Research Article

Dispersal and adaptive radiation of *Bidens* (Compositae) across the remote archipelagoes of Polynesia

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Received 4 September 2020; Accepted 29 October 2020; Article first published online 9 November 2020

Abstract The genus *Bidens* (Compositae) comprises c. 230 species distributed across five continents, with the 41 Polynesian species displaying the greatest ecomorphological variation in the group. However, the genus has had a long and complicated taxonomic history, and its phylogenetic and biogeographic history are poorly understood. To resolve the evolutionary history of the Polynesian *Bidens*, 152 individuals representing 91 species were included in this study, including 39 of the 41 described species from Polynesia. Four chloroplast and two nuclear DNA markers were utilized to estimate phylogenetic relationships, divergence times, and biogeographic history. *Bidens* was found to be polyphyletic within *Coreopsis*, consistent with previous assessments. The Polynesian radiation was resolved as monophyletic, with the initial dispersal into the Pacific possibly from South America to either the Hawaiian or Marquesas Islands. From the Marquesas, *Bidens* dispersed to the Society Islands, and ultimately to the Austral Islands. The initial diversification of the crown group in the Pacific is estimated to have occurred ~1.63 mya (0.74–2.72, 95% HPD), making Polynesian *Bidens* among the youngest and most rapid plant diversification events documented in the Pacific. Our findings suggest that relatively rare long-distance dispersal and founder-event speciation, coupled with subsequent loss of dispersal potential and within-island speciation, can explain the repeated and explosive adaptive radiation of *Bidens* throughout the archipelagoes of Polynesia.

Key words: Asteraceae, Coreopsideae, ecology, evolution, extinction, geologic history, Heliantheae Alliance, Island biogeography, speciation.

1 Introduction

The publication of The Theory of Island Biogeography (MacArthur & Wilson, 1963, 1967), and subsequently Island Biology (Carlquist, 1974), inspired multiple generations of scientists to formally study the ecology and evolution of island taxa. Among other taxa, Carlquist studied the diversity and distribution of the Compositae genus Bidens L. in the remote archipelagoes of Polynesia, where most Bidens species are single-island endemics. Upon examination of the fruit morphology (achenes, which are indehiscent dry fruits, that likely attach to bird feathers with barbed awns as a means of long-distance dispersal), Carlquist found what he considered to be a perfect example of the loss of dispersal potential, a common pattern in island taxa (Carlquist, 1966a, 1974). Polynesian *Bidens* have a wide range of achene morphologies as compared with their mainland relatives with traits that reduce their dispersibility, such as vestigial or lost barbs, as well as shortened awn length (Carlquist, 1966a). The Polynesian *Bidens*, therefore, present an apparent paradox, in that they appear to have lost dispersal potential in the achenes, relative to their continental ancestors, but have widely dispersed and evolved into one of the largest plant radiations in Polynesia, with 41 described species distributed throughout the Hawaiian, Marquesas, Society, and Austral Islands. MacArthur & Wilson (1967) considered these remote archipelagoes, among others, to be in what they coined the "radiation zone" where *in situ* speciation is

expected to play a relatively large role, in addition to immigration and local extinction rates, in explaining island biodiversity patterns. However, the evolutionary history of the Polynesian *Bidens* radiation has yet to be adequately resolved.

Bidens and the closely related genera Coreopsis L., Coreocarpus Benth., Cosmos Cav., Dahlia Cav., Thelesperma Less., and several smaller genera are part of the Compositae tribe Coreopsideae (Heliantheae Alliance). This tribe has approximately 550 species with a worldwide distribution; however, most species are found in the Americas. Panero (2006) provided descriptions of these genera, but there has been no comprehensive treatment of either Bidens or Coreopsis. Bidens is the largest genus of the tribe, with estimates of 150-235 species (Sherff, 1937; Strother & Weedon, 2006), but the monophyly of the genus and number of species are in doubt. Attempts to develop a phylogenetic hypothesis for the tribe using morphological characters have resulted in limited resolution (Ryding & Bremer, 1992; Karis & Ryding, 1994), prompting a number of researchers to use molecular techniques to address their evolutionary history.

In a phylogenetic assessment of Bidens and Coreopsis, based solely on the nuclear ribosomal internal transcribed spacer (ITS), Kim et al. (1999) included 50 ingroup taxa, of which two species were from the Hawaiian Islands, and found a split between north temperate and subtropical Bidens within Coreopsis, suggesting that Bidens is polyphyletic and Coreopsis is paraphyletic. The two Hawaiian species were placed in a clade with Bidens pilosa from Mexico (Kim et al., 1999). This study was followed by Ganders et al. (2000), who used data from the ITS region and included three unidentified Bidens species from the Marquesas and seven taxa from the Hawaiian Islands, of which two were purported hybrids. Their results agreed with the split between north temperate and subtropical Bidens and led to the conclusion that the continental sister group of Polynesian Bidens appeared to be a group of Central American herbaceous species with determinate growth. This suggests that the woodiness and indeterminate growth found in Polynesian Bidens are apomorphic character states not found in their ancestors. In addition, the study by Ganders et al. (2000) found support for the Marquesan taxa nested within the Hawaiian radiation, indicating that the Polynesian radiation originated in the Hawaiian Islands before dispersal to the South Pacific. Ganders et al. (2000) also indicated that an unknown species collected on Starbuck Island (Line Islands in the Central Pacific) was not a part of the main Polynesian radiation. Lastly, their study suggested that a clade containing B. pilosa and B. alba from Mexico and the Caribbean was sister to the Polynesian species (other than the Starbuck Island taxon), but this relationship had low branch support. Kimball & Crawford (2004) further documented that neither Bidens nor Coreopsis are monophyletic, and that some elements of Coreopsis are more closely related to other genera of Coreopsideae than they are to other Bidens or Coreopsis. Their ITS tree had two Hawaiian taxa that were recovered as the sister group to an unresolved clade consisting of B. alba, B. pilosa, and B. hintonii, but the grouping of these two clades was also not well supported. The goal of their study was to elucidate the

groups within Bidens and Coreopsis and produced support for many of the clades, but there was a relatively little structure among them. Mort et al. (2008) used the ITS region and added two chloroplast markers (*matK* and *trnL*-F), and found that the monophyly of Bidens and Coreopsis was not supported; however, this study did not include any Pacific taxa. Knope et al. (2012) sampled all 19 endemic Hawaiian species and included Bidens henryi Sherff and one undescribed Marguesan species from Ganders et al. (2000). They found further evidence based on ITS that the Hawaiian radiation and the two Marguesan species were descendants of a single recent common ancestor that colonized the Pacific from in or around Mexico based on the placement of B. pilosa and B. alba as the sister clade, supporting the results of previous studies. However, the direction of colonization between the Hawaiian and Marquesan Islands was unresolved. Most recently, Knope et al. (2020) sequenced complete chloroplast genomes and the nuclear ribosomal complex for 18 of the 19 endemic Hawaiian Bidens species and four outgroup species, including B. pilosa and B. alba. This genomic-level sequencing provided the first fully bifurcating phylogenetic hypothesis for the Hawaiian taxa. However, the authors also found strong nuclear-plastome conflict, indicating that ongoing hybridization and/or incomplete lineage sorting has potentially played an important role in the evolution of the group.

The goals of this project were to (i) test the monophyly of Bidens and of Coreopsis, the monophyly of the Polynesian Bidens radiation, and the monophyly of the individual archipelago-level radiations; (ii) determine the location of the most recent common ancestor(s) of the Polynesian Bidens species; and (iii) determine the timing and sequence of colonization events among the remote archipelagoes of the Pacific. These goals led us to a 15-year collecting effort of the Polynesian members (Polynesia is the geographic area of the Pacific generally defined by connecting the three points of the Hawaiian Islands, New Zealand, and Easter Island) of the tribe along with a broad sampling of related genera occurring in the Pacific Basin and elsewhere. This resulted in largely complete taxon sampling of the Polynesian Bidens radiation, and by far the greatest sampling of Bidens, Coreopsis, and related taxa undertaken to date.

2 Material and Methods

2.1 Taxon sampling

Sampling within *Bidens* was built on the earlier work of Knope et al. (2012), adding 74 taxa from across the distributional range of the genus (Africa, North America, Central America, South America, Asia, the Caribbean, and the Pacific; Appendix I). Multiple accessions of widely distributed species were included, when possible. Representatives from genera that have been shown to be closely related or intermingled with *Bidens* (*Coreopsis, Cosmos, Coreocarpus, Fitchia, Oparanthus, Henricksonia,* and *Glossocardia*) according to earlier phylogenetic studies (e.g., Kimball & Crawford, 2004; Mort et al., 2008) were included to root the phylogeny and to test for monophyly. In total, 152 accessions representing 91 species and 103 taxa were incorporated in this study (82 *Bidens,* 13 *Coreopsis,* two each of *Coreocarpus*

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and Fitchia, and one each of Cosmos, Oparanthus, Henricksonia, and Glossocardia). Following Kim et al. (1999) and Kimball & Crawford (2004), we refer to the clade of Bidens that includes the Pacific species and closely related taxa as Bidens sensu stricto (s.s.) and the more distantly related north temperate Bidens as Bidens sensu lato (s.l.). Leaf tissue was collected in the field and preserved in silica gel, and voucher specimens were deposited in various herbaria (see Appendix I).

2.2 Molecular methods

Genomic DNA was extracted from silica-dried leaf tissue using either Qiagen DNeasy Plant Mini Kits (Qiagen, Valencia, CA, USA) or a modified CTAB procedure (Doyle & Doyle, 1987). The following protocol of Knope et al. (2012; appendix S1) was used for amplifying the nuclear ribosomal internal and external transcribed spacer (ITS and ETS) regions, as well as the *ndhC-trnV*, *rpl32-trnL*, *psbA-trnH*, and *trnQ-rps1*6 chloroplast (cp) regions. Double-stranded DNA was amplified in 25- μ L volume reactions. Each polymerase chain reaction (PCR) contained 18.1- μ L PCR water, 2.5- μ L 10× Accuzyme Buffer (Bioline USA Inc., Taunton, MA, USA), 1- μ L 10-mM dNTP, 1- μ L 25-mM MgCl₂, 1 μ L 10 mM of each primer for ITS and ETS amplifications, and 0.3- μ L Accuzyme DNA Polymerase (Bioline USA Inc., Taunton, MA, USA).

Amplifications were obtained for ITS with the primer pair ITS-4 (White et al., 1990) and ITS-5a (Stanford et al., 2000). Reactions were run with an initial denaturation temperature of 96 °C for 2 min, and subsequent cycles at 96 °C for 60 s, 51 °C for 60 s, and 72 °C for 45 s with an additional 4 s each cycle, for 35 cycles. PCR was performed for the ETS locus with the primer pair 18S-ETS and ETS-Hel-1 (Baldwin & Markos, 1998). Thermal cycling was performed with an initial denaturation temperature of 94 °C for 2 min, and subsequent cycles at 94 °C for 60 s, 63 °C for 60 s, and 72 °C for 2 min with an additional 4s each cycle, for 39 cycles and a final extension of 72 °C for 7 min. Amplifications were obtained for plastid loci with the following primer pairs: trnV^(uacX2)_ndhC, rpl32f-trnL^(uug), trnQ-rps16, rpl32r-ndhF, and trnH^(gug)-psbA (Shaw et al., 2005,). Reactions for plastid loci were run with an initial denaturation of 80 °C for 5 min, and subsequent cycles at 95 °C for 60 s, 50-55 °C for 60 s, ramping at 65% to 65 °C for 4 min, for 30 cycles with a final extension of 65 °C for 5 min (Shaw et al., 2007). PCR amplification of the psbAtrnH cp region differed only in that the initial ramp was converted to a touchdown of 94 °C for 30 s, 56 °C for 30 s, and 72 $^{\circ}$ C for 60 s (and repeated 10×) (Shaw et al., 2005).

PCR products were visualized by electrophoresis in 1% agarose gels with subsequent GelStar DNA staining (Lonza, Rockland, ME, USA) and UV transillumination. PCR products were cleaned of unincorporated dNTPs and excess primer by ExoSap-It enzymatic reactions (USB Corporation, Cleveland, OH, USA) following the manufacturer's protocol. Double-stranded PCR products were sequenced directly in both directions with the same primers used for the PCR amplifications. DNA sequencing was performed using the Applied Biosystems (ABI) 3730XL DNA Analyzer capillary electrophoresis-based sequencer, using BigDye Terminator v3.1 for cycle sequencing reactions (Applied Biosystems, Carlsbad, CA, USA). Cycle sequencing products were cleaned

using NaAc + EDTA + EtOH, according to ABI manufacturer's protocol. Hi-Di formamide was used to dissolve the precipitated DNA in 96-well plates, and then loaded on a 3730XL sequencer for electrophoresis analysis. The raw data were automatically processed using KB basecaller to generate chromatograph and quality files.

All sequences were edited in SEQUENCHER 4.8 (Gene Codes Corp., Ann Arbor, MI, USA) and were aligned with CLUSTALW (Larkin et al., 2007) or MUSCLE (Edgar, 2004), followed by manual editing by eye. Alignments and tree files are available upon request. Double peaks in nuclear gene sequences, reflecting heterozygous positions, were coded with International Union of Pure and Applied Chemistry (IUPAC) degeneracy codes and were treated as polymorphisms. Target sequence authenticity was verified by Basic Local Alignment Search Tool (BLAST) searching sequences in the National Center for Biotechnology Institute (NCBI) GenBank database for appropriate target locus and taxonomic affinity. All sequences have been deposited in GenBank (Appendix I).

2.3 Data partitioning, model testing, and maximum likelihood (ML)

The search for the best-fit partitioning scheme, model testing, and ML analyses were all conducted in the CIPRES Science Gateway v. 3.3 (Miller et al., 2010). PartitionFinder v. 2.1.1 (Guindon et al., 2010; Lanfear et al., 2017) was used to determine the appropriate partitioning scheme for the concatenated alignment. We used the greedy algorithm (Lanfear et al., 2012) and the Akaike information criterion (AIC) to find the optimal scheme from nine partitions that were determined a priori based on coding and non-coding regions. The best scoring partition scheme (Table S1) was used for ML and Bayesian inference (BI). The best-fit model of nucleotide evolution for each genic region was selected using the AIC criterion as implemented in jModelTest v. 2.1.6 (Darriba et al., 2012; see Table S1). The total number of characters, number of variable characters, and number and percentage of parsimony-informative characters were calculated in PAUP* v. 4.0a (Swofford, 2020). ML analyses were conducted with RAxML v. 8.2.12 (Stamatakis, 2006; Stamatakis et al., 2008) using the GTRGAMMA model of sequence evolution. The search for the optimal ML tree was done using default search parameters and a rapid bootstrap analysis of 1000 replicates. Clades with bootstrap support $(BS) \ge 80\%$ were considered well supported. ML analyses were initially conducted on individual genic regions to assess congruence, with areas of conflict determined by examining the placement of individual taxa on each gene tree. Relationships were considered incongruent if the placement of taxa varied among the individual gene trees and exhibited BS values \geq 80%. An additional ML analysis was conducted on the concatenated (nuclear + cp) partitioned data set. Multiple RAxML runs (using a random starting seed to test the consistency of tree topology and node support) produced identical results.

2.4 Bayesian inference and divergence times

BI and divergence times were estimated using a timecalibrated phylogeny generated in BEAST v. 2.6.1 (Drummond et al., 2012), as implemented in the CIPRES Science Gateway v. 3.3 (Miller et al., 2010). The tree was modeled under a Yule process using a random starting tree and an uncorrelated relaxed clock with a lognormal distribution. Substitution model parameters for each of the six partitions were based on the estimated best-fit model of nucleotide evolution. Two independent MCMC analyses were run for 300 million generations each and sampled every 10,000 generations. The phylogeny was constrained using a combination of geologic ages and secondary calibration points. The geological history of the Hawaiian Islands is well known, being formed in a linear chronological sequence (with islands increasing in age toward the WNW from Hawai'i Island) by a hotspot in the Pacific plate (e.g., Price & Clague, 2002). The Hawai'i Island calibration point was assigned a uniform distribution, with an upper bound of 0.46 Ma (corresponding to the age of the oldest surface rocks, as estimated by Obbard et al., 2012) and no lower bound. For the second geologic calibration point, we used the age of Socorro Island, which is a volcanic island off the coast of Mexico. The Socorro Island calibration point was assigned a uniform distribution, with an upper bound of 0.54 Ma (corresponding to the age of the oldest surface rocks, as estimated by Bohrson & Reid, 1998) and no lower bound. As an additional calibration point, we used the date estimated by Knope et al. (2020) for the Hawaiian Bidens crown node. We used a lognormal distribution with a mean of 1.82 Ma and a standard deviation of 0.3 (approximating the 95% highest posterior density of Knope et al., 2020). Convergence of runs and adequacy of MCMC sampling were checked using Tracer v.1.6 (Rambaut et al., 2014), ensuring that ESS values were >200 for each parameter. After removing 25% of the trees as burnin, a maximum clade credibility tree was constructed using TreeAnnotator v. 2.3.2 (Drummond et al., 2012). The maximum clade credibility tree was then visualized in FigTree v. 1.4.2, 2014 (http://tree.bio.ed.ac.uk/software/ figtree/), along with mean node heights and the 95% highest posterior density interval of each node (Fig. 1).

2.5 Ancestral range estimation

The package BioGeoBEARS (BioGeography with Bayesian (and likelihood) Evolutionary Analysis in R Scripts'; Matzke, 2013) was used to estimate ancestral areas for Bidens s.s. under the DEC (Dispersal-Extinction-Cladogenesis; Ree et al., 2005; Ree & Smith,), DIVALIKE (Dispersal-Vicariance Analysis; Ronquist,), and BayArea (Bayesian Inference of Historical Biogeography for Discrete Areas; Landis et al., 2013) models in the R statistical computing environment (R Core Team, 2019). Each of the different models allows for a subset of biogeographic processes (e.g., dispersal, extinction, vicariance), which are implemented in a maximum likelihood framework. To each of these base models, we also added two free parameters: founder events ("j" parameter; Matzke, 2014) and dispersal distance ("x" parameter; Van Dam & Matzke, 2016). Distances between areas were determined using ArcGIS software (ESRI, 2011), with x being defined as the distance between the centers of two areas measured in kilometers. Distances were then rescaled (dividing by the smallest distance), such that the units of measurement would not influence the outcome of likelihood searches.

The ultrametric BEAST tree was pruned to include only a single representative of each taxon. Taxa were assigned to a set of 10 geographic areas based on collection localities: Africa, Asia, North America, South America, Central America, Line Islands, Society Islands, Austral Islands, Marquesas Islands, and the Hawaiian Islands. We set the maximum number of areas that can be explored together in state space for any given taxon to three (based on species distribution data), and then compared these models for statistical fit using the AIC and a Likelihood Ratio Test (LRT). Lastly, we used BioGeoBEARS to perform a biogeographic stochastic mapping (BSM) analysis (Matzke, 2016). We conducted 500 stochastic mapping simulations on the best model to get event counts for biogeographic processes involving anagenesis (range switching and range expansion dispersal) and cladogenesis (narrow sympatry, subset sympatry, widespread sympatry, vicariance, and founder events), and to infer the direction of dispersal events.

3 Results

3.1 Phylogenetic relationships

The results of the independent ML analyses were largely congruent; none of the relationships that differed between trees were well supported (>80 BS) and the majority of those that differed below this threshold were between closely related taxa (i.e., at the tips of tree), such that they did not affect the interpretation of relationships among major clades and inference of biogeographical patterns. The phylogenetic structure was greatly improved with the concatenation of the six gene regions, relative to that achieved with individual genes; we, therefore, focus on results from the concatenated data set for the remainder of this paper. The concatenated matrix consisted of 5737 bp of aligned sequence data, with 152 accessions representing the 103 taxa of Bidens, Coreopsis, Coreocarpus, Fitchia, Cosmos, Oparanthus, Henricksonia, and Glossocardia. Summary statistics for each marker are presented in Table 1.

Our phylogenetic results largely corresponded with those from earlier studies, with Bidens being polyphyletic and Coreopsis being both polyphyletic and paraphyletic (Fig. 2). At the base of the tree, there exists two clades that are strongly supported as sister to one another in the ML analysis (100 BS), but weakly supported in the BI analysis (53 PP; Fig. 2, node 1), and comprise taxa from N. America. Clade 2 (Fig. 2, node 2) is weakly supported in both the ML (73 BS) and BI (0.79 PP) analyses, and contains Cosmos bipinnatus (Mexico), seven species of Coreopsis (Mexico and N. America), Glossocardia bidens (Australia), Bidens aurea (N. America), Henricksonia mexicana (Mexico), Oparanthus hivoanus (Marquesas), and the two Fitchia species (Society Islands and Cook Islands). Clade 3 (Fig. 2, node 3) is strongly supported (100 BS, 1.0 PP; Fig. 2) and comprises the remaining N. American Coreopsis that are strongly supported as a clade (96 BS, 1.0 PP; Fig. 2, node 4), as well as most of the remaining North American Bidens and B. cernua from China (100 BS, 1.0 PP; Fig. 2, node 5).

At the base of Bidens s.s., there exist three African taxa, with *B. schimperi* strongly supported as sister to all remaining *Bidens* (100 BS, 0.91 PP; Fig. 2, node 6). *Bidens prestinaria* and



Fig. 1. Photos of representative taxa from Pacific archipelagoes are outlined and colored corresponding to their archipelago; islands are not to scale. Islands and islets that do not contain *Bidens* species are filled with gray. Taxa in photos are as follows: Hawaiian Islands: **A**, O'ahu endemic *B. asymmetrica* (D. Eickhoff); **B**, *B. campylotheca* subsp. *campylotheca* (J. VanDeMark); **C**, Maui Nui endemic *B. mauiensis* (F. and K. Starr); **D**, *B. hillebrandiana* subsp. polycephala from Maui Nui (F. and K. Starr); **E**, endangered Kaua'i endemic *B. cosmoides* (T. Kroessig); **F**, critically endangered Kaua'i endemic *B. sandvicensis* subsp. *confusa* (M. Clark); **G**, vulnerable Maui Nui endemic *B. micrantha* subsp. *micrantha* (F. and K. Starr); and **H**, Hawai'i Island endemic *B. menziesii* subsp. *filiformis* (J. Latsha). Marquesas islands: **I**, Fatu Hiva endemic *B. wichmanii* (F. Jacq); J, Eiao and Hatu Taa endemic *B. beckiana* (F. Jacq); **K**, Hiva Oa and Tahuata endemic *B. henryi* (J-Y. Meyer); and **L**, *B. polycephala* (J-Y. Meyer). Society Islands: **M**, Tahiti endemic *B. orofenensis* (J-Y. Meyer); **N**, Ra'iātea endemic *B. raiateensis* (F. Jacq); and **O**, *B. australis* (J-Y. Meyer). Austral Islands: **P**, Rapa Iti endemic *B. meyeri* (J-Y. Meyer).

B. pachyloma are strongly supported as sister (100 BS, 1.0 PP; Fig. 2), which, in turn, are placed but not supported as sister to all remaining taxa (60 BS, 74 PP; Fig. 2, node 7). A clade comprising eight taxa from five geographic areas is then

strongly supported as sister to all remaining taxa (95 BS, 0.99 PP; Fig. 2, node 8). Within this strongly supported clade (100 BS, 1.0 PP; Fig. 2, node 9), *Bidens sp.* from the Line Islands is strongly supported as belonging to a clade with *B. cynapifolia*

| Summary statistic | ETS | ITS | psbA-trnH | rpl32-trnL | trnQ-rps16 | ndhC-trnV |
|-----------------------|------|-----|-----------|------------|------------|-----------|
| Total length (bp) | 1221 | 705 | 509 | 1049 | 1166 | 1087 |
| Variable sites (n) | 663 | 362 | 194 | 457 | 362 | 286 |
| Informative sites (n) | 469 | 278 | 116 | 258 | 163 | 160 |
| Informative sites (%) | 38 | 39 | 23 | 25 | 14 | 15 |
| Coverage (%) | 100 | 100 | 96 | 88 | 86 | 92 |

Table 1 Summary statistics of nuclear and plastid data sets



Fig. 2. The Bayesian chronogram from the concatenated partitioned analysis conducted in BEAST (basal branching lineages only). Blue bars represent the 95% highest posterior density, and node support is indicated as maximum likelihood bootstrap support (BS) and Bayesian posterior probabilities (PP). Support values are not shown for nodes that had <70 BS and <90 PP. A dash indicates that the branch was not supported in one of the analyses (<50% BS or <0.50 PP values). Node numbers are shown in black circles and taxa are color-coded by geographic region to the right. The chronogram is continued at top arrow (above node 8) to Fig. 3 to enable best view.

(Americas and Caribbean) and *B. bipinnata* (N. America; 100 BS, 1.0 PP; Fig. 2, nodes 10 and 11, respectively), which are, in turn, supported as sister to a clade comprising five species from C. America, S. America, and the Caribbean (100 BS, 1.0 PP; Fig. 2, node 12). Sister to all remaining taxa (100 BS, 1.0 PP; Fig. 3, node 13) is a well-supported clade comprising *B. andicola* and *B. ferulifolia* from N. America (100 BS, 1.0 PP; Fig. 3, node 14). A clade comprising taxa predominantly from Mexico (with some now invasive on many continents), as well as *B. biternata* (Asia, Africa, and India), *B. alba* (N. America), and *B. subalternans* (S. America) is strongly supported in the BI but not the ML analysis as sister to the remaining Pacific taxa (58 BS, 1.0 PP; Fig. 3, node 15). The monophyly of this South/North American clade is not supported (Fig. 3, node 16).

The large, strongly supported Polynesian clade (100 BS, 1.0 PP; Fig. 3, node 18) contains all *Bidens* taxa sampled from the Hawaiian Islands, the Marquesas Islands, the Society Islands, and the Austral Islands. This clade is divided into two large groups: one well-supported clade comprising all taxa from the Marquesas, the Society, and the single Austral Islands' species sampled (99 BS, 1.0 PP; Fig. 3, node 19), and a second clade comprising all Hawaiian taxa (70 BS, 1.0 PP; Fig. 3, node 22). The majority of species-level relationships in these two groups are unresolved. The Marquesas taxa are grouped

together in a grade within the larger Marquesas/Society/ Austral Islands clade. The Society Islands taxa are grouped together (Fig. 3, node 21), with the exception of *B. raiateensis*, which is placed but not supported as sister to the Austral Islands' *B. meyeri* from Rapa Iti (Fig. 3, node 20), and these are, in turn, placed but not supported with two Marquesan taxa (<50 BS, 67 PP; Fig. 3). Throughout the tree, taxa for which multiple samples were included in the analyses are generally placed together, with the exception of several taxa from the Hawaiian Islands (*B. sandvicensis*, *B. hillebrandiana*, *B. valida*, *B. cosmoides*, and *B. macrocarpa*), the Marquesas Islands (*B. wichmanii*, *B. polycephala*), and Central America (*B. pilosa*).

3.2 Divergence times

Divergence time estimates suggest that the crown age of *Bidens* s.s. is 5.77 Ma (2.28–9.97, 95% HPD; Fig. 2, node 6). The Pacific clade is estimated to have split from its closest relatives 3.14 mya (1.28–5.35, 95% HPD; Fig. 3, node 15), with the crown group emerging 1.63 Ma (0.74–2.72, 95% HPD; Fig. 3, node 18). The crown age of the Marquesas, Society, and Austral Islands clade was estimated as 1.29 Ma (0.54–2.19, 95% HPD; Fig. 3, node 19). The Hawaiian lineage of *Bidens* is estimated to have a crown age of 1.32 Ma (0.66–2.10, 95% HPD; Fig. 3, node 22). *Bidens* sp. from the Line



Fig. 3. The Bayesian chronogram from the concatenated partitioned analysis conducted in BEAST, continued from Fig. 2 at arrow to bottom left. Blue bars represent the 95% highest posterior density, and node support is indicated as maximum likelihood bootstrap support (BS) and Bayesian posterior probabilities (PP). Support values are not shown for nodes that had <70 BS and <90 PP. A dash indicates that the branch was not supported in one of the analyses (<50% BS or <0.50 PP values). Node numbers are shown in black circles and calibration points are indicated by red stars (Node 17: Socorro Island, Node 22: Hawaiian Islands, Node 23: Hawai'i Island). Taxa are color-coded by geographic region to the right. Inset shows the maximum likelihood tree with branch lengths.

Islands emerged around 0.55 Ma (0.10–1.15, 95% HPD; Fig. 3, node 11).

3.3 Ancestral range estimation

A significant improvement was seen in the three base models with the addition of founder events and dispersal distance. Of the 12 models evaluated, three were considered plausible on the basis of Δ AIC values < 7 (Burnham et al., 2010), and these included the DEC + j, DEC + j + x, and DIVA + j + x models (Table 2). Given that these models were largely congruent and only varied slightly in the probability of a few backbone nodes, we focus on results from the best model on the basis of LRT and Δ AIC values. The best model was determined to be DEC + j + x, which was significantly better

Table 2 Model parameters (d = anagenetic dispersal, e = extinction, j = founder events, x = dispersal distance), log likelihood (LnL) values, and Akaike Information Criterion (AIC) values for each of the biogeographic analyses conducted in BioGeoBEARS on Pacific *Bidens* and its sister clade. Models were compared for goodness of fit using Likelihood Ratio Test (LRT) and Δ AIC values. The model with the highest likelihood and lowest Δ AIC value is highlighted in bold

| Model | d | e | j | х | LnL | AIC | ΔΑΙΟ | p Value |
|---------------|--------|--------|--------|---------|---------|----------|-------|-------------------------|
| DEC | 0.0174 | 0 | 0 | 0 | -91.37 | 186.7390 | 24.23 | 1 |
| DEC + j | 0.0057 | 0 | 0.0107 | 0 | -80.29 | 166.5872 | 4.53 | 2.52×10^{-6} |
| DEC + x | 0.0502 | 0 | 0 | -0.4835 | -88.03 | 182.0587 | 19.55 | 9.75×10^{-3} |
| DEC + j + x | 0.0490 | 0 | 0.0637 | -0.8762 | -77.26 | 162.5126 | 0 | 7.43 × 10 ⁻⁷ |
| DIVA | 0.0222 | 0 | 0 | 0 | -88.97 | 181.9485 | 19.44 | 1 |
| DIVA + j | 0.0107 | 0 | 0.0097 | 0 | -83.85 | 173.7033 | 11.19 | 1.37×10^{-3} |
| DIVA + x | 0.1668 | 0 | 0 | -0.8617 | -84.20 | 174.3930 | 11.88 | 1.99×10^{-3} |
| DIVA + j + x | 0.0883 | 0 | 0.0490 | -0.8355 | -80.67 | 169.3362 | 6.82 | 2.47×10^{-4} |
| BayArea | 0.0163 | 0.2482 | 0 | 0 | -110.94 | 225.8883 | 63.38 | 1 |
| BayArea+j | 0.0041 | 0.0318 | 0.0129 | 0 | -87.43 | 180.8684 | 18.36 | 7.03×10^{-12} |
| BayArea+x | 0.0373 | 0.2512 | 0 | -0.3439 | -109.27 | 224.5416 | 62.03 | 0.067 |
| BayArea+j + x | 0.0308 | 0 | 0.0677 | -0.7327 | -84.76 | 177.5131 | 15.00 | 4.24×10^{-12} |

than the null model (DEC) according to the LRT value (LnL = -77.26 vs. -91.37, df = 2, p < 0.001). The parameters of the DEC + j + x model include the following: anagenetic dispersal rate (d) = 0.0490, extinction rate (e) = 0, founder event dispersal rate (j) = 0.0637, and dispersal distance rate (x) = -0.8762. On the basis of the parameters of the DEC + j + x model, the BSM analysis recovered a total of 65 cladogenetic events, with 75% of these resulting from speciation within areas (narrow sympatry), 14% from founder-event speciation, 8% from subset sympatric speciation, and 4% from vicariance (Table S2).

The most recent common ancestor of the Pacific Bidens radiation appears to be located in South America (62% probability), but there is little statistical support for the placement of B. subalternans from S. America, which is driving this result (Fig. 4). The initial colonization of the Pacific was either to the Marquesas/Society Islands (43% probability) or Hawai'i (39% probability), with the order of colonization between the two archipelagoes unresolved (Fig. 4). Within the Pacific, each of the Marquesan and Hawaiian radiations were the result of single colonization events. The Hawaiian radiation is recovered as monophyletic and the Marquesan radiation as paraphyletic, with respect to the Society Islands radiation that is nested within it (Fig. 4). For the taxa sampled, we recover one colonization of the Society Islands from the Marquesas with a high probability (100%). Nested within the Marquesan clade are B. cf. raiateensis (Raiatea, Society Islands) and B. meyeri (Rapa Iti, Austral Islands), which are placed but not supported as sister to one another. The ancestral area for these two taxa is uncertain (Society Islands with 56% probability and Austral Islands with 44% probability). The Starbuck Island species (Bidens sp.) in the Line Islands of the Central Pacific is recovered as a separate colonization of the Pacific from the main radiation and has closest affinity to B. bipinnata, native to North America and possibly to eastern Asia as well. In addition, B. socorrensis from Socorro Island 600 km off the western coast of Mexico is also recovered as a separate colonization event in the Pacific and has closest affinity to B. hintonii with a center of distribution in Mexico. Both

species appear to have no extant closely related taxa within the Pacific.

4 Discussion

Despite a long history of study (e.g., Sherff, 1937; Sherff & Alexander, 1955; Steussy, 1977; Panero & Funk, 2002; Kimball & Crawford, 2004), the evolutionary relationships among taxa in the Coreopsidae tribe have been difficult to ascertain using morphological characters alone or in combination with few molecular markers. The present study included 103 taxa sequenced across two nuclear and four chloroplast markers, representing the most complete molecular study of the group to date. In addition, this study also represents the first attempt to resolve the evolutionary and biogeographic history of the explosive *Bidens* radiation throughout Polynesia.

4.1 Testing the monophyly of *Bidens* and *Coreopsis,* Polynesian *Bidens*, and archipelago-level radiations

Within the Coreopsideae, the evolutionary relationships of the taxa in the two largest genera, Bidens and Coreopsis, have been particularly problematic and difficult to reconstruct (e.g., Ganders & Nagata, 1990; Kim et al., 1999; Tadasse, 1984, 1986, 1993; Tadesse et al., 1995, 1996, 2001). In line with previous assessments, we recover Bidens s.l. as polyphyletic and Coreopsis as both polyphyletic and paraphyletic with respect to Bidens (Kim et al., 1999; Kimball & Crawford, 2004). Kim et al. (1999) and Kimball & Crawford (2004) called for a systematic revision of the two genera based on ITS sequences. Both studies recovered Bidens as having originated twice within Coreopsis, with north temperate Bidens (Bidens s.l.) more closely related to North American temperate Coreopsis rather than Bidens s.s. (comprising taxa from Africa, Central/South America, and the Hawaiian Islands), which were similarly nested within Coreopsis. Our results support these general conclusions, as we recover Bidens s.s. as monophyletic with strong support (Fig. 2, node 6) and the north temperate Bidens s.l. nested



Fig. 4. Ancestral range estimation for *Bidens s.s.* under the best model determined in BioGeoBEARS (DEC + j + x), based on the divergence times estimated in BEAST and the distribution of extant species. Areas are color-coded for the geographic regions (single and multiple area ranges) depicted in the map. Pie graphs at each node indicate the relative probability of a given area (or combined areas). Arrows on the map depict the direction and number of dispersal events (both founder events and range expansion events) as determined in a biogeographic stochastic mapping analysis. Black arrows indicate dispersal events with a high relative probability, whereas gray arrows reflect uncertainty in the reconstructed ancestral ranges.

within a basal branching clade that includes taxa from multiple genera, including *Coreopsis* (Fig. 2, node 1). However, in contrast to these prior studies, we do not find *Bidens s.s.* nested within *Coreopsis*. Clearly though, all evidence to date points toward the need for a systematic revision of the group, which is beyond the scope of the present study.

We recovered strong support for the monophyly of the Polynesian *Bidens* radiation (comprising taxa from the Hawaiian, Marquesan, Society, and Austral Islands) within *Bidens s.s.* (Fig. 3, node 18). We recover the Hawaiian radiation as monophyletic (Fig. 2), consistent with previous assessments (Helenurm & Ganders, 1985; Knope et al., 2012; Knope et al., 2020). However, given that the direction of colonization between the Hawaiian and Marquesas Islands could not be resolved, it is important to note that the monophyly of the Hawaiian radiation remains in question. If the Marquesas were colonized first with subsequent dispersal to the Hawaiian Islands, the Hawaiian radiation would remain as a monophyletic clade. However, if the Hawaiian Islands were the initial colonization point in the Pacific, then the Hawaiian species would be paraphyletic with respect to the Marquesan, Society, and Austral Island species, which would then be descended from the Hawaiian lineage. A third possibility is that two dispersal events gave rise to the Hawaiian and Marquesan lineages independently from a single common ancestor in Central/South America in quick succession of one another, but this is unlikely, given the extremely long distances for colonization for such events to occur coincidently.

Within Bidens s.l., we do find support for the possibility of two separate, independent colonizations of the Pacific that

are not part of the main Polynesian radiation. These separate colonizations are B. socorroensis from Socorro Island off the west coast of Mexico and the Starbuck Island Bidens sp. in the Line Islands of the Central Pacific (Figs. 2 and 3, nodes 11 and 17, respectively). Bidens socorroensis is recovered as nested within the Central American clade and appears to likely be the result of a dispersal event from mainland Mexico (only ~500 km away), followed by allopatric speciation resulting in this single Socorro Island endemic species. Ganders et al. (2000) first indicated that an unknown species collected on Starbuck Island was not part of the main Polynesian radiation. Subsequently, in an unpublished master's thesis based on both ITS sequences and morphological data, Sayre (2001, unpublished data) further suggested that the Starbuck Island population represented a new, undescribed species and proposed that the closest sampled relative to this population was B. cynapifolia, native to Central and South America but weedy around the including, besides being a common weed in the Hawaiian Islands. In fact, the Starbuck Island population differed from B. cynapifolia collected in Kona, Hawai'i, by only 12 bp of the 519 ITS bp sequenced. Starbuck Island is an extremely small, low-lying, and uninhabited coral atoll, with a total land area of just over 16 km² and ~1000 km due south of Hawai'i. We find strong support for this population as sister to B. pinnata from North America (Fig. 2, node 11), which are, in turn, both strongly supported as sister to B. cynapifolia (Fig. 2, node 10). This may help explain why the Starbuck Island population has morphologically distinct achenes from B. cynapifolia. Future studies comparing morphological characters (e.g., achenes, among others) of these taxa in a common garden setting, along with broad-scale genomic data, may help to determine if the Starbuck Island population is indeed a natural colonization and endemic species, or a more recent human introduction. Until then, we suggest it is prudent to refrain from a new species designation for this enigmatic population.

4.2 Determining the location of the MRCA of the Polynesian *Bidens*

On the basis of ITS sequences, Ganders et al. (2000) suggested that the MRCA of the five Hawaiian species, two Hawaiian hybrids, and three unidentified Marquesan specimens sampled was located in Central America. Subsequently, Knope et al. (2012 and 2020) have supported this result, but Knope et al. (2020) cautioned that more complete taxon sampling of Bidens from across the Pacific Basin and potential source regions would be necessary to determine the location (and possible number) of MRCA of the Hawaiian and South Pacific radiations. With more inclusive taxon sampling in the present study, our results suggest a single MRCA of the Hawaiian/Marquesan/Society/Austral Island clade, but with a possible South American (62% probability in BSM analysis; Fig. 4), rather than Central American origin. However, caution is warranted in this conclusion, as this result is being driven solely by the placement of B. subalternans in the otherwise Central American clade that is immediately basal to the Polynesian radiation (Fig. 3, node 16), a result that is not statistically supported in either the BI or ML analyses. Further study with broad-scale phylogenomic data may help to resolve this question.

4.3 The timing and sequence of colonization events among the remote archipelagoes of Polynesia

Given the great ecomorphological diversity within Hawaiian Bidens (greater than the rest of the entire genus found on five continents combined), Gillett (1975) proposed that the initial colonization of the Hawaiian Islands occurred before the formation of Kaua'i (c. 5 Ma, and the oldest of the current high-elevation Hawaiian Islands; Price & Clague, 2002), as he surmised that substantial time in the archipelago would have been necessary for this degree of ecomorphological differentiation to occur. The oldest of the current Northwestern Hawaiian Islands is presently Kure Atoll, which formed ~29 Ma, and it is believed that there was an approximately 4 My gap before its formation and after the submergence of Koko Seamount when no Hawaiian Islands (presently the Emperor Seamounts) were above sea level, and colonization of the archipelago would have started over ~23–29 Ma (Clague et al., 2010). Furthermore, when Kaua'i formed, only relatively small islands in the archipelago were available as a source, and the largest of these (Nihoa, Necker, LaPerouse, and Gardner) were relatively distant to the northwest in comparison to the spacing of the present high islands (Price & Clague, 2002). Gillett (1975) also suggested that B. cosmoides (restricted to high-elevation rainforests on Kaua'i and the only Hawaiian species that is bird-pollinated) was the result of a separate older colonization event that failed to radiate beyond the single species, and that the remaining 18 Hawaiian species were the descendants of a second later colonization event. In contrast, Helenurm and Ganders (1985) sampled 15 Hawaiian species and found little divergence at isozyme loci, pointing toward recent colonization and subsequent rapid radiation. Similarly, in the study of Ganders et al. (2000), all five of the Hawaiian species and two hybrids sampled had identical ITS sequences, suggesting that the radiation had occurred recently. Knope et al. (2012) found little divergence in the ITS locus across all 19 Hawaiian species (including 6 subspecies) and two hybrids. On the basis of island age constraints and ITS molecular clock estimates, their study placed the age of the Hawaiian radiation at ~2.1 Ma (1.3-3.1 Ma, 95% HPD). Knope et al. (2020) expanded the study of Hawaiian taxa using a phylogenomic approach and next-generation sequencing techniques to examine complete plastomes and ~11,570 kb of the nuclear ribosomal complex. Using this expanded data set along with a secondary calibration point from Knope et al. (2012) and an age constraint for the colonization of Hawai'i Island (the youngest of the main islands), their study estimated that the Hawaiian crown group emerged ~1.82 Ma (1.11–2.55, 95% HPD). This placed the diversification of the entire group likely after shield emergence of West Moloka'i (2.58 Ma) and West Maui (2.15 Ma), but before shield emergence of Hawai'i Island (1.04 Ma; Obbard et al., 2012).

The present study places the crown age of *Bidens s.s.* at 5.77 Ma (2.28–9.97, 95% HPD; Fig. 2, node 6), with the Pacific group splitting from its closest continental relatives 3.14 Ma (1.28-5.35, 95% HPD; Fig. 3, node 15) and the crown group in Polynesia emerging 1.63 Ma (0.74-2.72, 95% HPD; Fig. 3, node 18). The Hawaiian lineage of *Bidens* is estimated to have a crown age of 1.32 Ma (0.66-2.10, 95% HPD; Fig. 3, node 22), which is younger than previous estimates, but still before

shield emergence of Hawai'i Island. This younger age estimate for the crown group of the Hawaiian radiation results in an increase in the diversification rate of the radiation, which was already considered among the fastest known in plants, especially on a per-unit-area basis (Knope et al., 2012). The Marquesas appear to have been colonized around 1.29 Ma (0.54-2.19, 95% HPD, Fig. 3 node 19), which is relatively recent when considering the beginning of the formation of the island chain at 5.5 Ma. This slightly younger age of antiquity of the ten Marguesan Islands species, plus those descended from the Marguesan radiation, makes the South Pacific diversification of 22 described species of Bidens slightly faster than the Hawaiian radiation with 19 species and a slightly older age of antiquity (assuming the same extinction rates for both, which are estimated to be negligible in the BSM analyses; Table 2). In addition to the Polynesian radiation, Bidens sp. from the Line Islands emerged around 0.55 Ma (0.10–1.15, 95% HPD, Fig. 2; node 11), which could lend support to it being a new undescribed taxon. Alternatively, this population could have split with its continental common ancestor with B. pinnata at that time, followed by a more recent introduction to Starbuck Island (either by natural means or human-mediated transport).

On the basis of the parameter estimates for the best model (DEC + j + x), extinction has yet to play an important role in the biogeographic history of Polynesian Bidens. This supports the idea that the radiation has yet to reach any ecological limits to clade diversity (e.g., Rabosky, 2009) and is likely still in the expansive phase of the radiation, as was suggested for the Hawaiian taxa in earlier analyses (Knope et al., 2012, 2020). We also found that the three plausible models included the jump dispersal (j) parameter, emphasizing the importance of founder-event speciation among archipelagoes. The DEC+j model has recently received criticism for possibly being a poor model for estimating founder-event speciation, and in some cases having a tendency to inflate the role of cladogenetic events and underestimate the role of anagenetic events (Ree & Sanmartín, 2018). However, we find no obvious departures from intuitive dispersal patterns across Polynesia, consistent with Knope et al. (2020) for the Hawaiian taxa.

Of the 65 cladogenetic events recovered in the BSM analysis of the of the DEC + j + x model, 75% resulted from speciation within areas (in this case defined as archipelagoes), 14% resulted from founder-event speciation (among archipelagoes), 8% from subset sympatric speciation, and just 4% from vicariance (Table 2). These results are consistent with relatively rare long-distance dispersal among the archipelagoes resulting in founder-event speciation, with almost all cladogenetic events occurring within individual archipelagoes. Of course, this does not preclude the importance of founder-event speciation between islands within archipelagoes. The BSM analysis also suggested that the initial colonization of the Pacific was either to the Marguesas (43% probability) or Hawai'i (39% probability), with the order of colonization between the two archipelagoes unresolved (Fig. 4). This is likely indicative of the relatively short interval of time that elapsed between subsequent colonization of the two archipelagoes, as suggested by the statistically indistinguishable crown age estimates for the two archipelagoes (Hawaiian lineage at 1.32 Ma [0.66–2.10, 95% HPD] and Marquesan lineage at 1.29 Ma [0.54–2.19, 95% HPD]).

4.4 Evolutionary patterns of dispersal potential

Although long-distance dispersal of plant lineages between the Hawaiian and French Polynesian archipelagoes is actually quite common (Price & Wagner, 2018), many Polynesian taxa appear to have evolved with a presumably adaptive reduced dispersal potential. For example, Beccari & Rock (1921) noted in their study of Hawaiian Pritchardia (Arecaceae) that loss of dispersal potential, or what they termed "precinctiveness," could lead to propagules remaining in the specialized habitat of the parent plants. Carlquist (1966a) further pointed out that the Hawaiian flora as a whole displays a general trend for endemic species to have lower dispersal potential than their mainland or continental island relatives. Carlquist (1966a) postulated that an extreme function of precinctiveness would be to lower the probability that propagules are lost by being blown out to sea. However, he suggested that this was not likely to be the common adaptive function of loss of dispersal potential in Hawaiian flowering plants, because most taxa with lowered dispersal ability do not occupy windy sites, but rather are commonly found in protected forest habitats. Similarly, Perkins (1913) suspected wind pressure to be insufficient to explain the repeated evolution of flightlessness in Hawaiian insects. Carlquist (1965, 1966b) pointed toward a second probable factor for the loss of dispersal potential for immigrants to oceanic islands; many colonists are "weedy" plants capable of longdistance dispersal and of establishing in novel environments, and that these lineages often evolve characteristics advantageous in stable forest habitats. Carlquist (1966b) considered the Compositae to be a prime example of the evolution of weedy, herbaceous ancestors often giving rise to shrubs and trees in forest habitats. Furthermore, Carlquist (1966b) described a third possible factor for the failure to maintain the dispersal mechanism that facilitated the original colonization of oceanic islands, with the Pacific insular species of Bidens being an excellent example. The species of Bidens in Polynesia that have retained dispersal mechanisms most similar to the likely ancestral types are found on open sites like cliffs, suggesting that the attachment of achenes to feathers was the original vector for immigration. Subsequently, with dispersal and establishment in upland island interior habitats, contact with the original dispersal vector can be lost, and either the old mechanism is lost or a new mechanism is developed, or both may occur. The loss of contact with the original dispersal vector, in this case likely shorebirds or possibly seabirds, may be a byproduct of evolutionary opportunity and ecological shifts that are commonplace during adaptive radiation, especially on oceanic islands with disharmonic biotas and presumably open niche space (Carlquist, 1966c).

The Pacific *Bidens* conform to the idea that the basic ecology of the species is correlated with their dispersal potential (Carlquist, 1966b). Only species found in open areas retain a fully developed dispersal apparatus in the structure of the achenes, and the degree of modification is roughly proportional to adaptation to stable, island interior environments; however, the presumably adaptive specializations can be unique to individual habitats. The Hawaiian species appear to offer a particularly strong example of evolution from seacoast to island interior habitats with accompanying adaptive shifts by loss of dispersal mechanism (Carlquist, 1966b). Similarly, the Society Island species that occupy grassy ridges and open forest retain barbed awns (stiff needle-like element of the pappus on the achenes), and the species that have adapted to the dense upland rainforest, such as B. raiateensis, have the poorest dispersal means of any of the South Pacific Bidens taxa. Furthermore, it appears that none of the Pacific species of Bidens have dispersal mechanisms as efficient as that of their closely related continental taxa. Of those that have been studied (Carlquist, 1966b, 1980), the general trends in loss of dispersal potential of the achenes in Pacific Bidens relative to B. pilosa are as follows: awns become shorter and closer together (are less spreading); awns lose retrorse barbs; awns lost entirely; upward-pointing hairs on achene body diminished or lost; achenes increase in size; and achene shape changes from narrow and needle-like to various shapes, including some that are twisted or contorted. It appears that Pacific Bidens have retained long-distance dispersal potential in many of the coastal species, facilitating colonization of other remote oceanic archipelagos likely by attachment to bird feathers. Additionally, repeated and generally predictable evolution in the loss of dispersal potential can be observed as individual island radiations occur and taxa speciate into island interior habitats.

4.5 Conservation status of Polynesian Bidens

While Bidens of the Pacific represent one of the best examples of explosive adaptive radiation in plants, they are also one of the many highly imperiled groups of native plants in the region. According the International Union for the Conservation of Nature Red List (IUCN, 2020), of the 27 taxa (19 species and 8 subspecies) endemic to Hawai'i, 12 are considered Vulnerable or worse, with B. cosmoides, B. forbesii, and B. valida listed as Endangered, and B. campylotheca pentamera, B. sandvicensis confusa, and B. wiebkei listed as Critically Endangered with the highest risk of extinction in the wild. Although the IUCN has not yet made formal assessments of the Marquesan taxa, Wagner et al. (2014) evaluated them using the IUCN criteria for endangerment (IUCN, 2001) and determined that all ten species of Marquesan Bidens fall into the Endangered and Critically Endangered categories, based on having narrow geographic ranges and continued decline in habitat quality. Additionally, the authors noted that the IUCN area criterion for single-island endemic species on small oceanic islands may force these species to fall into these two categories, even when they can be locally quite abundant. Funk & Wood (2014) similarly used the IUCN criteria (IUCN, 2001) to assess the conservation status of B. meyeri (recently described from Rapa in the Austral Islands), finding that it easily falls into the Critically Endangered category with very high risk of extinction in the wild (<50 individuals known). Only six of the ten species of Bidens from the Society Islands have been assessed by the IUCN (IUCN France, 2015), with B. glandulifera and B. mooreensis listed as Critically Endangered, B. lantanoides listed as Endangered, B. orofenesis listed as Vulnerable, and B. aoraiensis as Data-Deficient.

Although the remaining four described species are yet to be assessed, it is likely that they too are of high conservation concern based on their small ranges and ongoing declines in habitat quality. Although we were unable to include *B. saint-johniana* from neighboring Marotiri in the Austral Islands, it is listed as Near Threatened (IUCN France, 2015). Similarly, we were also unable to include *B. mathewsii* or *B. hendersonensis* from the Pitcairn Islands, and while none have been evaluated by the IUCN, we expect they would likely fall in the Endangered or Critically Endangered threat categories on the basis of the same criteria listed for the taxa above. Also, inclusion of these taxa in future phylogenetic assessments of the Polynesian *Bidens* should be of high priority.

4.6 Conclusions and future directions

The present study contributes the first generally wellresolved phylogenetic and historical biogeographic hypotheses for Bidens of the Pacific and its relationships to other Bidens and closely related genera in the Coreopsideae tribe. We found Bidens to be polyphyletic within Coreopsis, consistent with previous works (Kim et al., 1999; Kimball & Crawford, 2004). However, we find the Polynesian Bidens radiation to be monophyletic, with the initial colonization of the Pacific being either to the Hawaiian or the Marguesas Islands, possibly from South America. Additional work is needed to substantiate this ancestral location and to determine the order of colonization between the Hawaiian and the Marquesas Islands. From the Marquesas, it appears that Bidens dispersed to the Society Islands twice, followed by colonization of the Austral Islands apparently from the Society Islands, but statistical support for this hypothesis is weak. The estimated age of diversification for the crown group in the Pacific is 1.63 Ma (0.74–2.72, 95% HPD), making Polynesian Bidens among the youngest and most rapid plant diversification events documented in the Pacific. Our findings suggest that relatively rare long-distance dispersal and founder-event speciation, coupled with subsequent loss of dispersal potential in the achenes coincident with speciation into island interior habitats, can explain the repeated and explosive adaptive radiation of Bidens throughout Polynesia. Our findings also illustrate how nearly complete taxon sampling is necessary for a better understanding of the phylogenetic and biogeographic history of a clade of interest.

Acknowledgements

The authors thank many people from all over the world who helped with collections and sent samples. They also thank T. Chong, C. Kelloff, and D. Koizumi for administrative support. This material is based upon work supported by the National Science Foundation under Grant No. 1345247 and a University of Hawai'i at Hilo Faculty SEED Grant to M.L.K. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. Authors are also grateful for funding support from the McBryde Fund at the National Tropical Botanical Garden. This is publication #2 from the School of Life Sciences, University of Hawai'i at Mānoa.

Appendix I. 5 Individuals sampled in this study of Pacific Bidens. For each sample, the species name, collector(s) and voucher number, voucher information, place of origin, and GenBank accession numbers (ETS, ITS, *ndhC-trnV*, *rpl32-trnL*, *psbA-trnH*, and *trnQ-rps16*) are provided. An X indicates sequence data for that marker were not obtained.

Bidens alba (L.) DC., USA, Moloka'i, Herbst, D 9874 (BISH), MK545542, MK545673, MK545804, MK545931, MK546045, MK546200. Bidens alba (L.) DC. var. radiata (Sch. Bip.) Ballard ex Melchert, USA, Kaua'i, Knope, J & K McMillan 2009.104 (BISH), MW152219, MW145359, MW152197, MW152249, MK546046, MW152176. Bidens amplectens Sherff, USA, O'ahu, Perlman, S 5843 (US), MK545543, MK545674, MK545806, MK545932, MK546048, MK546201. Bidens amplectens Sherff, USA, O'ahu, Knope, M 13 (BISH), MW152212, MW145342, MK545805, MW152240, MK546047, MW152169. Bidens amplissima Greene, Canada, BC, Klinkenberg, B 1, 9, 17 (UBC), MK545544, MK545675, MK545807, MK545933, MK546049, X. Bidens andicola Kunth, Peru, Cuzco, Norrbom, AL, GJ Steck, BD Sutton 13-PE-06 (US), MK545547, MK545678, MK545808, MK545936, MK546052, X. Bidens andicola Kunth var. andicola, Peru, Cuzco, Franquemont, CE 341a (UBC), MK545545, MK545676, MK545809, MK545934, MK546050, MK546202. Bidens andicola Kunth var. decomposita Kuntze, Peru, Cuzco, Franquemont, CE 341b (UBC), MK545546, MK545677, MK545810, MK545935, MK546051, MK546203. Bidens aristosa (Michx.) Britton, USA, Illinois, Chase,VH 17109 (UBC), MK545549, MK545680, MK545812, MK545937, MK546054, MK546205. Bidens asymmetrica Sherff, USA, O'ahu, Knope, M 28 (BISH), MK545550, MW145350, MW152196, MW152242, MK546055, MW152175. Bidens asymmetrica Sherff, USA, O'ahu, Knope, M 29 (BISH), MK545551, MK545681, MK545813, MK545938, MK546056, MK546206. Bidens aurea (Aiton) Sherff, USA, AZ, Makings 1406 (DAV), MK545552, X, MK545814, MK545939, MK546057, MK546207. Bidens australis Spreng., Society Islands, Tahiti, Meyer, J-Y. s.n. (PAP), MK545556, MK545685, MK545818, MK545943, MK546061, MK546211. Bidens australis Spreng., Society Islands, Tahiti Iti, Meyer, J-Y. s.n. (PAP), MK545560, MK545689, MK545822, X, MK546065, MK546215. Bidens beckiana (F.Br.) Sherff, Marquesas Islands, Hatutaa, Meyer, J-Y. 3170 (PAP), MK545561, MK545690, MK545823, MK545947, MK546066, X. Bidens beckii Torr. ex Speng., Canada, BC, Newroth, PR s.n. (UBC), MK545562, MK545691, X, MK545948, MK546067, MK546216. Bidens bipinnata L., Australia, NT, Dixon, D 1342 (NT), MK545563, MK545692, MK545824, MK545949, MK546068, MK546217. Bidens bipontina x polycephala Sch. Bip., Marquesas Islands, Nuku Hiva, Butaud, J-F 2587 (PAP), MK545620, MK545749, MK545880, MK545994, MK546138, MK546263. Bidens biternata (Lour.) Merr. & Sherff, China, Shandong, Guocheng-yong 2006-15232 (US), MK545566, MK545695, MK545827, MK545952, MK546070, MK546220. Bidens biternata (Lour.) Merr. & Sherff, China, Shandong, Guocheng-yong 2006-44983 (US), MK545565, MK545694, MK545826, MK545951, X, MK546219. Bidens boquetiensis Roseman, USA, PR, Kennedy, H 4566 (UBC), MK545567, MK545696, MK545828, MK545953, MK546071, MK546221. Bidens campylotheca Sch. Bip. subsp. campylotheca, USA, O ´ahu (cult), Knope, M & S Hinard 17 (BISH), MW152215, MW145357, MW152192, MW152228, MK546072, MW152171. Bidens campylotheca Sch. Bip. subsp. pentamera (Sherff) Ganders & Nagata, USA, East Maui, Wood, KR 6607 (PTBG), X, MW145355, X, MW152238, X, MW152162. Bidens campylotheca Sch. Bip. subsp. pentamera (Sherff) Ganders & Nagata, USA, West Maui, Oppenheimer, HL H-40,802 (BISH, PTBG), MK545568, MK545697, MK545829, MK545954, MK546073, MK546222. Bidens cernua L., China, Tibet, Tibet McArther 1 (US), MK545570, MK545699, MK545830, MK545956, MK546075, MK546224. Bidens cernua L., Canada, BC, Klinkenberg, B & R 51 (UBC), MK545569, MK545698, X, MK545955, MK546074, MK546223. Bidens cervicata Sherff, USA, O'ahu, Morden, CW 2223 (HAW), MW152218, X, MW152195, MW152248, MK546076, MW152174. Bidens cervicata Sherff, USA, Kaua'i, Ganders, FR 81-11 (UBC), MK545571, MK545700, MK545831, MK545957, MK546077, MK546225. Bidens cf. aoraiensis M.L. Grant in Sherff, Tahiti, Meyer, J-Y. 3233 (PAP), MK545548, MK545679, MK545811, X, MK546053, MK546204. Bidens cf. australis Spreng., Mo'orea, Meyer, J-Y. 3098 (PAP), MK545555, MK545684, MK545817, MK545942, MK546060, MK546210. Bidens cf. australis Spreng., Mo´orea, Butaud, J-F 2970 (PAP), MK545553, MK545682, MK545815, MK545940, MK546058, MK546208. Bidens cf. australis Spreng., Mo'orea, Meyer, J-Y. & V Funk 3220a (US), MK545558, MK545687, MK545820, MK545945, MK546063, MK546213. Bidens cf. australis Spreng., Mo'orea, Meyer, J-Y. & V Funk 3220b (US), MK545559, MK545688, MK545821, MK545946, MK546064, MK546214. Bidens cf. australis Spreng., Tahiti, Meyer, J-Y. 3090 (PAP), MK545554, MK545683, MK545816, MK545941, MK546059, MK546209. Bidens cf. australis Spreng., Mo'orea, Meyer, J-Y. & V Funk 3216 (US), MK545557, MK545686, MK545819, MK545944, MK546062, MK546212. Bidens cf. bipontina Sherff, Nuku Hiva, Meyer, J-Y. 3099 (PAP), MK545564, MK545693, MK545825, MK545950, MK546069, MK546218. Bidens cf. mooreensis M.L. Grant in Sherff, Mo'orea, Meyer, J-Y. s.n. (PAP), X, MK545734, MK545864, MK545981, MK546123, MK546250. Bidens cf. raiateensis J.W. Moore, Raiatea, Meyer, J-Y 3089 (PAP), MK545626, MK545755, MK545885, MK545999, MK546144, MK546268. Bidens cf. wichmanii W.L. Wagner, J.R. Clark & Lorence, Marquesas Islands, Meyer, J-Y. s.n. (PAP), MK545580, MK545709, MK545840, MK545963, MK546088, X. Bidens conjuncta Sherff, USA, West Maui, Perlman, S 15767 (PTBG), MK545572, MK545701, MK545832, MK545958, MK546079, MK546226. Bidens conjuncta Sherff, USA, West Maui, Perlman, S 12419 (PTBG, UBC), MW152226, MW145349, MW152204, MW152247, MK546078, MW152182. Bidens connata Muhl. ex Wild., USA, OH, Roberts, ML 6052 (KANU), MK545574, MK545703, MK545834, MK545959, MK546081, MK546227. Bidens cordifolia Sch. Bip., Nuku Hiva, Butaud, J-F 1776 (PAP, destroyed), MK545573, MK545702, MK545833, X, MK546080, X. Bidens cosmoides Sherff, USA, Kaua'i, Wood, KR & A Willyard 13050 (BISH, PTBG), MK545575, MK545704, MK545835, X, MK546083, MK546228. Bidens cosmoides Sherff, USA, Kaua'i (cult), Harbinirman, M ASC s.n. (HPDL-3787), MW152222, MW145352, MW152200, MW152230, MK546082, MW152178.

Bidens cynapifolia Kunth, USA, O'ahu, Krajina, VJ 30 (UBC), MK545578, MK545707, MK545838, X, MK546086, MK546231. Bidens cynapifolia Kunth, USA, HW (cult), Sayre, CM 202 (UBC), MK545577, MK545706, MK545837, MK545961, MK546085, MK546230. Bidens dahlioides S. Watson, New Zealand, Massy, Hammett, KRW s.n. (CHR), MK545579, MK545708, MK545839, MK545962, MK546087, MK546232. Bidens ferulifolia (Jacq.) Sweet, Canada, BC (cult), Straley, GB 9106 (UBC), MK545584, MK545713, MK545845, MK545965, MK546092, MK546234. Bidens forbesii Sherff subsp. forbesii, USA, Kaua'i (cult), Knope, M 15 (BISH), MW152213, MW145343, MW152190, MW152241, MK546093, MK546235. Bidens forbesii Sherff subsp. kahiliensis Ganders & Nagata, USA, Kaua'i, Perlman, S 18739 (PTBG), MW152206, MW145358, MW152186, MW152239, MK546094, MW152163. Bidens frondosa L., New Zealand, Christchurch, Banks, Daphne s.n. (CHR), MK545585, MK545714, MK545846, MK545966, MK546095, MK546236. Bidens hawaiensis A. Gray, USA, HW, Wood, KR & S Perlman 529 (PTBG), MK545587, MK545716, MK545848, Х, MK546098, MK546238. Bidens hawaiensis A. Gray, USA, HW, Knope, M 37 (BISH), MW152221, MW145356, MW152199, X, MK546096, MW152177. Bidens hawaiensis A. Gray, USA, HW, O'ahu (cult), Knope, M 53 (BISH), MK545586, MK545715, MK545847, MK545967, MK546097, MK546237. Bidens henryi Sherff, Hiva Oa, Lorence, D et al. 8932 (PAP, PTBG), MK545590, MK545718, MK545849, X, MK546100, X. Bidens henryi Sherff, Hiva Oa, Perlman, S 19759 (PTBG), MK545591, MK545719, MK545850, MK545968, MK546101, MK546239. Bidens henryi Sherff, Hiva Oa, Perlman, S & KR Wood 19207 (BISH, PTBG), MK545589, MK545717, X, X, MK546099, X. Bidens hillebrandiana (Drake) O. Deg. ex Sherff subsp. hillebrandiana, USA, HW, Perlman, S 15190 (PTBG), MW152207, X, X, X, X, X. Bidens hillebrandiana (Drake) O. Deg. ex Sherff subsp. polycephala Nagata & Ganders, USA, Moloka'i, Perlman, S 17524 (PTBG), MK545593, X, X, MW152232, X, MW152164. Bidens hintonii (Sherff) Melchert, Mexico, Guerrero, Villaseñor & Soto s.n. (MEXU, UARK), MK545594, MK545721, MK545852, MK545969, MK546103, MK546240. Bidens holwayi Sherff & S.F. Blake, Pico Zunil, Guatemala (cult), Quedensley, TS 2764 (TEX), MK545595, MK545722, MK545853, MK545970, MK546104, MK546241. Bidens laevis (L.) Britton, Sterns & Poggenb., USA, FL, Ganders, FR & H Kennedy s.n. (UBC), MK545598, MK545725, MK545973, MK546107, MK546244. Bidens lantanoides A. Gray, Mo'orea, Meyer, J-Y. & V Funk 3218 (US), MK545599, MK545726, MK545856, MK545974, MK546108, MK546245. Bidens lantanoides A. Gray, Society Islands, Mo'orea, Meyer, J-Y. & V Funk, MK545600, MK545727, MK545857, MK545975, MK546109, MK546246. Bidens macrocarpa Sherff, USA, O'ahu, Morden, CW 2221 (BISH, HAW), X, MW145338, MW152185, MW152227, MK546111, MW152161. Bidens macrocarpa Sherff, USA, O ´ahu, Funk, V, CM Morden, & J Boutain 12806 (PTBG), X, MK545728, MK545858, MK545976, MK546110, X. Bidens mauiensis Sherff, USA, Maui (cult), Knope, M 18 (BISH), MK545602, MK545729, MK545859, MK545977, MK546112, MK546247. Bidens mauiensis Sherff, USA, Maui (cult), Knope, M 44 (BISH), MW152223, MW145339, MW152201, MW152235, MK546113, MW152179. Bidens menziesii Sherff subsp. filiformis (Sherff) Ganders & Nagata, USA, HW, Perlman,

S 10284 (PTBG), MW152208, MW145351, MW152187, MW152233, MK546115, MW152165. Bidens menziesii Sherff subsp. menziesii, USA, Moloka'i, Wood, KR 6029 (PTBG), MW152209, MW145341, MK545860, MW152244, MK546116, MW152166. Bidens menziesii Sherff subsp. menziesii, USA, Moloka'i, Cantley, J, M Chou, S Walsh & Garnett 416 (US), MK545603, MK545730, X, MK545978, MK546114, X. Bidens meyeri V.A. Funk & K.R. Wood, Austral Islands, Rapa, Wood, KR 9515 (PTBG), MK545642, MK545772, X, X, MK546164, MK546284. Bidens micrantha Gaudich. subsp. ctenophylla (Sherff) Nagata & Ganders, USA, HW, Perlman, S 16803 (PTBG), MW152210, MW145345, MW152188, MW152234, MK546118, MW152167. Bidens micrantha Gaudich. subsp. kalealaha Nagata & Ganders, USA, Maui, Oppenheimer, HL H-89905 (PTBG), MW152211, MW145340, MW152189, MW152236, MK546117, MW152168. Bidens microcephala W.L. Wagner, J.R. Clark & Lorence, Fatu Hiva, Price, J 231 (PAP, PTBG, US), MK545604, MK545731, MK545861, MK545979, MK546119, MK546248. Bidens molokaiensis Sherff, USA, Moloka'i (cult), Knope, M & S Hinard 45 (BISH), MW152224, MW145353, MW152202, MW152245, MK546120, MW152180. Bidens molokaiensis Sherff, USA, Moloka'i (cult), Knope, M & S Hinard 46 (BISH), MK545605, MK545732, MK545862, MK545980, MK546121, X. Bidens mooreensis M.L. Grant in Sherff, Mo'orea, Meyer, J-Y. s.n. (PAP), MK545606, MK545733, MK545863, X, MK546122, MK546249. Bidens orofenensis M.L. Grant in Sherff, Tahiti, Pitohiti, Meyer, J-Y. & V Funk 3194 (US), MK545608, MK545736, MK545866, MK545983, MK546125, MK546251. Bidens orofenensis M.L. Grant in Sherff, Tahiti, Mt. Orohena, Meyer, J-Y. & V Funk 3214bis (US), MK545609, MK545737, MK545867, MK545984, MK546126, MK546252. Bidens pachyloma (Oliv. & Hiern) Cufod., Ethiopia (cult) no voucher, Mesfin, T s.n. (OS), MK545610, MW145360, MW152205, MW152251, MK546127, MW152184. Bidens paniculata Hook. & Arn., Tahiti, Florence, J 6962 (BISH, US), X, MK545738, MK545868, X, MK546128, MK546253. Bidens pilosa L., Belize, Cayo Dist., Arvigo, R 894 (US), MK545611, MK545739, MK545869, MK545985, X, X. Bidens pilosa L., USA, Kaua'i, Wagner, W 4948 (US), MK545615, MK545744, MK545874, MK545990, MK546133, MK546258. Bidens pilosa L., Australia, NSW, Hosking, JR 3309 (CANB, NSW, US), X, MK545742, MK545872, MK545988, MK546131, MK546256. Bidens pilosa L., Mexico, Oaxaca, Zarate-Marcos, A 612 (TEX), MK545614, MK545743, MK545873, MK545989, MK546132, MK546257. Bidens pilosa L., USA, O'ahu, Funk, V & Cantley 12775 (HAW, US), MK545613, MK545741, MK545871, MK545987, MK546130, MK546255. Bidens polycephala Sch. Bip., Ua Huka, Perlman, S 19750 (BISH, MPU, NY, P, PAP, PTBG, US), MK545622, MK545751, MK545881, MK545995, MK546140, MK546264. Bidens polycephala Sch. Bip., Tahuata, Price, J 218 (BISH, P, PAP, PTBG, US), MK545619, MK545748, MK545875, MK545993, MK546137, MK546262. Bidens polycephala Sch. Bip., Ua Huka, Wood, KR & J-Y. Meyer 10515 (PTBG), MK545621, MK545750, MK545876, X, MK546139, X. Bidens polylepis S.F. Blake, USA, VA, Funk, V 12727 (US), MK545623, MK545752, MK545882, MK545996, MK546141, MK546265. Bidens populifolia Sherff, USA, O'ahu, Ganders, FR 81-23 (UBC), MK545624, MK545753, MK545883, MK545997, MK546142, MK546266. Bidens prestinaria (Sch. Bip.) Cufod., Ethiopia (cult) no voucher, Mesfin, T s.n. (OS), MK545625,

MK545754, MK545884, MK545998, MK546143, MK546267. Bidens reptans (L.) G. Don, USA, PR, Kennedy, H, G Breckon & M Breckon 4784 (UBC), MK545627, MK545756, MK545886, MK546000, MK546145, MK546269. Bidens reptans (L.) G. Don, USA, PR, Kennedy, H, G Breckon & M Breckon 4787 (UBC), MK545628, MK545757, X, MK546001, MK546146, MK546270. Bidens rubifolia Kunth, Ecuador, Loja, Kennedy, H, & FR Ganders 4514 (UBC), MK545629, MK545758, MK545887, MK546002, MK546147, MK546271. Bidens sandvicensis Less., USA Kaua'i, Lorence, D 5372 (US), X, MK545762, MK545891, MK546006, MK546153, MK546275. Bidens sandvicensis Less., USA, Kaua'i (cult), Harbinirman, M ASC s.n. (HPDL-3786), MK545630, MK545759, MK545888, MK546003, MK546148, MK546272. Bidens sandvicensis Less. subsp. confusa Nagata & Ganders, USA, Kaua'i, Herbst, D 1004 (BISH), MK545632, MK545761, MK545890, MK546005, MK546151, X. Bidens sandvicensis Less. subsp. sandvicensis, USA, Kaua'i, Funk, V 12800 (PTBG, US), MK545631, MK545760, MK545889, MK546004, MK546149, MK546274. Bidens sandvicensis Less. subsp. sandvicensis, USA, Kaua'i, Knope, M 21 (BISH), MW152216, MW145347, MW152193, MW152237, MK546152, MW152172. Bidens sandvicensis Less. subsp. sandvicensis, USA, Kaua'i, Knope, J & K McMillan 36 (BISH), MW152220, MW145354, MW152198, MW152243, MK546150, MK546273. Bidens schimperi Sch. Bip. ex Walp., Africa, Mesfin, T s.n. (OS), MK545634, MK545763, MK545893, MK546007, MK546155, MK546276. Bidens schimperi Sch. Bip. ex Walp., Ethiopia (cult) no voucher, Mesfin, T s.n. (OS), MK545633, MW145361, MK545892, MW152250, MK546154, MW152183. Bidens socorrensis Moran & G.A. Levin, Mexico, Socorro Island, Moran, R 29509 (US), MK545636, MK545765, MK545895, MK546009, MK546157, MK546278. Bidens socorrensis Moran & G.A. Levin, Mexico, Socorro Island, Moran, R 5781 (US), MK545635, MK545764, MK545894, MK546008, MK546156, MK546277. Bidens sp., Line Islands, Starbuck Island (cult), Sayre, CM 198 (UBC), MK545596, MK545723, MK545854, MK545971, MK546105, MK546242. Bidens sp., Line Islands, Starbuck Island (cult), Sayre, CM 198 (UBC), MK545597, MK545724, MK545855, MK545972, MK546106, MK546243. Bidens sp. nov ., Huahine, Wood, KR 11056 (PTBG, US, BISH, PAP, UC), X, MK545769, MK545899, MK546012, MK546161, MK546282. Bidens sp. nov . Lyon, USA, O'ahu, Funk, V 12810, MK545640, MK545770, MK545900, X, MK546162, X. Bidens sp. nov ., Mo'orea, Taputuarai & Meyer s.n. (PAP), MK545641, MK545771, MK545901, MK546013, MK546163, MK546283. Bidens sp. nov ., Mo'orea, Butaud, J-F 2978 (PAP), MK545637, MK545766, MK545896, MK546010, MK546158, MK546279. Bidens squarrosa Kunth, Mexico, Veracruz, Nee, M & J Calzada 22429 (UBC), MK545773, Х, MK546014, MK546165, MK545643, MK546285. Bidens subalternans DC., Australia, Queensland, Hosking, JR 2929 (US, NSW), MK545644, MK545774, MK545902, MK546015, MK546166, MK546286. Bidens subalternans DC., Australia, Calala, Hosking, JR 3335 (US, NSW), MK545645, MK545775, MK545903, MK546016, MK546167, MK546287. Bidens torta Sherff, USA, O'ahu, Morden, CW, J Lau & R Randell 1536 (HAW), MW152214, MW145344, MW152191, MW152231, MK546168, MW152170. Bidens torta Sherff, USA, O'ahu, Morden, CW 1931 (HAW), MK545646, MK545776, MK545904, MK546017, MK546169, MK546288. Bidens tripartita L., USA, OH, Roberts, ML 6050 (KANU), MK545576, MK545705, MK545836, MK545960, MK546084, MK546229. Bidens uapensis (F.Br.) Sherff, Ua Pou, Lorence, D 9098 (BISH, P, PAP, PTBG, US), MK545616, MK545745, MK545877, MK545991, MK546134, MK546259. Bidens uapensis (F.Br.) Sherff, Ua Pou, Dunn et al. 241 (P, PAP, PTBG, US), MK545649, MK545779, MK545906, X, MK546172, X. Bidens uapensis (F.Br.) Sherff, Ua Pou (cult), Lorence, DH 9474 (PTBG), MK545618, MK545747, MK545879, X, MK546136, MK546261. Bidens uapensis (F.Br.) Sherff, Ua Pou, Perlman, S & KR Wood 19083 (BISH, PTBG), MK545648, MK545778, MK545905, MK546019, MK546171, MK546290. Bidens valida Sherff, USA, Kaua'i, Wood, KR 1351 (PTBG, US), MK545651, MK545781, MK545908, MK546021, MK546175, X. Bidens valida Sherff, USA, Kaua'i (cult), Wood, KR 10930 (PTBG), MW152217, MW145348, MW152194, MW152229, MK546174, MW152173. Bidens wichmanii W.L. Wagner, J.R. Clark & Lorence, Fatu Hiva, Wood, KR 10139 (PTBG), MK545650, MK545780, MK545907, MK546020, MK546173, MK546291. Bidens wichmanii W.L. Wagner, J.R. Clark & Lorence, Fatu Hiva, Lorence, DH & B Nishek 8813 (PTBG), MK545583, X, MK545842, X, MK546090, X. Bidens wiebkei Sherff, USA, Moloka'i, Knope, M & S Hinard 47 (BISH), MW152225, MW145346, MW152203, MW152246, MK546176, MW152181. Bidens wiebkei Sherff, USA, Moloka'i, Knope, M & S Hinard 48 (BISH), MK545652, MK545782, MK545909, MK546022, MK546177, MK546292. Bidens woodii W.L. Wagner, J.R. Clark & Lorence, Ua Pou, Wood, KR 10806 (HPDL, BISH, P, PAP, PTBG, US), MK545582, MK545712, MK545844, MK545964, X, X. Coreocarpus congregatus (S.F. Blake) E.B. Sm, Mexico, Sinaloa, Smith, E 3959 (UARK), MK545654, MK545784, MK545911, MK546024, MK546179, MK546294. Coreocarpus sonoranus Sherff, Mexico, Sonora, Smith, E 3928 (UARK), MK545655, MK545785, MK545912, MK546025, MK546180, MK546295. Coreopsis auriculata L., USA, NC, Smith, E 3514 (UARK), MK545656, MK545786, MK545913, MK546026, MK546181, MK546296. Coreopsis bigelovii (A. Gray) Voss, USA, CA, Crawford, D 1477 (KANU), MK545657, MK545787, MK545914, MK546027, MK546182, MK546297. Coreopsis connata Cabrera, Peru, Celendin, Stuessy et al. 12517 (OS), MK545658, MK545788, MK545915, MK546028, MK546183, X. Coreopsis cyclocarpa S.F. Blake, Mexico, Jalisco, Crawford et al. 1395 (OS), MK545653, MK545783, MK545910, MK546023, MK546178, MK546293. Coreopsis delfiniifolia Lam., USA, SC, Crawford, D & P Lewis 1461, MK545659, MK545789, MK545916, MK546029, MK546184, MK546298. Coreopsis floridana E.B. Sm., USA, FL, Crawford, D & D Giannasi 1806 (GA), MK545660, MK545790, MK545917, MK546030, MK546185, MK546299. **Coreopsis gigantea** (Kellogg) H.M. Hall, USA, CA, No voucher, Elisens, W. s.n., MK545661, MK545791, MK545918, MK546031, MK546186, MK546300. Coreopsis gladiata Walter, USA, FL, Crawford, D & D Giannasi 1802, MK545662, MK545792, MK545919, MK546032, MK546187, MK546301. Coreopsis lanceolata L., Cook Island, Buelow, GP 1463 (CHR), MK545663, MK545793, MK545920, MK546033, MK546188, MK546302. Coreopsis latifolia Michx., USA, NC, Crawford, D & P Lewis 1466, MK545664, X, MK545921, MK546034, MK546189, X. Coreopsis petrophila A. Gray, Mexico, Jalisco, Crawford et al. 1389 (OS), MK545665, MK545794, MK545922, MK546035, MK546190, MK546303. Coreopsis rhyacophila Greenm., Mexico, Morelos, Yahara 225 (OS), MK545666,

MK545795, MK545923, MK546036, MK546191, MK546304. Coreopsis verticillata L., USA, Delande 5409, X, MK545796, MK545924, MK546037, MK546192, MK546305. Cosmos bipinnatus Cav., Mexico (cult), Ganders, FR 95-3, MK545667, MK545797, MK545925, MK546038, MK546193, MK546306. Fitchia speciosa Cheeseman, USA, O'ahu (cult), Funk, V 12444 (US), MK545668, MK545798, MK545926, MK546039, MK546194, MK546307. Fitchia tahitensis Nadeaud, Tahiti, Florence, J 3881 (BISH, US), MK545669, MK545799, X, MK546040, MK546195, X. Glossocardia bidens (Retz.) Veldkamp, Australia, Woodsreef, Hosking, JR 3306 (US, NSW), X, MK545801, MK545928, MK546042, MK546197, MK546309. Glossocardia bidens (Retz.) Veldkamp, Australia, Hosking, JR 3325 (US, NSW), MK545670, MK545800, MK545927, MK546041, MK546196, MK546308. Henricksonia mexicana B.L.Turner, Mexico, Durango, Villarreal, JA, A Rodriguez Gamez & MA Carranza 6173 (TEX), MK545671, MK545802, MK545929, MK546043, MK546198, MK546310. Oparanthus hivoanus (O. Deg. & Sherff) R.K. Shannon & W.L. Wagner, Hiva Oa, Perlman, S 18347 (BISH, US), MK545672, MK545803, MK545930, MK546044, MK546199, MK546311.

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Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse. 12704/suppinfo:

Table S1. The best-scoring partition scheme as defined by PartitionFinder2 under the Aikake Information Criterion (AIC), consisting of eight data subsets. The best model for each partition was determined in jModelTest.

Table S2. Event counts (mean and standard deviations) for Pacific *Bidens* from 500 biogeographic stochastic mappings in BioGeoBEARS. Mapping was performed using parameters from the DEC+j+x model of biogeography.