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APPLICATION

PleistoDist: A toolbox for visualising and quantifying the effects of Pleistocene sea-level change on island archipelagos

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Abstract

1. Pleistocene sea-level change played a significant role in the evolution and assembly of island biotas. The formation of land bridges between islands during Quaternary glacial maxima, when sea levels were more than 120 metres below present-day sea levels, often facilitated historical dispersal and gene flow between islands that are today geographically disconnected.
2. Despite the importance of Pleistocene sea-level change, few software packages exist that model the effects of this phenomenon in a standardised and generalised manner.
3. Here, we present PleistoDist, an R package that allows users to visualise and quantify the effects of Pleistocene sea-level change on islands over time, and test multiple temporally explicit hypotheses of inter-island dispersal and community assembly.
4. Re-analysing published datasets, we demonstrate how using PleistoDist to account for historical sea-level change can provide greater explanatory power when analysing extant island communities, and show how population genetic simulations can be used to generate spatiotemporally explicit neutral expectations of population genetic structure across island archipelagos.

KEYWORDS
bathymetry, biogeography, gene flow, islands, land bridges, phylogeography, Pleistocene, sea level

1 | INTRODUCTION

One of the key insights of the theory of island biogeography (MacArthur & Wilson, 1967) is that the size and orientation of islands play a significant role in structuring the evolution and assembly of island communities. Specifically, the theory predicts that proximate islands experience higher inter-island immigration, and consequently increased gene flow and community similarity (Kimura & Weiss, 1964; Simberloff, 1974), and that larger islands tend to have more species (Gleason, 1922). Yet, empirical species distributions across island archipelagos highlight numerous exceptions. At macroecological scales, the distributions of terrestrial megafauna across the Sundaic and Wallacean regions (Lohman et al., 2011; Wallace, 1869) and the decoupling of species–area correlations on land-bridge islands in the Aegean Sea (Hammoud et al., 2021) illustrate how land bridges can facilitate dispersal, colonisation and biotic homogenisation between distant islands. Phylogeographic studies have also demonstrated that the patterns of intraspecific genetic differentiation within island archipelagos are correlated with land-bridge connectivity (Cros et al., 2020; Leonard et al., 2015).

Incorporating the historical effects of Pleistocene sea-level change into models of island biogeography is thus essential to better understanding the patterns of community assembly and gene flow observed in island archipelagos (Lohman et al., 2011). However, while many studies have qualitatively and quantitatively described the impact of transient land bridges in island systems (Cros et al., 2020; Reilly et al., 2019), few software packages exist that allow for such analyses to be performed in a generalised and standardised manner. To address the need for generalised methods that quantify the effects of sea-level change on islands, we present PleistoDist (https://github.com/g33k5p34k/PleistoDistR), an R package that allows users to visualise sea-level change over time and calculate multiple metrics of island shape, inter-island distance, net inter-island migration and inter-island visibility, all normalised over time. This tool generalises workflows akin to those developed by Norder et al. (2018) and Rijsdijk et al. (2014) by simplifying the effect of sea-level change using a eustatic sea-level reconstruction, which assumes that sea-level change is globally uniform, and applying it to high-resolution bathymetric datasets to reconstruct the geographical extents of islands at different time points. This software is designed to be applicable across a wide range of geographical contexts, and the maps and island metrics generated by this workflow can be used to generate null expectations and hypotheses for ecological and evolutionary analyses. We demonstrate this with a nonexhaustive series of worked examples spanning a variety of taxa and localities, showing how PleistoDist can help address various biogeographic questions and be used in conjunction with other software packages.

2 | PleistoDist WORKFLOW

2.1 | Input files

PleistoDist requires two main input files: a bathymetry raster to generate maps of island extents at different historical sea levels and a shapefile of source points from which to calculate island metrics and/or pairwise distances. By default, users are advised to use bathymetry data from the General Bathymetric Chart of the Oceans (GEBCO: https://www.gebco.net), a global database of Earth's terrestrial and undersea terrain at 15-arc-second resolution, although PleistoDist can accept any type of ASCII-formatted bathymetry data as input. Users must also specify a map projection appropriate to their area of interest, as well as a time cut-off to set the temporal scope of the analysis.

2.2 | Generating the interval file

PleistoDist models historical sea-level change by decomposing eustatic Pleistocene sea levels (by default from Bintanja and van de Wal (2008)) into a number of discrete intervals for a user-defined period of time (3000 kya by default, depending on the range of the sea-level reconstruction). These intervals can be calculated in two different ways: by binning over time with the *getintervals_time* function or by binning over sea level with the *getintervals_sealvl* function (Figure 1). Binning over time involves dividing the timespan of interest into several equal time intervals and calculating the mean sea level for each interval (Figure 1a). In contrast, binning over sea level involves calculating the total range of sea-level change for the timespan of interest and dividing this range into several equal bins (Figure 1b). For the latter method, the mean sea level of each bin is the average of the minimum and maximum sea level for that bin, without respect to time. Once calculated, the intervals are written to an 'interval file' (Figure 1) in comma-separated value (CSV) format in the output folder.

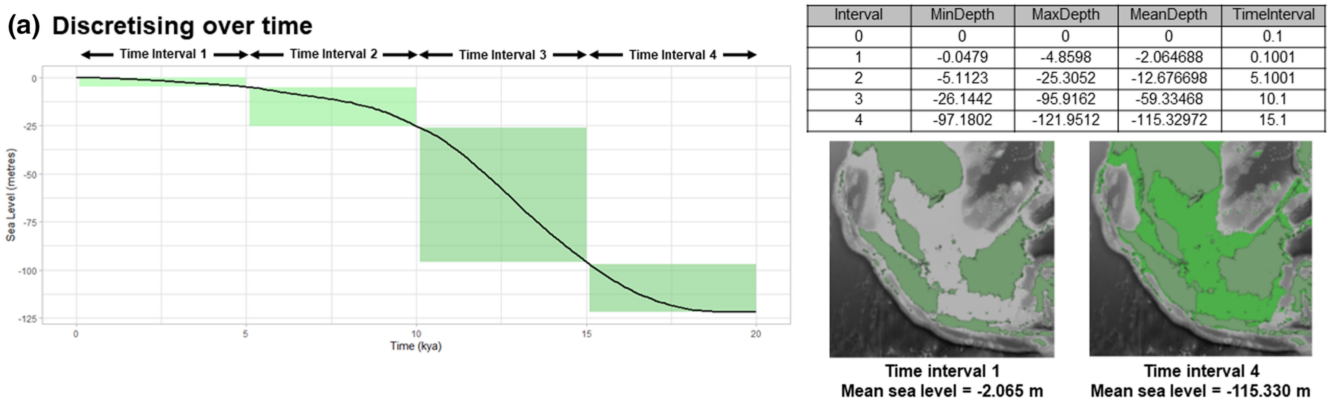
2.3 | Generating maps of island extents

Users can generate maps of island extents based on mean sea levels specified in the interval file (Figure 1) using the *makemaps* function. This function reprojects the input bathymetry raster into the user-specified map projection using a bilinear resampling method and generates raster and shapefile outputs of island extents in three formats: a shapefile of island polygons, an ASCII flat raster with no topography and an ASCII topographic raster that preserves the original elevations of each land pixel. Since the *makemaps* function reads intervals and mean sea levels directly from the interval file, users can customise the output maps generated by this module by manually editing the interval file. Users can also specify an offset value that accounts for constant rates of tectonic uplift or subsidence across the entire modelled region (Ali & Aitchison, 2014; Kealy et al., 2017).

2.4 | Calculating intra- and interisland metrics

Based on the maps generated, PleistoDist can calculate a variety of intra- and interisland metrics for each time or sea-level interval specified in the interval file, as well as calculate the weighted mean of these values over time. For metrics of island shape, PleistoDist includes functions that calculate island perimeter, area and surface area for each interval. As for interisland distances, PleistoDist can calculate three kinds of island-to-island distances (centroid-to-centroid, least shore-to-shore and mean shore-to-shore distances; Figure 2), as well as two kinds of point-to-point distances (Euclidean and least-cost distances; Figure 3) for each interval. Islands that merge at particular intervals are considered fused for these metrics.

In addition to metrics of island shape and interisland distance, PleistoDist includes two higher level functions that calculate the expected equilibrium net migration between island pairs based on a model described by MacArthur and Wilson (1967), as well as the visibility of an island relative to an observer on another based on an estimate of the maximum sightline (i.e. horizon distance) of the observer (Figure 4). Details on how the calculations are performed can be found in the Supporting Information.

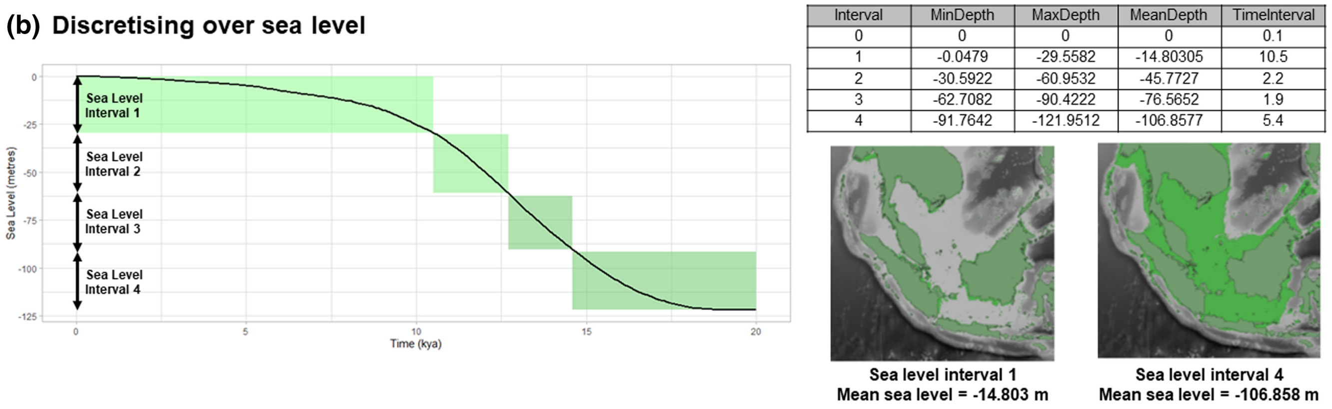


(a) Discretising over time

Interval	MinDepth	MaxDepth	MeanDepth	TimeInterval
0	0	0	0	0.1
1	-0.0479	-4.8598	-2.064688	0.1001
2	-5.1123	-25.3052	-12.676698	5.1001
3	-26.1442	-95.9162	-59.33468	10.1
4	-97.1802	-121.9512	-115.32972	15.1

Time interval 1
Mean sea level = -2.065 m

Time interval 4
Mean sea level = -115.330 m



(b) Discretising over sea level

Interval	MinDepth	MaxDepth	MeanDepth	TimeInterval
0	0	0	0	0.1
1	-0.0479	-29.5582	-14.80305	10.5
2	-30.5922	-60.9532	-45.7727	2.2
3	-62.7082	-90.4222	-76.5652	1.9
4	-91.7642	-121.9512	-106.8577	5.4

Sea level interval 1
Mean sea level = -14.803 m

Sea level interval 4
Mean sea level = -106.858 m

FIGURE 1 PleistoDist provides two different methods for discretising sea-level change, either by time (a) or by sea level (b), as illustrated here for Sundaland with a time cut-off of 20 kya over five intervals.

3 | PleistoDist APPLICATIONS AND CASE STUDIES

3.1 | Isolation-by-distance in Caribbean flightless ground crickets *Amphiacusta sanctaecrucis*

Papadopoulou and Knowles (2015) studied the effects of Pleistocene island connectivity on the genetic differentiation patterns of *Amphiacusta sanctaecrucis* populations in the Virgin Islands, and found that population divergence times broadly correlate with a period of fluctuating sea levels and interisland land-bridge connections (~75–115 kya). In addition, all Virgin Island populations appeared to exhibit a pattern of isolation-by-distance, except those from St. Croix.

Because these analyses were based on present-day Euclidean distances, we used PleistoDist to replicate the landscape genetic analyses using geographical distance matrices that account for sea-level change over time, for a time cut-off of 20 kya (corresponding to the last glacial maximum [LGM]) and 20 time intervals. Similar to Papadopoulou and Knowles (2015), Mantel tests show no significant correlation between genetic and Euclidean distance ($R^2 = 0.228$, $p = 0.0521$; Table 1) when all populations are included in the analysis (Table 1). None of the other geographic distance metrics showed a significant Mantel correlation with genetic distance either. However, given the susceptibility of Mantel tests to spatial autocorrelation (Legendre et al., 2015), it is probable that genetic variation is nonlinearly distributed across geographic space. Using distance-based redundancy analyses (dbRDA), which account for spatial autocorrelation, we found that unlike Papadopoulou and Knowles (2015), we observed a highly significant correlation between genetic distance and time-corrected least shore-to-shore and centroid-to-centroid distances ($p = 0.00661$ and 0.00704, respectively; Table 1), while Euclidean distance showed a marginally significant correlation with genetic distance ($p = 0.0348$; Table 1). Further model selection indicated that the time-corrected centroid-to-centroid distance best fit the variation observed in the genetic data, suggesting that genetic divergence patterns were likely structured by broad-scale isolation-by-distance driven by interisland overwater dispersal between panmictic populations.

3.2 | Species–area relationships of Aegean Island angiosperms

Hammoud et al. (2021) examined the relationship between island area and species richness in the Aegean Islands across multiple angiosperm taxa, accounting for historical sea-level change over the Quaternary. They find that true islands, which were historically unconnected to the mainland, exhibit stronger correlations between

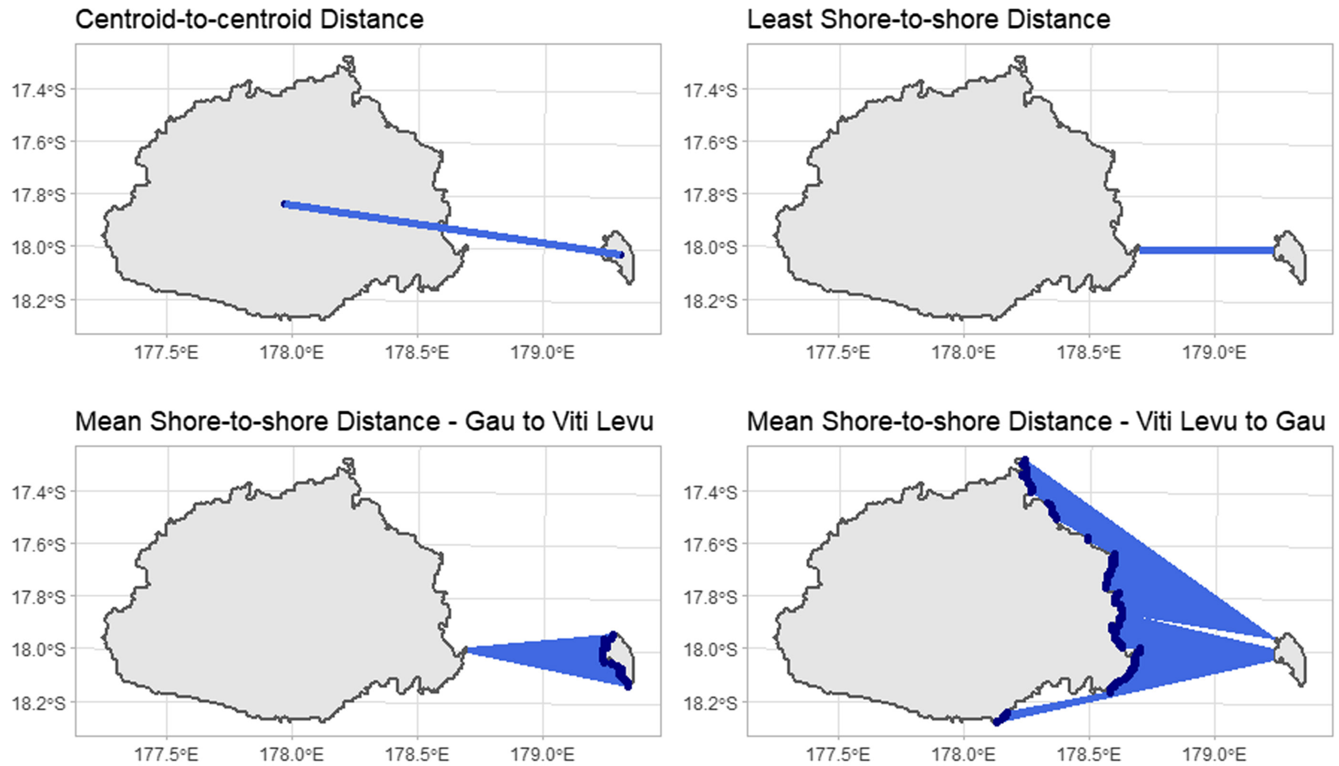


FIGURE 2 PleistoDist calculates three interisland distances: centroid-to-centroid distance, least shore-to-shore distance and mean shore-to-shore distance, illustrated here with Viti Levu (left) and Gau islands, Fiji. Note how interisland distances are asymmetric for the mean shore-to-shore distance.

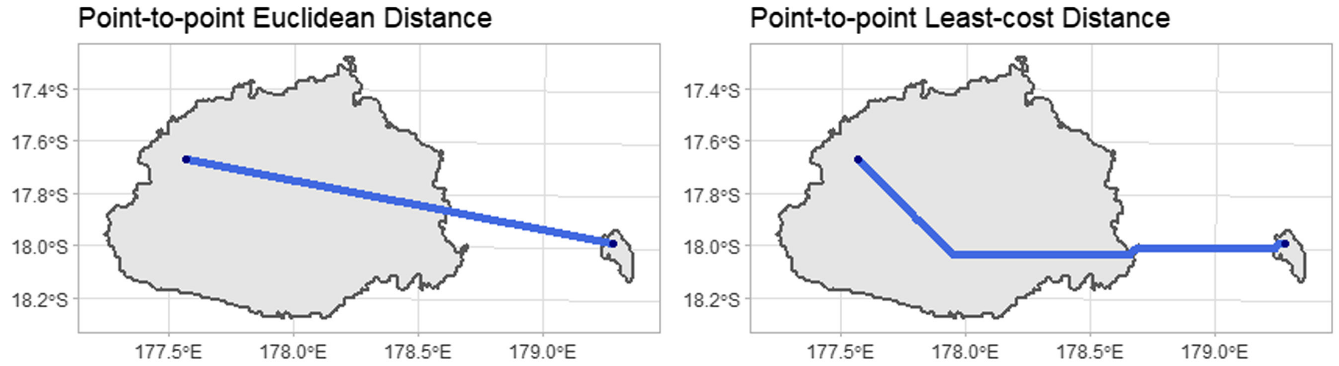


FIGURE 3 PleistoDist calculates two distance measures between source points: Euclidean distance between points (as the crow flies, invariant across all intervals) and least-cost distance (which minimises overwater movement).

island area and endemic species richness relative to land-bridge islands.

Using PleistoDist, we reanalysed angiosperm species–area relationships on the true islands of the Aegean Sea using both contemporary and time-corrected estimates of island area for 40 depth intervals over the last 20 kya. We found that species richness is significantly positively correlated with island area for all angiosperm chorotypes (Table 2), consistent with the findings of Hammoud et al. (2021). However, unlike Hammoud et al. (2021), our extended analyses suggest that present-day 2D island area is the best predictor of angiosperm species richness instead of time-corrected 2D area (Table 2). Our re-evaluation suggests that species turnover rates on true islands may be fast, resulting in a rapid equilibration of species richness to contemporary island extents.

3.3 | Interisland migration of *Horornis* bush-warblers across the Fijian archipelago

One of the predictions of the theory of island biogeography (MacArthur & Wilson, 1967) is that the relative rate of migration between island pairs can be predicted by the size, relative orientation and distance of source islands. Gyllenhaal et al. (2020) tested this

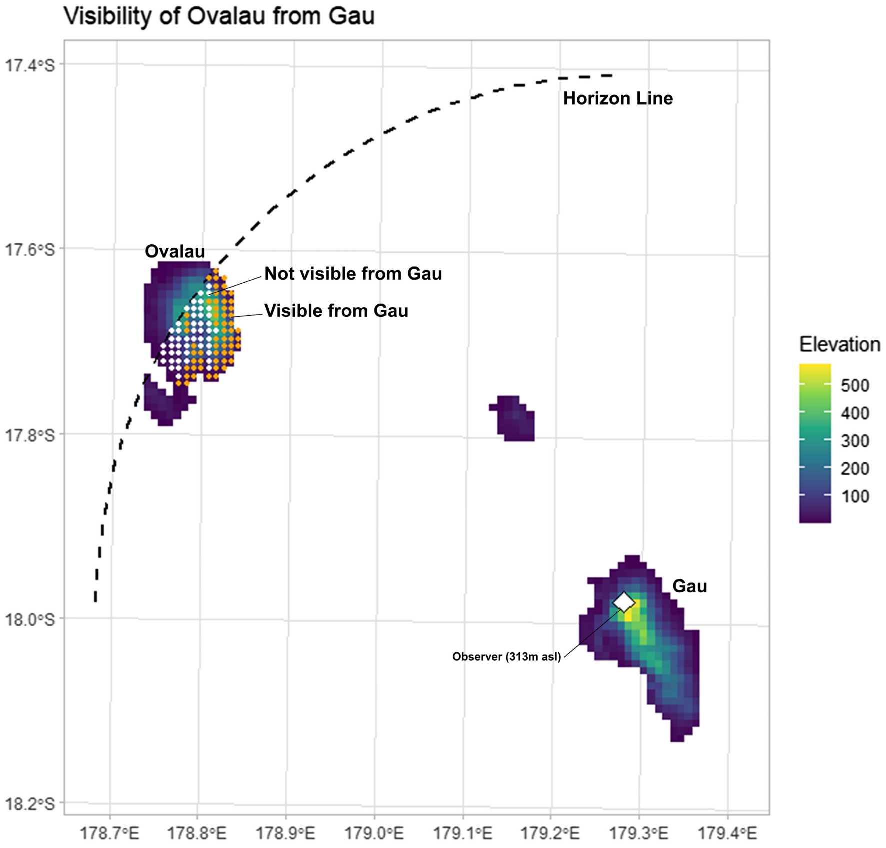


FIGURE 4 PleistoDist estimates the visibility of a destination island relative to an observer on an origin island by calculating the horizon distance and performing a viewshed analysis to estimate the visible nonoccluded area of the destination island, illustrated here with Ovalau and Gau islands, Fiji.

TABLE 1 Results of Mantel tests and dbRDA for *Amphiacusta sanctaecrucis* populations across the Virgin Islands for different metrics of geographic distance

Distance type	Mantel R^2	Mantel *p*-value	dbRDA R^2_{adj}	dbRDA *p*-value
Euclidean distance	0.228273	0.0521429	0.3509484	0.034779
Least-cost distance	0.2203824	0.0521409	0.1387593	0.3025617
Least shore-to-shore distance	0.0426482	0.1997118	0.4736347	0.00661
Centroid-to-centroid distance	0.0090014	0.2004748	0.5933486	0.007043
Mean shore-to-shore distance	0.0035279	0.2976187	−0.4337182	0.9366181

TABLE 2 Results of simple linear regressions between species richness and island area, for different angiosperm chorotypes and island area metrics

Chorotype	Present-day 2D area R^2_{adj}	*p*-value	AIC	Time-corrected 2D area R^2_{adj}	*p*-value	AIC
Total species richness	0.7621572	8.51e-17	22.043369	0.3917022	7.04e-7	68.9961019
Native nonendemics	0.7445056	4.80e-16	26.3768068	0.3873976	8.38e-7	70.1025982
Endemics	0.4888763	9.80e-9	81.6361191	0.2662759	7.45e-5	99.7121938

expectation by estimating the rates of interisland migration in the Fiji bush warbler *Horornis ruficapilla* between the four large islands of Fiji, concluding that rates of interisland migration are largely consistent with neutral expectations. This neutral expectation can now be easily and accurately calculated using PleistoDist while accounting for the effect of sea-level change over time.

Re-running this analysis using time cut-off of 115 kya, corresponding with the start of the last glacial period, for 40 sea-level depth intervals, we found that empirical ratios of migrants for $\frac{\textit{Kadavu} \rightarrow \textit{Viti Levu}}{\textit{Viti Levu} \rightarrow \textit{Kadavu}}$ broadly correspond with neutral expectations, suggesting that net migration rates are unlikely to have changed much over the last 115,000 years (Figure 5). In contrast, empirical

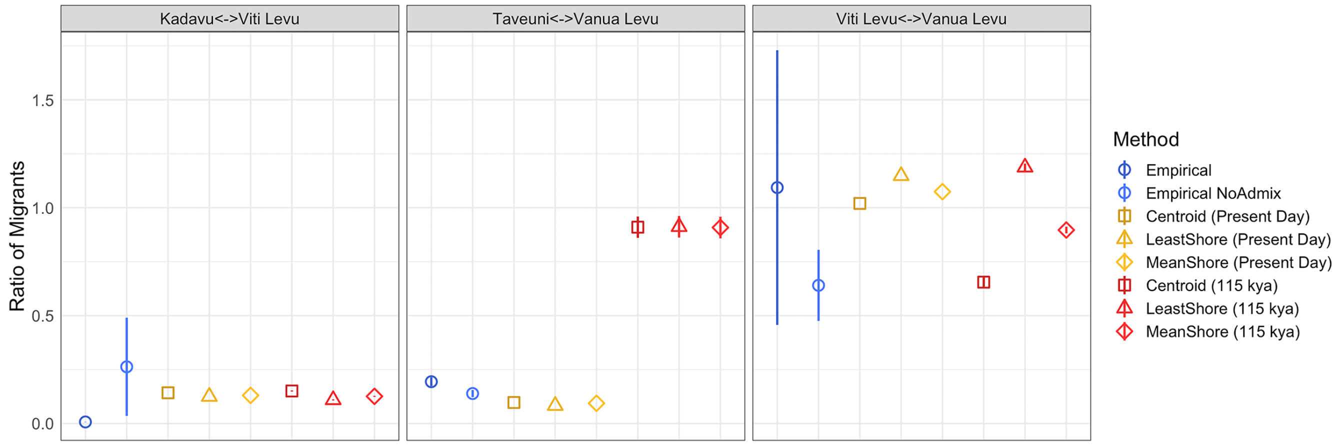


FIGURE 5 Comparison of empirical estimates of net interisland migration with contemporary and time-corrected neutral expectations from MacArthur and Wilson (1967), figure adapted from Gyllenhaal et al. (2020).

migration ratios for $\frac{\textit{Taveuni} \rightarrow \textit{Vanua Levu}}{\textit{Vanua Levu} \rightarrow \textit{Taveuni}}$ seem consistent with neutral expectations based on present-day sea levels but not expectations averaged over the last 115,000 years (Figure 5). The empirical net migration ratios for $\frac{\textit{Viti Levu} \rightarrow \textit{Vanua Levu}}{\textit{Vanua Levu} \rightarrow \textit{Viti Levu}}$ are challenging to interpret given the broad confidence intervals of the empirical data, but the mean empirical migration ratio from the model removing a putatively admixed individual is similar to the value inferred from the centroid-to-centroid distance model averaged over 115,000 years (Figure 5).

3.4 | Spatially explicit forward population genetic simulations

To demonstrate the utility of PleistoDist for spatially explicit simulations, we ran forward-in-time, spatially explicit Wright–Fisher simulations in SliM3 (Haller & Messer, 2019) across the Samoan archipelago using maps generated by PleistoDist, with a metapopulation size of 20,000, for 50,000 generations. We ran simulations both with and without sea-level change for eight mean dispersal distances, for 100 replicates per sea-level regime/dispersal distance combination (full model parameters in Supporting Information). As expected, F_{ST} was negatively correlated with dispersal distance (Figure 6), and π was positively correlated. The impact of accounting for change in sea level was most noticeable for islands that were much closer at glacial maxima (i.e. Savai'i and Upolu islands, Samoa), but not when dispersal distance was high.

To demonstrate the utility of PleistoDist for modelling simple archipelagic colonisations, we simulated the colonisation of the Solomon Archipelago using the SLiM GUI (Haller & Messer, 2019), with initial colonists arriving on Buka/Bougainville islands (Mayr & Diamond, 2001). To simulate an expanding colonising population, we used a non-Wright–Fisher simulation, starting with 50 individuals on the easternmost large island in the archipelago. We used a mean long-distance dispersal distance of ~46.7 km (100 pixels), an exponential long-distance dispersal kernel, and offspring long-distance dispersal probability of 1%. For all simulations (two shown at https://github.com/g33k5p34k/PleistoDistR/tree/main/simulation_scripts), Makira Island was colonised last due to its relative isolation and location at the far eastern end of the archipelago, demonstrating the utility of the script in generating null expectations against which complex empirical patterns can be compared.

3.5 | Parameterizing migration rates for backwards population genetic simulations

To demonstrate the utility of accounting for migration rate variation between nonconnected populations, we used msprime v1.0.0 (Baumdicker et al., 2022) to model dispersal between Viti Levu and Kadavu islands, Fiji. We used PleistoDist to estimate per interval migration rates using least shore-to-shore distance (Figure 2) and an exponential dispersal kernel with means of 0 (no dispersal), 10, 20, 40 and 80 km. We calculated population size by multiplying island area for each interval by a density of 10 individuals/km^2. We either held migration rates and population sizes constant (based on current sea level) or changed them based on sea level in intervals of 5000 years (2500 generations). The initial population split was set to 200,000 generations. At the end of the simulation, we calculated F_{ST} and per-island π for each sea-level regime. As with the SLiM simulations, the impact of sea-level change was more notable when dispersal was low or not present (Figure 7). These simulations also demonstrate how sea-level change and interisland dispersal can benefit π on less isolated small island populations (i.e. Kadavu).

4 | LIMITATIONS

Despite its broad utility, PleistoDist nonetheless relies on a simplification of Pleistocene sea-level change, and users should be aware of its limitations. One major assumption is that bathymetry remains constant, or changes at constant rates, throughout

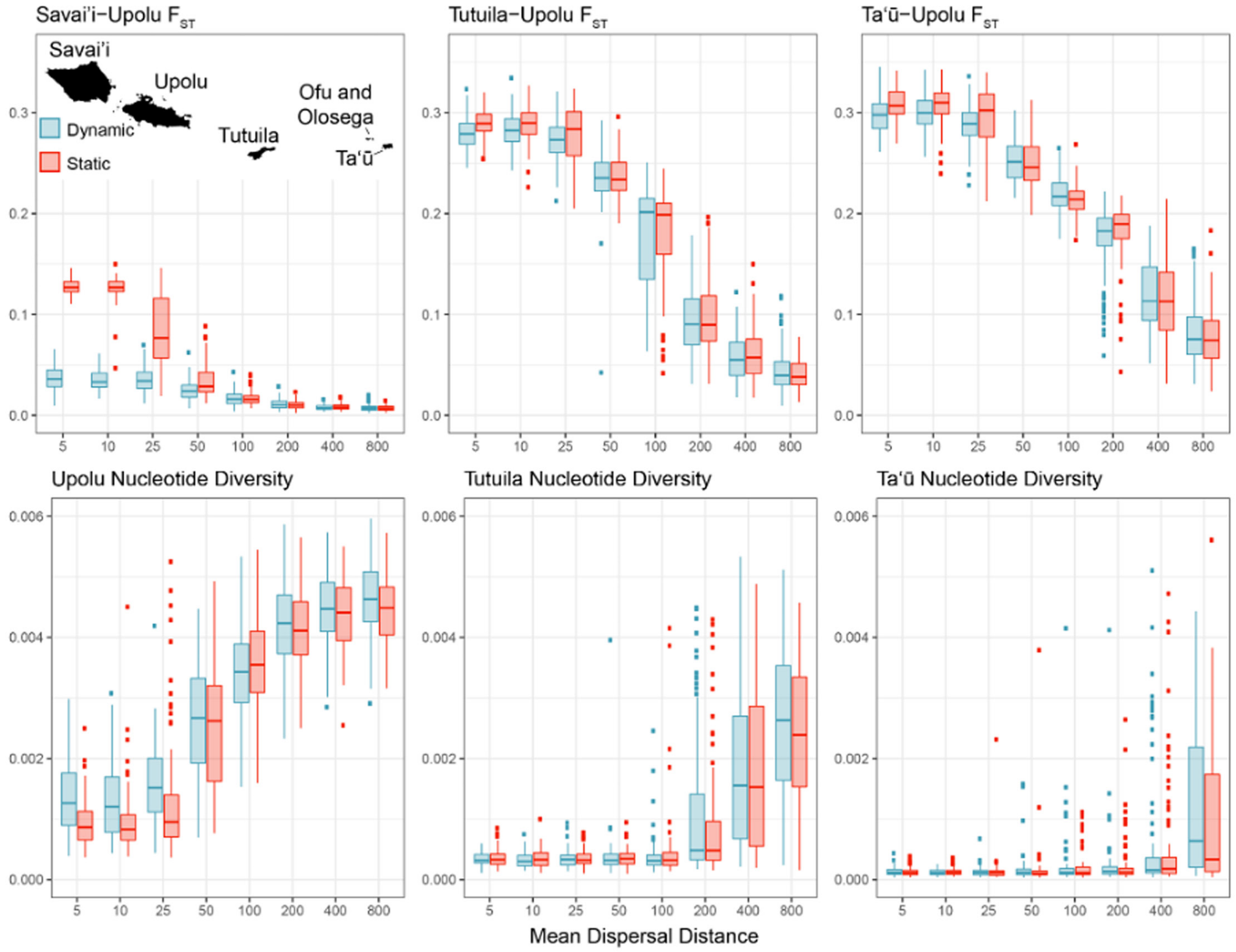


FIGURE 6 F_{ST} (top row) and π (bottom row) values from spatially explicit simulations across the Samoan Archipelago. Dispersal distance is listed in pixels (~4.78 pixels/km). Each dispersal distance tested has the results from the dynamic (left, blue) and static (right, red) sea-level models. Inset map has all islands included in the analysis labelled.

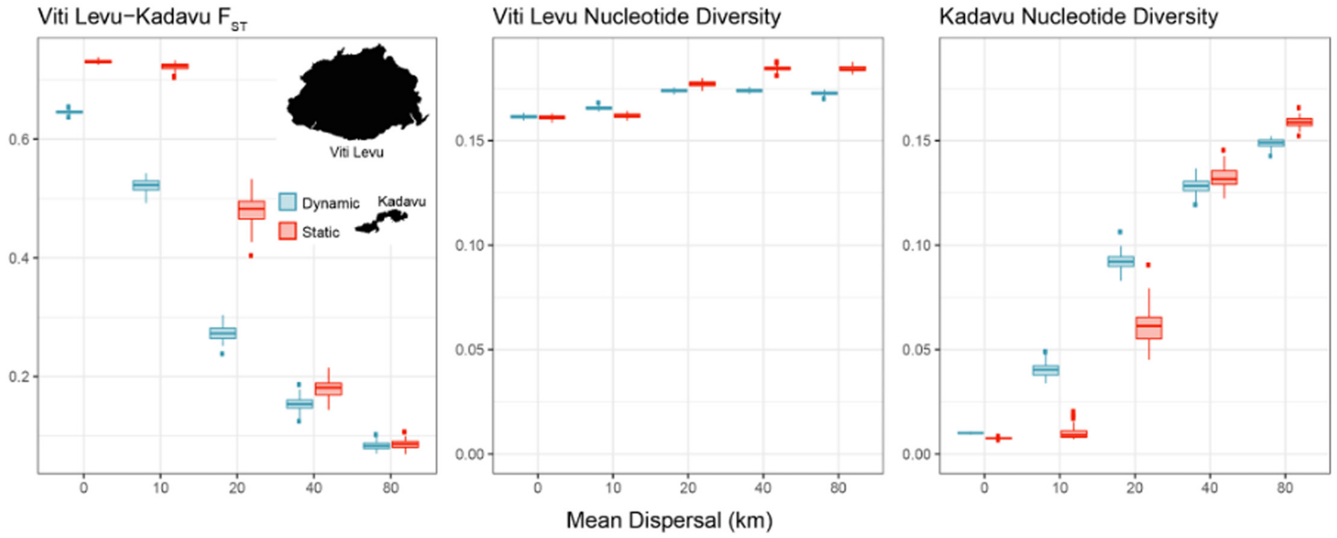


FIGURE 7 F_{ST} (left panel) and π (middle and right panels) values from msprime simulations for Viti Levu and Kadavu islands, Fiji. Each dispersal distance tested has the results from the dynamic (left, blue) and static (right, red) sea-level models.

the time-scale of the analysis, and PleistoDist therefore does not account for the effect of localised tectonic activity or transport-based processes such as sedimentation and erosion. For example, PleistoDist analyses of Taveuni island in Fiji with a cut-off time close to and exceeding 700 kya are unlikely to be accurate since the island likely emerged around that time (Cronin & Neall, 2001). Furthermore, although PleistoDist lets users account for region-wide uplift or subsidence effects, the cumulative effects of localised bathymetry changes are more likely to be amplified the further one goes back in time. Studies involving deep time reconstructions of island morphologies are therefore more likely to diverge from reality and may need to account for the increased uncertainty of deeper time slices.

Another limitation is the assumption that local sea levels can be accurately modelled by eustatic reconstructions. As demonstrated by Simaiakis et al. (2017), local gravitational and deformational effects of ice sheets can lead to local sea levels diverging from eustatic estimates, with sea levels exhibiting a 25-m difference between the northern and southern Aegean Sea islands during the LGM. While PleistoDist's inability to model local (isostatic) sea levels could explain the divergence between our model outputs and that of Hammoud et al. (2021), it also highlights the limitation of eustatic sea-level reconstructions in regions where ice sheets and other forces cause localised deviations in sea level. PleistoDist is therefore less likely to be accurate at high latitudes compared to sites located further away from Pleistocene ice sheets. This limitation can be overcome by using rasters generated with isostatic sea-level reconstructions such as those presented in De Groeve et al. (2022) instead of using the makemaps function.

5 | SUMMARY

Although simple in concept, PleistoDist provides users with the ability to calculate island metrics that account for the effects of Pleistocene sea-level change, allowing biogeographers to test multiple hypotheses of evolution and community assembly when coupled with georeferenced empirical data. The flexibility and extensibility of the software, coupled with its numerous possible use cases, should facilitate the development of more quantitative approaches to the study of island biogeography, and a better understanding of the patterns of species diversification across island archipelagos.

AUTHOR CONTRIBUTIONS

David J. X. Tan, Ethan F. Gyllenhaal and Michael J. Andersen conceived the methodology and concept. David J. X. Tan and Ethan F. Gyllenhaal developed and tested case studies and applications. David J. X. Tan developed the package and led the writing of the manuscript, with substantial input from all authors.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

PleistoDist is a free and open-source package written in R, available at https://github.com/g33k5p34k/PleistoDistR (Tan & Gyllenhaal, 2022). The case studies described above are available as vignettes from https://davidbirdtan.com/pleistodist/ and archived on Zenodo at https://doi.org/10.5281/zenodo.7241068 (Tan, 2022). The original package version (v1.1.0) is available from Zenodo at https://doi.org/10.5281/zenodo.7154836. We are submitting PleistoDist to the Comprehensive R Archive Network (CRAN), where it will also be available for future download.

REFERENCES

Ali, J. R., & Aitchison, J. C. (2014). Exploring the combined role of eustasy and oceanic Island thermal subsidence in shaping biodiversity on the Galápagos. *Journal of Biogeography*, *41*(7), 1227–1241.

Baumdicker, F., Bisschop, G., Goldstein, D., Gower, G., Ragsdale, A. P., Tsambos, G., Zhu, S., Eldon, B., Ellerman, E. C., Galloway, J. G., Gladstein, A. L., Gorjanc, G., Guo, B., Jeffery, B., Kretzschumar, W. W., Lohse, K., Matschiner, M., Nelson, D., Pope, N. S., … Kelleher, J. (2022). Efficient ancestry and mutation simulation with msprime 1.0. *Genetics*, *220*(3), 1–19. https://doi.org/10.1093/genetics/iyab229

Bintanja, R., & van de Wal, R. S. W. (2008). North American ice-sheet dynamics and the onset of 100,000-year glacial cycles. *Nature*, *454*(7206), 869–872.

Cronin, S. J., & Neall, V. E. (2001). Holocene volcanic geology, volcanic hazard, and risk on Taveuni, Fiji. *New Zealand Journal of Geology and Geophysics*, *44*(3), 417–437.

Cros, E., Chattopadhyay, B., Garg, K. M., Ng, N. S. R., Tomassi, S., Benedick, S., Edwards, D. P., & Rheindt, F. E. (2020). Quaternary land bridges have not been universal conduits of gene flow. *Molecular Ecology*, *29*(14), 2692–2706.

De Groeve, J., Kusumoto, B., Koene, E., Kissling, W. D., Seijmonsbergen, A. C., Hoeksema, B. W., Yasuhara, M., Norder, S. J., Cahyarini, S. Y., van der Geer, A., Meijer, H. J. M., Kubota, Y., & Rijsdijk, K. F. (2022). Global raster dataset on historical coastline positions and shelf sea extents since the Last Glacial Maximum. *Global Ecology and Biogeography: A Journal of Macroecology*, *31*(11), 2162–2171.

Gleason, H. A. (1922). On the relation between species and area. *Ecology*, *3*(2), 158–162.

Gyllenhaal, E. F., Mapel, X. M., Naikatini, A., Moyle, R. G., & Andersen, M. J. (2020). A test of Island biogeographic theory applied to estimates of gene flow in a Fijian bird is largely consistent with neutral expectations. *Molecular Ecology*, *29*(21), 4059–4073.

Haller, B. C., & Messer, P. W. (2019). SLiM 3: Forward genetic simulations beyond the Wright–Fisher model. *Molecular Biology and Evolution*, *36*, 632–637. https://academic.oup.com/mbe/article-abstract/36/3/632/5229931

Hammoud, C., Kougioumoutzis, K., Rijsdijk, K. F., Simaiakis, S. M., Norder, S. J., Foufopoulos, J., Georgopoulou, E., & Van Loon, E. E. (2021). Past connections with the mainland structure patterns of insular species richness in a continental-shelf archipelago (Aegean Sea, Greece). *Ecology and Evolution*, *11*(10), 5441–5458.

Kealy, S., Louys, J., & O'Connor, S. (2017). Reconstructing palaeogeography and inter-Island visibility in the Wallacean archipelago during the likely period of Sahul colonization, 65–45 000 years ago. *Archaeological Prospection*, *24*(3), 259–272.

Kimura, M., & Weiss, G. H. (1964). The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics*, *49*(4), 561–576.

Legendre, P., Fortin, M.-J., & Borcard, D. (2015). Should the Mantel test be used in spatial analysis? *Methods in Ecology and Evolution/British Ecological Society*, *6*(11), 1239–1247.

Leonard, J. A., den Tex, R.-J., Hawkins, M. T. R., Muñoz-Fuentes, V., Thorington, R., & Maldonado, J. E. (2015). Phylogeography of vertebrates on the Sunda Shelf: A multi-species comparison. *Journal of Biogeography*, *42*(5), 871–879.

Lohman, D. J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P. K. L., Shih, H.-T., Carvalho, G. R., & von Rintelen, T. (2011). Biogeography of the Indo-Australian Archipelago. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 205–226.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.

Mayr, E., & Diamond, J. M. (2001). *The birds of Northern Melanesia: Speciation, ecology & biogeography*. Oxford University Press.

Norder, S. J., Baumgartner, J. B., Borges, P. A. V., Hengl, T., Kissling, W. D., van Loon, E. E., & Rijsdijk, K. F. (2018). A global spatially explicit database of changes in Island palaeo-area and archipelago configuration during the late Quaternary. *Global Ecology and Biogeography: A Journal of Macroecology*, *27*(5), 500–505.

Papadopoulou, A., & Knowles, L. L. (2015). Genomic tests of the species-pump hypothesis: Recent Island connectivity cycles drive population divergence but not speciation in Caribbean crickets across the Virgin Islands. *Evolution; International Journal of Organic Evolution*, *69*(6), 1501–1517.

Reilly, S. B., Stubbs, A. L., Karin, B. R., Bi, K., Arida, E., Iskandar, D. T., & McGuire, J. A. (2019). Leap-frog dispersal and mitochondrial introgression: Phylogenomics and biogeography of Limnonectes fanged frogs in the Lesser Sundas Archipelago of Wallacea. *Journal of Biogeography*, *46*(4), 757–769.

Rijsdijk, K. F., Hengl, T., Norder, S. J., Otto, R., Emerson, B. C., Ávila, S. P., López, H., van Loon, E. E., Tjørve, E., & Fernández-Palacios, J. M. (2014). Quantifying surface-area changes of volcanic islands driven by Pleistocene sea-level cycles: Biogeographical implications for the Macaronesian archipelagos. *Journal of Biogeography*, *41*(7), 1242–1254.

Simaiakis, S. M., Rijsdijk, K. F., Koene, E. F. M., Norder, S. J., Van Boxel, J. H., Stocchi, P., Hammoud, C., Kougioumoutzis, K., Georgopoulou, E., Van Loon, E., Tjørve, K. M. C., & Tjørve, E. (2017). Geographic changes in the Aegean Sea since the Last Glacial Maximum: Postulating biogeographic effects of sea-level rise on islands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *471*, 108–119.

Simberloff, D. S. (1974). Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics*, *5*(1), 161–182. https://doi.org/10.1146/annurev.es.05.110174.001113

Tan, D. J. X. (2022). PleistoDist Vignettes. *Zenodo*. https://doi.org/10.5281/zenodo.7241068

Tan, D. J. X., & Gyllenhaal, E. (2022). PleistoDist v1.1.0 (v1.1.0). Zenodo. https://doi.org/10.5281/zenodo.7154836

Wallace, A. R. (1869). *The Malay Archipelago: The land of the orang-utan, and the bird of paradise*. Macmillan and Co.

SUPPORTING INFORMATION

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

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