitat-associated dewlap divergence over small geographical scale in *A. sagrei* across the West Indies. While these populations do not appear to be in the process of speciation, our results strongly suggest that the anoline dewlap has enough micro-scale, local adaptive potential to participate in the build-up of reproductive isolation, should it be recruited for assortative mating.

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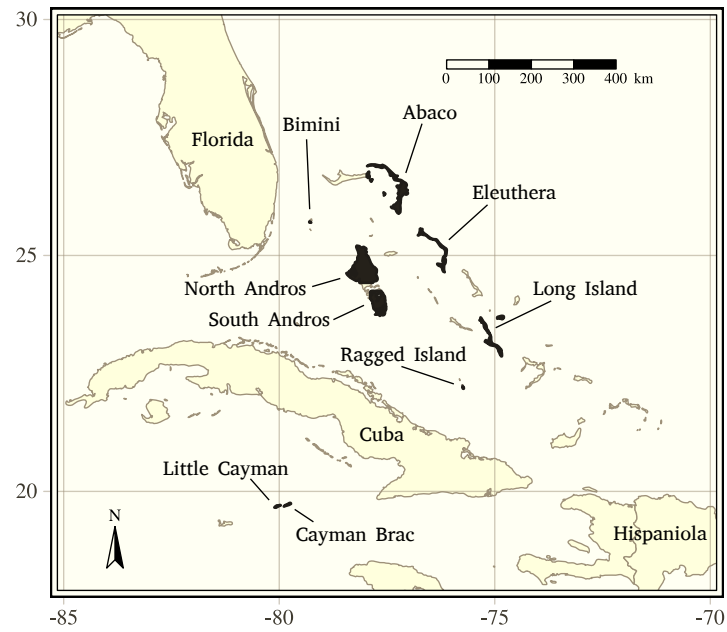


Figure 1: Map of the West Indies with sampled islands highlighted in black.

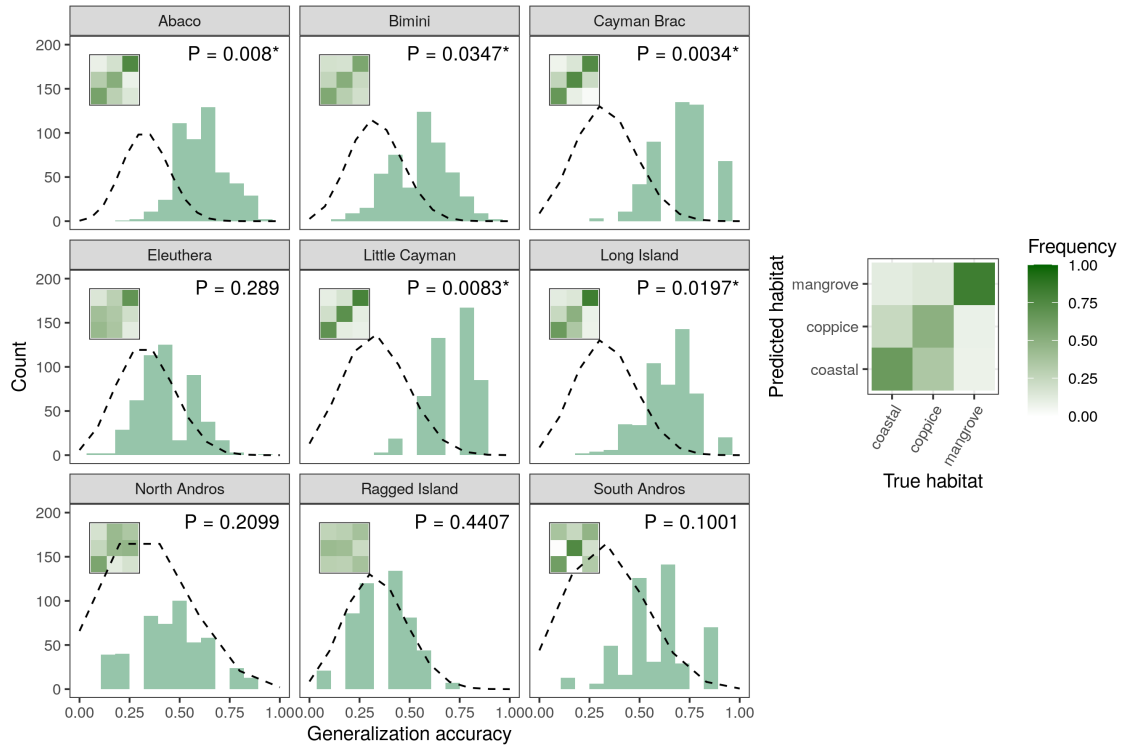


Figure 2: Distributions of classification accuracy across all SVM machines (100 replicates of 5 cross-validation bins each). The dashed line represents the density of a corresponding null binomial distribution, which would be expected under random guessing (testing sets with 20% of the observations for each island and success probability of 1/3). Inset plots show the corresponding average confusion matrices and represent the proportion of lizards from each habitat (columns) reassigned in each other habitat (rows), with an interpretation guide in the right panel. P-values indicate deviations of the mean classification accuracy to the expected null binomial distribution. *, $P < 0.05$

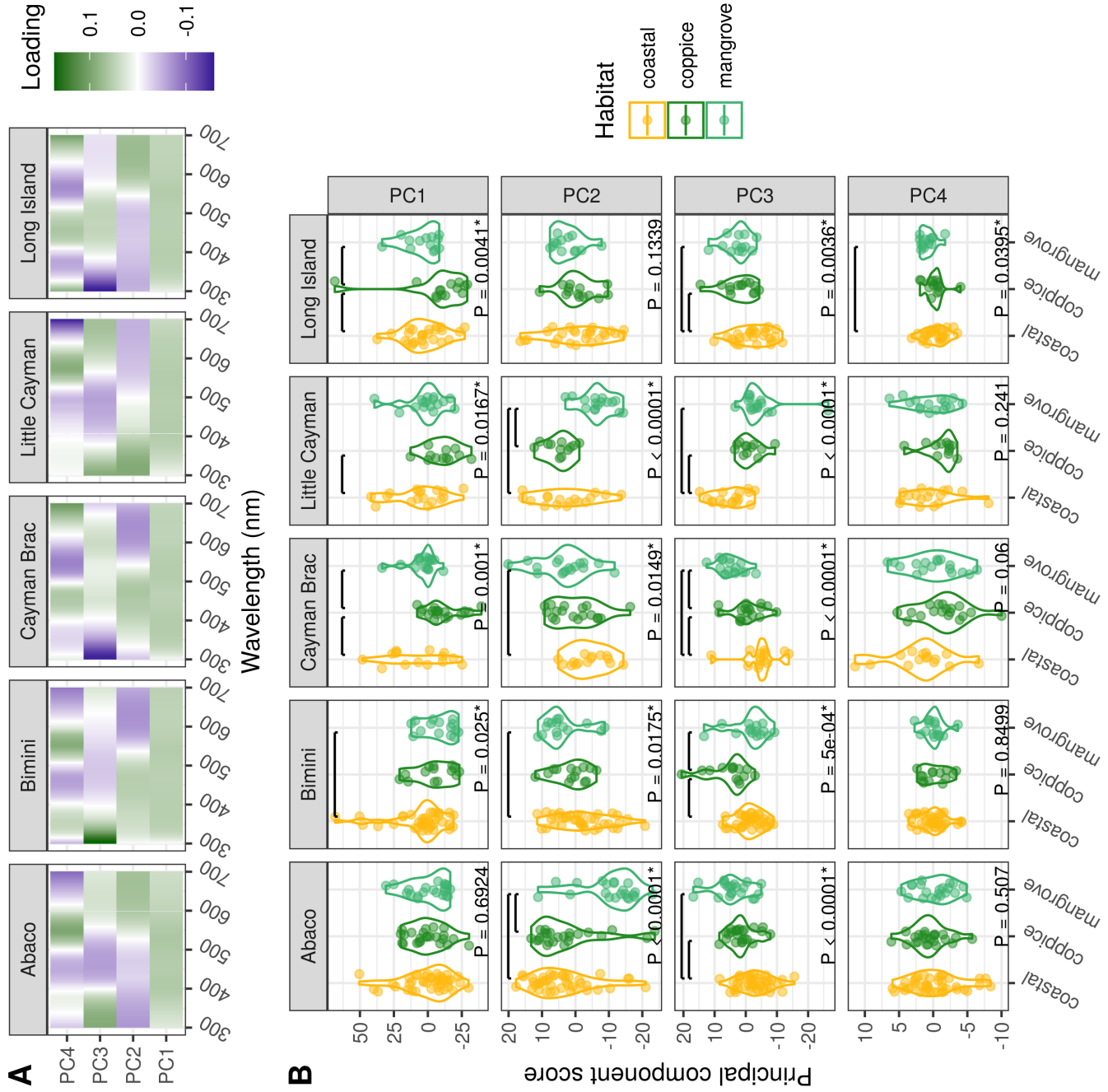


Figure 3: Dewlap coloration varies between habitat-types along different dimensions on different islands. (A) Boxplots show the distribution of the data for the five islands with significant differences in dewlap coloration between habitat (P-values in Fig. 2), along the first four principal components. We report the P-values of univariate analyses of variance conducted for each island (see Methods). Horizontal bars indicate *post hoc* significant contrasts at a 0.05 error rate (see Methods). *, $P < 0.05$. (B) Mapping of the reflectance at various wavelengths onto the principal components. Note that PC1 largely represents brightness.

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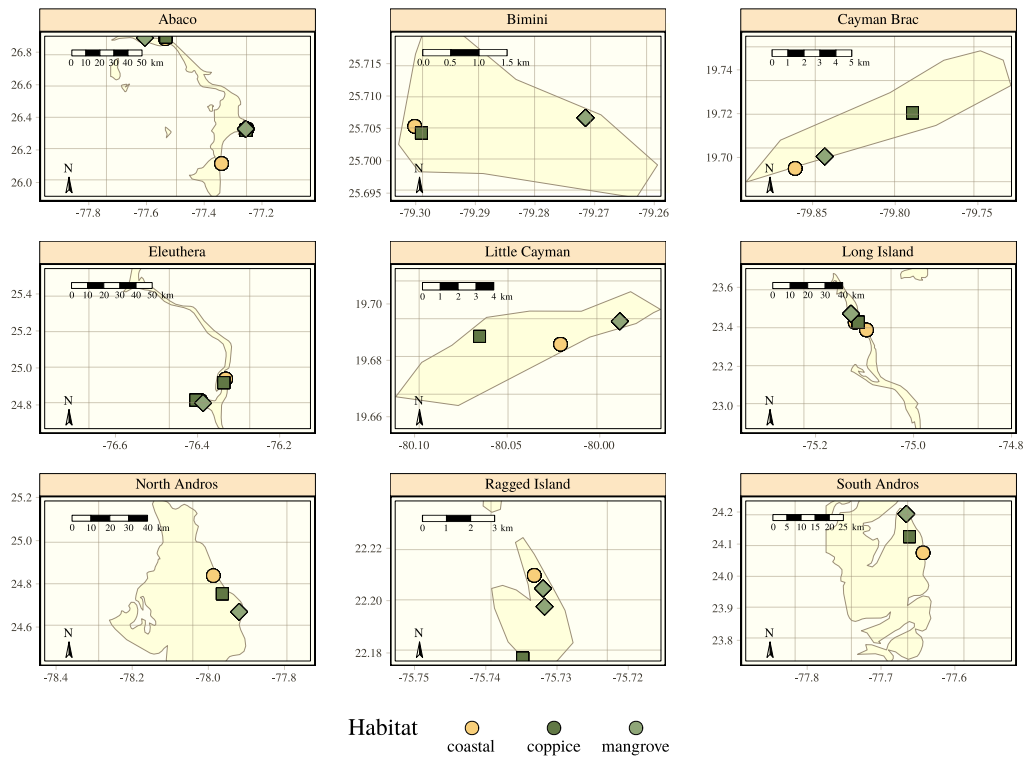


Figure S1: Map of the sampling sites and corresponding habitats across 9 islands of the West Indies.

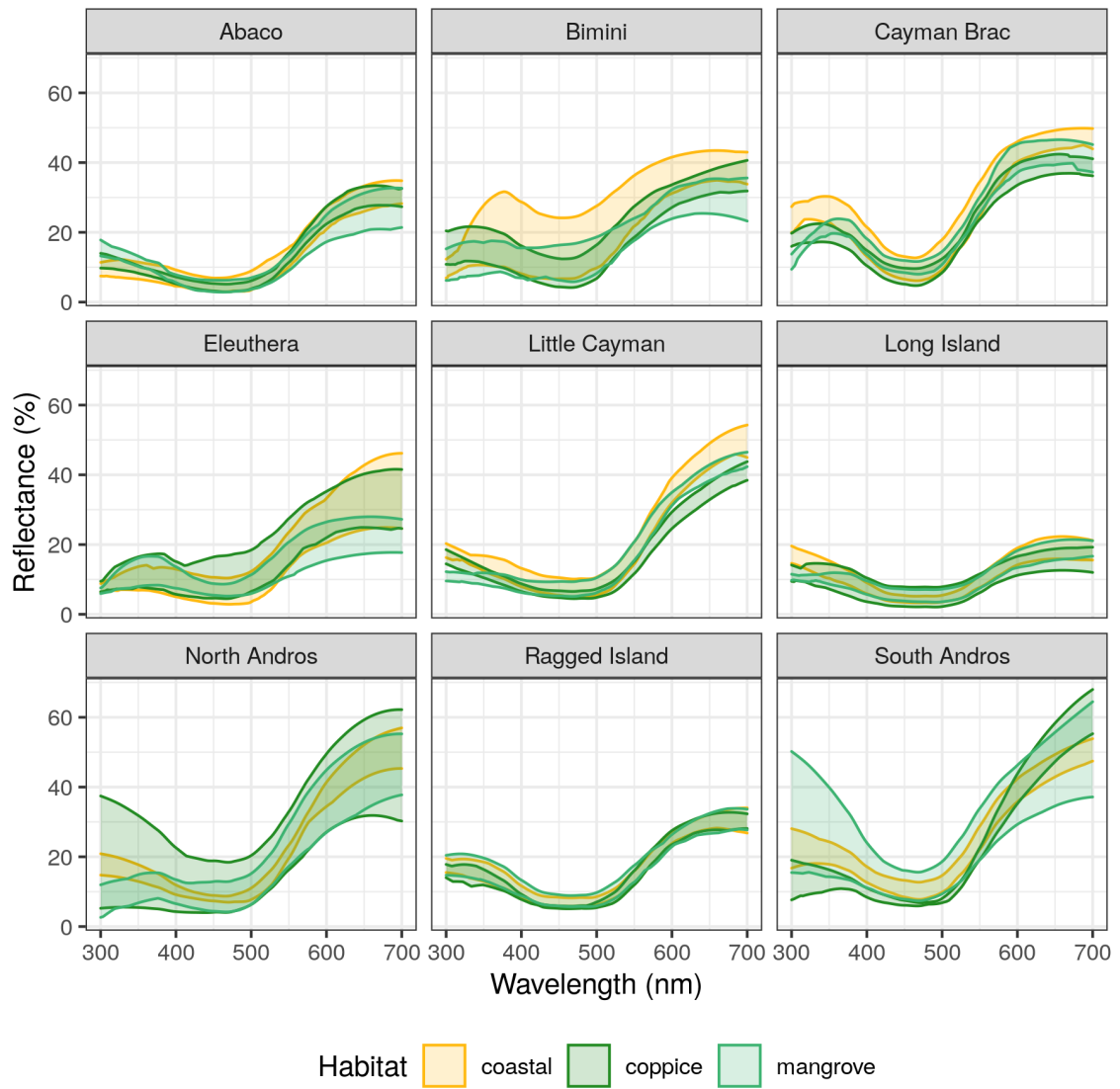


Figure S2: 5-95th percentile distributions of lizard dewlap reflectance values (in % of incoming light) across wavelengths for each island and each habitat.

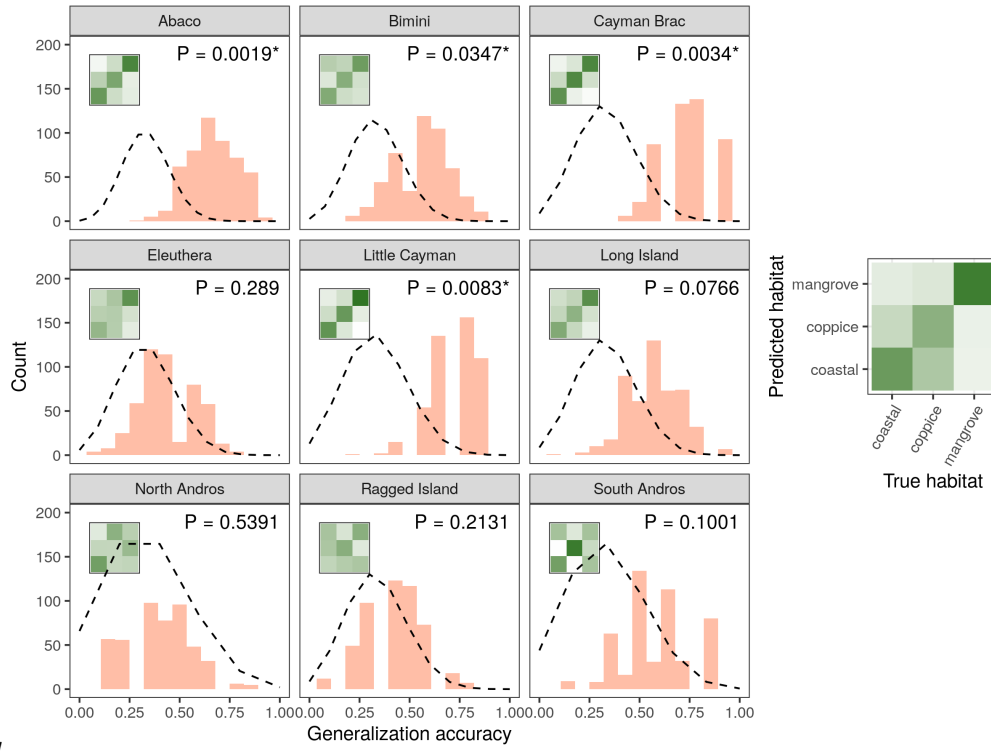


Figure S3: Distributions of classification accuracy across all LDA machines (100 replicates of 5 cross-validation bins each). The dashed line represents the density of a corresponding null binomial distribution, which would be expected under random guessing (testing sets with 20% of the observations for each island and success probability of 1/3). Inset plots show the corresponding average confusion matrices and represent the proportion of lizards from each habitat (columns) reassigned in each other habitat (rows), with an interpretation guide in the right panel. P-values indicate deviations of the mean classification accuracy to the expected null binomial distribution. *, $P < 0.05$

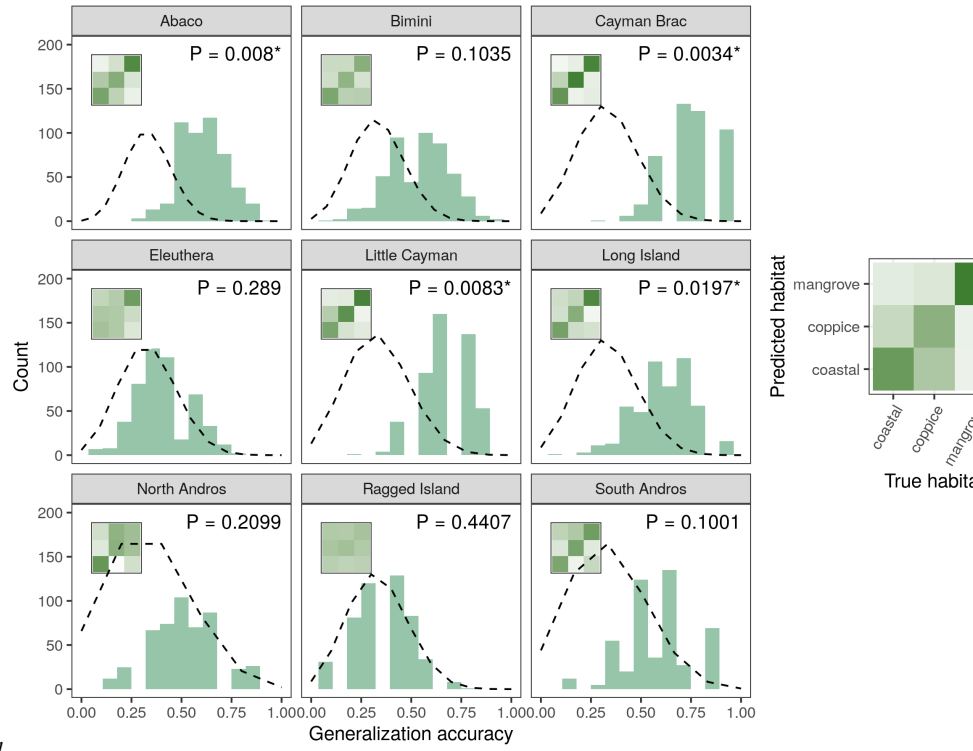
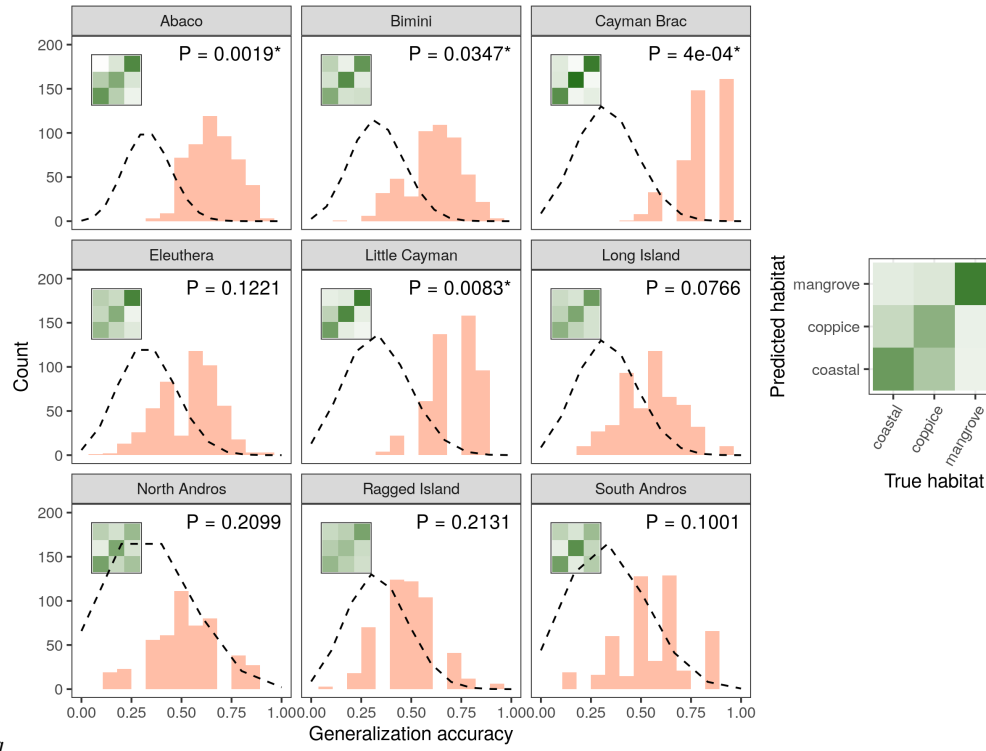


Figure S4: Distributions of classification accuracy across all SVM machines (100 replicates of 5 cross-validation bins each) trained directly on reflectance data from 300 to 700nm, at 50nm intervals. The dashed line represents the density of a corresponding null binomial distribution, which would be expected under random guessing (testing sets with 20% of the observations for each island and success probability of 1/3). Inset plots show the corresponding average confusion matrices and represent the proportion of lizards from each habitat (columns) reassigned in each other habitat (rows), with an interpretation guide in the right panel. P-values indicate deviations of the mean classification accuracy to the expected null binomial distribution. *, $P < 0.05$



learning/plots/classif_{lda}_{refl}.png

Figure S5: Distributions of classification accuracy across all LDA machines (100 replicates of 5 cross-validation bins each) trained directly on reflectance data from 300 to 700nm, at 50nm intervals. The dashed line represents the density of a corresponding null binomial distribution, which would be expected under random guessing (testing sets with 20% of the observations for each island and success probability of 1/3). Inset plots show the corresponding average confusion matrices and represent the proportion of lizards from each habitat (columns) reassigned in each other habitat (rows), with an interpretation guide in the right panel. P-values indicate deviations of the mean classification accuracy to the expected null binomial distribution. *, $P < 0.05$

Supplementary Tables

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Table S1: Locations of the sampling sites across islands, with mean principal component scores per site.

Island	Longitude	Latitude	Habitat	PC1	PC2	PC3	PC4
Abaco	-77.7256	26.9083	mangrove	-5.4905	1.3541	-0.4741	0.0083
Abaco	-77.5800	26.9020	coastal	1.8633	0.0365	-0.4475	0.0033
Abaco	-77.5763	26.9128	coppice	-1.6738	-1.7793	-0.0499	0.0012
Abaco	-77.1784	26.1045	coastal	1.1863	2.0408	-0.3468	0.0022
Abaco	-77.0055	26.3254	mangrove	-9.0319	-2.7460	0.4687	0.0077
Abaco	-77.0039	26.3170	coppice	0.9967	0.5161	-0.0267	-0.0118
Abaco	-76.9968	26.3260	coastal	7.6077	0.3186	0.1771	-0.0008
Bimini	-79.3022	25.5859	coastal	5.7537	-0.1593	-0.2505	0.0001
Bimini	-79.3014	25.7052	coastal	-3.1822	1.6617	-0.0460	0.0024
Bimini	-79.3002	25.7042	coppice	-1.3514	-3.8786	0.1027	-0.0027
Bimini	-79.2709	25.7066	mangrove	3.3656	0.6244	0.1569	-0.0021
Cayman Brac	-79.8627	19.6878	coastal	6.6606	-2.5670	0.0166	-0.0007
Cayman Brac	-79.8441	19.6949	mangrove	-1.0914	4.3607	0.0855	0.0001
Cayman Brac	-79.7887	19.7209	coppice	-4.5197	-1.9793	-0.0946	0.0004
Eleuthera	-76.3347	24.8146	coppice	3.2669	-1.2404	0.1018	-0.0085
Eleuthera	-76.3058	24.8127	coastal	0.4216	-3.5133	-0.0567	0.0009
Eleuthera	-76.2901	24.7981	mangrove	2.1881	0.7517	0.3957	-0.0055
Eleuthera	-76.1616	24.9129	coppice	-1.9136	1.0868	-0.4978	-0.0092
Eleuthera	-76.1492	24.9335	coastal	-3.1863	2.4270	0.1881	0.0218
Little Cayman	-80.0660	19.6906	coppice	0.8021	-1.9569	-0.0760	-0.0068
Little Cayman	-80.0205	19.6865	coastal	-6.6917	-1.2615	0.0659	0.0057
Little Cayman	-79.9871	19.6986	mangrove	6.5083	2.8079	-0.0129	-0.0010
Long Island	-75.2299	23.4740	mangrove	-1.2873	1.9371	-0.1880	-0.0029
Long Island	-75.2063	23.4282	coastal	2.3686	-0.9033	0.0215	0.0096
Long Island	-75.1884	23.4292	coppice	-4.6266	0.5060	0.1049	-0.0070
Long Island	-75.1408	23.3883	coastal	3.6139	-1.4521	0.0475	0.0025
North Andros	-77.8908	24.8391	coastal	-2.1881	-1.1236	0.0397	-0.0060
North Andros	-77.8428	24.7516	coppice	-1.8115	0.0012	-0.1678	0.0024
North Andros	-77.7540	24.6644	mangrove	3.5997	1.0101	0.1153	0.0033
Ragged Island	-75.7364	22.1768	coppice	3.2851	-0.3274	0.1911	-0.0013
Ragged Island	-75.7314	22.2097	coastal	-0.6412	-0.8878	-0.1293	-0.0033
Ragged Island	-75.7276	22.2045	mangrove	-2.9188	1.5792	-0.0034	0.0099
Ragged Island	-75.7270	22.1973	mangrove	-1.2210	0.7285	-0.0721	-0.0028
South Andros	-77.6050	24.2027	mangrove	-3.9253	0.4734	0.0477	-0.0005
South Andros	-77.5936	24.1289	coppice	6.1152	-0.4925	0.0349	0.0012
South Andros	-77.5453	24.0764	coastal	-0.7933	-0.1248	-0.0887	-0.0004

Table S2: Proportion of variance explained by the first four principal components on each island, as well as across the whole archipelago.

Island	PC1	PC2	PC3	PC4	Total
Abaco	0.400	0.279	0.147	0.079	0.906
Bimini	0.502	0.208	0.160	0.051	0.921
Cayman Brac	0.438	0.190	0.155	0.105	0.888
Eleuthera	0.490	0.233	0.138	0.066	0.926
Little Cayman	0.441	0.212	0.176	0.078	0.907
Long Island	0.515	0.205	0.161	0.043	0.925
North Andros	0.560	0.170	0.152	0.054	0.937
Ragged Island	0.483	0.226	0.127	0.072	0.907
South Andros	0.488	0.247	0.146	0.067	0.948
Archipelago	0.473	0.197	0.164	0.079	0.913

Table S3: Results of Henze-Zirkler's test of multivariate normality, performed on principal components in each habitat and on each island. HZ, test statistic. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Island	Habitat	HZ	P-value	
Abaco	coastal	1.083	0.0037	**
Abaco	coppice	1.081	0.002	**
Abaco	mangrove	1.072	0.0019	**
Bimini	coastal	1.287	< 0.0001	***
Bimini	coppice	0.864	0.0394	*
Bimini	mangrove	1.177	1e-04	***
Cayman Brac	coastal	0.647	0.5289	
Cayman Brac	coppice	0.745	0.2566	
Cayman Brac	mangrove	0.651	0.5573	
Eleuthera	coastal	1.873	< 0.0001	***
Eleuthera	coppice	1.450	< 0.0001	***
Eleuthera	mangrove	0.733	0.1347	
Little Cayman	coastal	0.624	0.6609	
Little Cayman	coppice	0.712	0.2422	
Little Cayman	mangrove	0.837	0.0703	
Long Island	coastal	0.880	0.0693	
Long Island	coppice	0.879	0.0309	*
Long Island	mangrove	0.791	0.1019	
North Andros	coastal	0.666	0.2921	
North Andros	coppice	0.716	0.1676	
North Andros	mangrove	0.649	0.3837	
Ragged Island	coastal	0.754	0.2323	
Ragged Island	coppice	0.771	0.1557	
Ragged Island	mangrove	0.603	0.7342	
South Andros	coastal	0.661	0.3409	
South Andros	coppice	0.641	0.3756	
South Andros	mangrove	0.903	0.0165	*

Table S4: Univariate Shapiro-Wilk's tests of normality performed on each island where significant differences were detected by SVM classification, in each habitat where deviations from multivariate normality were detected (Table S3). W , test statistic. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Island	Habitat	Variable	W	P-value	
Abaco	coastal	PC1	0.936	0.0224	*
Abaco	coastal	PC2	0.934	0.0194	*
Abaco	coastal	PC3	0.990	0.9764	
Abaco	coastal	PC4	0.964	0.2226	
Abaco	coppice	PC1	0.960	0.4433	
Abaco	coppice	PC2	0.823	0.0007	***
Abaco	coppice	PC3	0.960	0.4454	
Abaco	coppice	PC4	0.978	0.8580	
Abaco	mangrove	PC1	0.882	0.0157	*
Abaco	mangrove	PC2	0.882	0.0160	*
Abaco	mangrove	PC3	0.943	0.2447	
Abaco	mangrove	PC4	0.976	0.8497	
Bimini	coastal	PC1	0.836	< 0.0001	***
Bimini	coastal	PC2	0.978	0.6400	
Bimini	coastal	PC3	0.978	0.6348	
Bimini	coastal	PC4	0.967	0.3164	
Bimini	coppice	PC1	0.918	0.2047	
Bimini	coppice	PC2	0.956	0.6622	
Bimini	coppice	PC3	0.878	0.0541	
Bimini	coppice	PC4	0.937	0.3777	
Bimini	mangrove	PC1	0.881	0.0487	*
Bimini	mangrove	PC2	0.856	0.0213	*
Bimini	mangrove	PC3	0.869	0.0327	*
Bimini	mangrove	PC4	0.951	0.5448	
Long Island	coppice	PC1	0.685	0.0003	***
Long Island	coppice	PC2	0.952	0.5974	
Long Island	coppice	PC3	0.917	0.2007	
Long Island	coppice	PC4	0.861	0.0318	*

Table S5: Results of Box's M-test of homogeneity of covariance matrices across habitats on each island. χ^2 , test statistic. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Island	χ^2	df	P-value	
Abaco	47.74	20	0.0005	***
Bimini	35.23	20	0.0189	*
Cayman Brac	37.09	20	0.0114	*
Eleuthera	61.61	20	< 0.0001	***
Little Cayman	33.48	20	0.0298	*
Long Island	53.01	20	< 0.0001	***
North Andros	33.31	20	0.0312	*
Ragged Island	26.81	20	0.1406	
South Andros	46.31	20	0.0007	***

Table S6: Mean SVM classification accuracy per island, over all replicates and cross-validation bins. n , number of observations per island; p_{test} , proportion of the data sampled to form the training set; n_{test} , number of observations in the testing set. P-values indicate deviations from the expected null binomial distribution, with n_{test} events per island and random guess success probability 1/3. *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$.

Island	Mean accuracy	n	p_{test}	n_{test}	P-value	
Abaco	0.612	86	0.2	17	0.0080	**
Bimini	0.547	67	0.2	13	0.0347	*
Cayman Brac	0.721	50	0.2	10	0.0034	**
Eleuthera	0.437	56	0.2	11	0.2890	
Little Cayman	0.734	45	0.2	9	0.0083	**
Long Island	0.651	53	0.2	10	0.0197	*
North Andros	0.453	28	0.2	5	0.2099	
Ragged Island	0.364	50	0.2	10	0.4407	
South Andros	0.600	31	0.2	6	0.1001	

Table S7: Results of nonparametric Kruskal-Wallis tests performed on each variable on each island where deviations from normality were detected (Table S4).

Island	Variable	χ^2	df	P-value	
Abaco	PC1	0.74	2	0.6924	
Abaco	PC2	23.13	2	< 0.0001	***
Abaco	PC3	22.96	2	< 0.0001	***
Abaco	PC4	1.28	2	0.5268	
Bimini	PC1	7.38	2	0.0250	*
Bimini	PC2	6.95	2	0.0310	*
Bimini	PC3	15.17	2	0.0005	***
Bimini	PC4	0.13	2	0.9351	
Long Island	PC1	10.98	2	0.0041	**
Long Island	PC2	4.02	2	0.1339	
Long Island	PC3	9.26	2	0.0098	**
Long Island	PC4	7.13	2	0.0283	*

Table S8: Individual-based permutation tests of spatial autocorrelation within islands. P-values were computed from 1,000 permutations of individual site-labels. Pearson's coefficient r measures the correlation between distances in color space and geodesic distances among the sites. *, $P < 0.05$.

Island	r	P-value	No. sites	
Abaco	-0.213	0.817	7	
Bimini	0.044	0.510	4	
Cayman Brac	-0.010	0.465	3	
Eleuthera	0.816	0.015	5	*
Little Cayman	-0.688	0.684	3	
Long Island	-0.189	0.579	4	
North Andros	0.730	0.199	3	
Ragged Island	0.706	0.114	4	
South Andros	-0.852	0.776	3	

Table S9: Pairwise geographical distances and Wilcoxon tests between sites whose habitats were found to significantly differ from each other in at least one dimension of dewlap coloration. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. **Reduce to four digits for longitude and latitude.**
<https://bookdown.org/yihui/rmarkdown-cookbook/kable.html>

island	site1	site2	distance	habitat1	habitat2	variable	W
Abaco	26.912775, -77.576286	26.901974, -77.58002	1.25	coppice	coastal	PC3	21
Abaco	26.912775, -77.576286	26.104472, -77.1784	97.95	coppice	coastal	PC3	102
Abaco	26.31705, -77.003854	26.901974, -77.58002	86.56	coppice	coastal	PC3	51
Abaco	26.31705, -77.003854	26.104472, -77.1784	29.31	coppice	coastal	PC3	265
Abaco	26.912775, -77.576286	26.325994, -76.996839	86.93	coppice	coastal	PC3	90
Abaco	26.31705, -77.003854	26.325994, -76.996839	1.21	coppice	coastal	PC3	209
Bimini	25.704172, -79.3002	25.585934, -79.302184	13.10	coppice	coastal	PC3	124
Bimini	25.704172, -79.3002	25.705249, -79.301399	0.17	coppice	coastal	PC3	320
Cayman Brac	19.72092, -79.78869	19.68784, -79.86265	8.58	coppice	coastal	PC1	70
Cayman Brac	19.72092, -79.78869	19.68784, -79.86265	8.58	coppice	coastal	PC3	206
Little Cayman	19.69062, -80.06602	19.68647, -80.02047	4.80	coppice	coastal	PC1	44
Little Cayman	19.69062, -80.06602	19.68647, -80.02047	4.80	coppice	coastal	PC3	36
Long Island	23.429152, -75.188354	23.428201, -75.206269	1.83	coppice	coastal	PC3	92
Long Island	23.429152, -75.188354	23.38831, -75.140756	6.64	coppice	coastal	PC3	169
Abaco	26.908272, -77.725588	26.901974, -77.58002	14.48	mangrove	coastal	PC2	8
Abaco	26.908272, -77.725588	26.104472, -77.1784	104.43	mangrove	coastal	PC2	43
Abaco	26.325377, -77.005543	26.901974, -77.58002	85.76	mangrove	coastal	PC2	1
Abaco	26.325377, -77.005543	26.104472, -77.1784	29.96	mangrove	coastal	PC2	49
Abaco	26.908272, -77.725588	26.325994, -76.996839	97.10	mangrove	coastal	PC2	19
Abaco	26.325377, -77.005543	26.325994, -76.996839	0.87	mangrove	coastal	PC2	2
Abaco	26.908272, -77.725588	26.901974, -77.58002	14.48	mangrove	coastal	PC3	8
Abaco	26.908272, -77.725588	26.104472, -77.1784	104.43	mangrove	coastal	PC3	57
Abaco	26.325377, -77.005543	26.901974, -77.58002	85.76	mangrove	coastal	PC3	70
Abaco	26.325377, -77.005543	26.104472, -77.1784	29.96	mangrove	coastal	PC3	289
Abaco	26.908272, -77.725588	26.325994, -76.996839	97.10	mangrove	coastal	PC3	38
Abaco	26.325377, -77.005543	26.325994, -76.996839	0.87	mangrove	coastal	PC3	254
Bimini	25.706629, -79.270911	25.585934, -79.302184	13.73	mangrove	coastal	PC1	61
Bimini	25.706629, -79.270911	25.705249, -79.301399	3.06	mangrove	coastal	PC1	104
Bimini	25.706629, -79.270911	25.585934, -79.302184	13.73	mangrove	coastal	PC2	133
Bimini	25.706629, -79.270911	25.705249, -79.301399	3.06	mangrove	coastal	PC2	279
Cayman Brac	19.69494, -79.84407	19.68784, -79.86265	2.10	mangrove	coastal	PC2	199
Cayman Brac	19.69494, -79.84407	19.68784, -79.86265	2.10	mangrove	coastal	PC3	237
Little Cayman	19.69861, -79.98714	19.68647, -80.02047	3.74	mangrove	coastal	PC2	46
Little Cayman	19.69861, -79.98714	19.68647, -80.02047	3.74	mangrove	coastal	PC3	21
Long Island	23.473987, -75.229859	23.428201, -75.206269	5.61	mangrove	coastal	PC3	91
Long Island	23.473987, -75.229859	23.38831, -75.140756	13.15	mangrove	coastal	PC3	168
Long Island	23.473987, -75.229859	23.428201, -75.206269	5.61	mangrove	coastal	PC4	104
Long Island	23.473987, -75.229859	23.38831, -75.140756	13.15	mangrove	coastal	PC4	144
Abaco	26.908272, -77.725588	26.912775, -77.576286	14.84	mangrove	coppice	PC2	13
Abaco	26.325377, -77.005543	26.912775, -77.576286	86.41	mangrove	coppice	PC2	7
Abaco	26.908272, -77.725588	26.31705, -77.003854	97.25	mangrove	coppice	PC2	29
Abaco	26.325377, -77.005543	26.31705, -77.003854	0.94	mangrove	coppice	PC2	34
Bimini	25.706629, -79.270911	25.704172, -79.3002	2.95	mangrove	coppice	PC3	34
Cayman Brac	19.69494, -79.84407	19.72092, -79.78869	6.48	mangrove	coppice	PC1	255
Cayman Brac	19.69494, -79.84407	19.72092, -79.78869	6.48	mangrove	coppice	PC3	252
Little Cayman	19.69861, -79.98714	19.69062, -80.06602	8.32	mangrove	coppice	PC2	6

Island	df	Wilks's λ	Pseudo F	num. df	den. df	P-value	
Abaco	2	0.436	10.29	8	160	< 0.0001	***
Bimini	2	0.593	4.55	8	122	< 0.0001	***
Cayman Brac	2	0.272	10.08	8	88	< 0.0001	***
Eleuthera	2	0.674	2.72	8	100	0.0093	**
Little Cayman	2	0.217	11.17	8	78	< 0.0001	***
Long Island	2	0.605	3.36	8	94	0.002	**
North Andros	2	0.676	1.19	8	44	0.3263	
Ragged Island	2	0.712	2.03	8	88	0.0513	
South Andros	2	0.269	5.80	8	50	< 0.0001	***

Table S10: Results of MANOVA tests performed on principal components for each island. df, degrees of freedom; num. df and den. df, numerator and denominator degrees of freedom for the F-test, respectively. *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$.

Table S11: Results of ANOVAs performed on each principal component across the whole archipelago. Legend is the same as for Table ??.

Island	Variable	Best fit	df	AICc	Δ AICc	df _{LRT}	Log-lik.	χ^2	P-value	
PC1	3	5	3749.9	-228.3	0.61	2	-1874.7	8.69	0.0130	*
PC2	4	7	3002.2	-162.3	0.98	2	-1496.2	17.76	0.0001	***
PC3	4	7	2826.3	-175.4	0.97	2	-1407.8	7.03	0.0298	*
PC4	4	7	2015.7	-305.8	0.52	2	-1000.1	0.47	0.7914	

variable	chisq	df	pvalue	signif
PC1	3.13	2	0.2087	*
PC2	6.44	2	0.0399	
PC3	2.20	2	0.3328	
PC4	0.99	2	0.6101	

Table S12: Results of Kruskal-Wallis tests comparing principal components between habitats across the whole archipelago

habitat	variable	W	pvalue	signif
coastal	PC1	0.92	0.0000	***
coastal	PC2	0.99	0.1280	
coastal	PC3	0.96	0.0000	***
coastal	PC4	0.97	0.0003	***
coppice	PC1	0.95	0.0001	***
coppice	PC2	0.97	0.0083	**
coppice	PC3	0.96	0.0003	***
coppice	PC4	0.98	0.0591	
mangrove	PC1	0.93	0.0000	***
mangrove	PC2	0.96	0.0015	**
mangrove	PC3	0.85	0.0000	***
mangrove	PC4	0.96	0.0016	**

Table S13: Shapiro tests of univariate normality within each habitat across the whole archipelago

variable	K2	df	pvalue	signif
PC1	1.92	2	0	
PC2	3.86	2	0	
PC3	4.28	2	0	
PC4	2.06	2	0	

Table S14: Homogeneity of variance between habitats across the whole archipelago.