

Phylogeography, population genetics and distribution modelling reveal vulnerability of *Scirpus longii* (Cyperaceae) and the Atlantic Coastal Plain Flora to climate change

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Abstract

A proactive approach to conservation must be predictive, anticipating how habitats will change and which species are likely to decline or prosper. We use composite species distribution modelling to identify suitable habitats for 18 members of the North American Atlantic Coastal Plain Flora (ACPF) since the Last Glacial Maximum and project these into the future. We then use *Scirpus longii* (Cyperaceae), a globally imperiled ACPF sedge with many of the characteristics of extinction vulnerability, as a case study. We integrate phylogeographical and population genetic analyses and species distribution modelling to develop a broad view of its current condition and prognosis for conservation. We use genotyping-by-sequencing to characterize the genomes of 142 *S. longii* individuals from 20 populations distributed throughout its range (New Jersey to Nova Scotia). We measure the distribution of genetic diversity in the species and reconstruct its phylogeographical history using the SNAPP and RASE models. Extant populations of *S. longii* originated from a single refugium south of the Laurentide ice sheet around 25 ka. The genetic diversity of *S. longii* is exceedingly low, populations exhibit little genetic structure and the species is slightly inbred. Projected climate scenarios indicate that nearly half of extant populations of *S. longii* will be exposed to unsuitable climate by 2070. Similar changes in suitable habitat will occur for many other northern ACPF species—centres of diversity will shift northward and Nova Scotia may become the last refuges for those species not extinguished.

KEYWORDS

community modelling, conservation, genotyping-by-sequencing, niche modelling, RASE, SNAPP

1 | INTRODUCTION

Little doubt remains that we are in the midst of the sixth great extinction, with total species loss in the recent Holocene expected to be of the same magnitude as all five previous mass extinctions (Dirzo et al., 2014; Doughty et al., 2016; Glavin, 2006; Leakey & Lewin, 1995; Pimm & Brooks, 2000; Vamosi, Magallón, Mayrose, Otto, & Sauquet, 2018). Nearly all of the current threats to species are anthropogenic (Dirzo et al., 2014; Vellend, Baeten, &

Becker-Scarpitta, 2017; Young, McCauley, Galetti, & Dirzo, 2016), whether due to habitat destruction and fragmentation, pollution and eutrophication, alteration of hydrology, over-harvesting, introduction of invasive species and disease, invasive hybridization, or the consequences of climate change, to name a few. Strategies for conservation must anticipate which species are likely to decline given evolutionary history, standing genetic diversity, phenotypic plasticity, geographical barriers, ecology and current distribution (Davis, Willis, Primack, & Miller-Rushing, 2010; Heller

& Zavaleta, 2009; Oberle & Schaal, 2011; Parks, Jenkins, Ostry, Zhao, & Woeste, 2014). Understanding the processes that have contributed to the present distribution of diversity is critical for effective conservation. This is particularly true in this era of rapid climate change (Oberle & Schaal, 2011). The extent to which a species will be able to cope with this change depends on physiological tolerances to climate-related parameters, ability to migrate and genetic diversity (Bradshaw & Holzapfel, 2001; Etterson & Shaw, 2001; Franks, Sim, & Weis, 2007; Kelly, Sanford, & Grosberg, 2013; Mitchell, Sgro, & Hoffman, 2011; Reed et al., 2011; Visser, 2008; Walters, Blankenhorn, & Berger, 2012). Organisms with strict ecological requirements, low dispersibility and restricted geographical distributions may be unable to track their preferred habitat, leaving the survival of lineages contingent on physiological plasticity or evolutionary adaptation. Such species may be at greater risk of extinction from climate change than species that are ecological generalists, widespread and genetically diverse (Chevin, 2012; Kelly et al., 2013; Stelkens, Brockhurst, Hurst, & Greig, 2014). Similarly, rapid anthropogenic climate change will no doubt place entire ecosystems or elements thereof at risk of extinction.

The eastern North American Atlantic Coastal Plain Flora (ACPF) is one such element that faces risk from continued anthropogenic change. The geographical ranges of most members of this flora are at low elevations and near the coast from southern New Jersey to Maine, with disjunct populations of some species in or near the southern Great Lakes basin and in Nova Scotia (Wisheu & Keddy,

1989). Occupying a developed region of North America where 98 ACPF species are known to occur (S. Blaney, personal communication, 2016), ACPF habitat is highly fragmented, and many members of the flora are genetically depauperate and largely asexual in reproduction (Brochmann, Gabrielsen, Nordal, Landvik, & Elven, 2003; Noss et al., 2015; Rawinski, 2001). Members of the northern ACPF are generally of low competitive ability (Querry, Bordeleau, Harper, & Basquill, 2017; WisheuKeddy, Keddy, & Hill, 1994) and are either tolerant of stress (particularly low nutrient levels in freshwater habitat) or adapted to disturbance (such as fire and ice-scouring of shallow shorelines) (Grime, 1979).

One species of the northern ACPF, the globally imperiled (G2G3: NatureServe, 2015) sedge *Scirpus longii* Fern. (Cyperaceae; Figure 1), has many of the characteristics generally associated with vulnerability to extinction. *S. longii* is a diploid, monoecious species with a historical range from the pine barrens of southern New Jersey to the coastal plains of New York, Rhode Island, Connecticut, Massachusetts, New Hampshire, Maine and southwestern Nova Scotia (Figure 2). *S. longii* occurs on peaty soils in wetlands that tend to dry in late summer (Fernald, 1942; Schuyler, 1963a, 1963b; Wisheu et al., 1994). *S. longii* is listed as “special concern” in Canada although 45 populations are known in Nova Scotia and more are being discovered every year. Although federally unlisted in the United States, *S. longii* is considered “endangered” in every state except Massachusetts and Maine, where it is “threatened,” and New York and Connecticut, where it is believed to be extirpated.



FIGURE 1 Typical flora, vegetative and growth form characteristics of *Scirpus longii*. (a) Inflorescence. Note the pedicellate spikelets, long floral bristles, and blackened floral scales and bases of involucral bracts. (b) Vegetative leaf sheaths and base of whitish, thick rhizome. Photo credit: Jennifer Garrett. (c) Characteristic circular clonal growth pattern. Photo credit: Donald Cameron. (d) Aerial photograph of population of *S. longii* at Noquochoke, MA, USA. Note the circular growth patterns of clones throughout the population. Photo credit: Office of Geographic Information (MassGIS), Massachusetts [Colour figure can be viewed at wileyonlinelibrary.com]

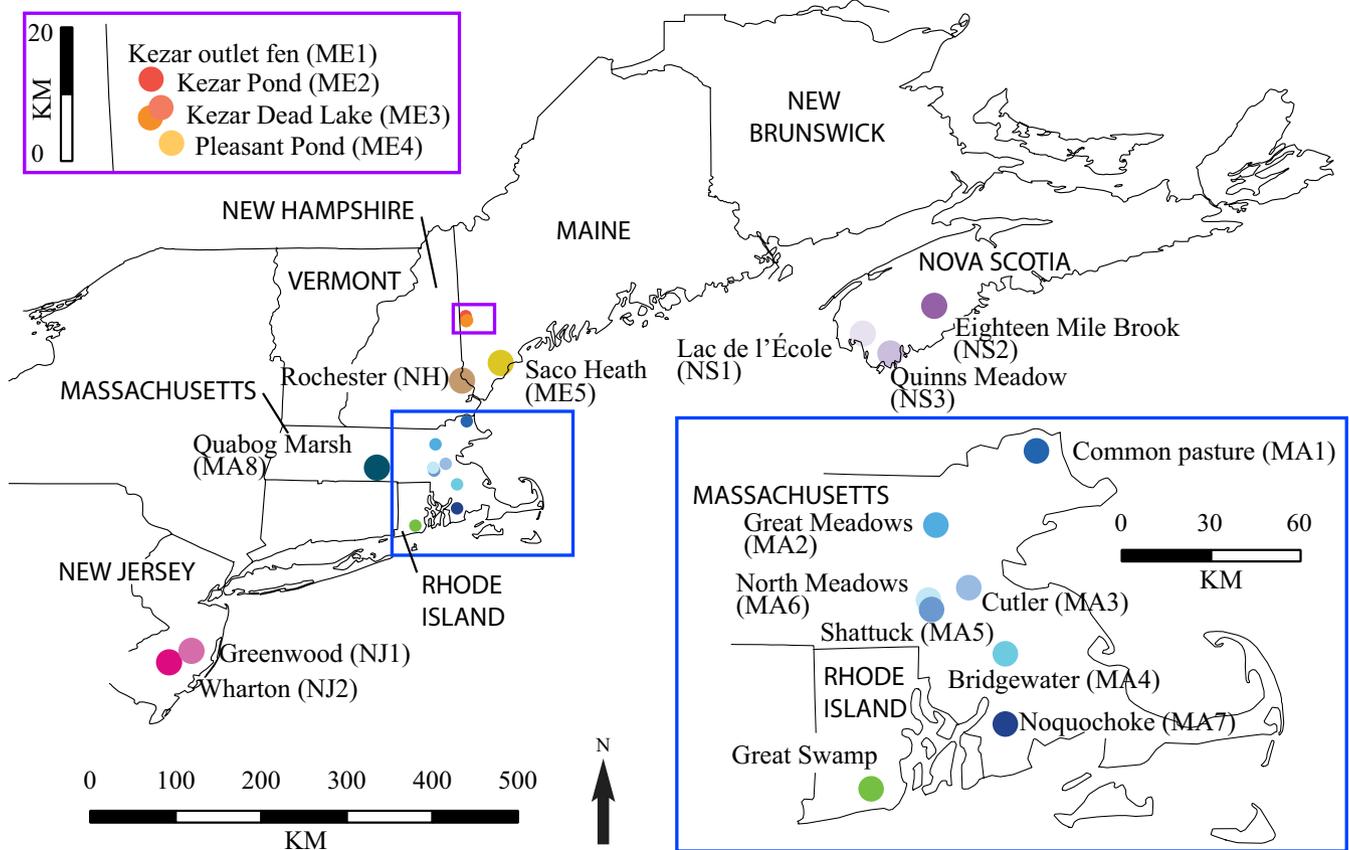


FIGURE 2 Map of sampled populations of *Scirpus longii*. These populations represent the majority of known localities of *S. longii*, with the exception of those in Nova Scotia where there are many known disjunct populations. Sizes of dots do not indicate population sizes. State and province names are presented in caps [Colour figure can be viewed at wileyonlinelibrary.com]

Similar to many species of the northern ACPF, *S. longii* reproduces primarily by asexual means (rhizomes) (Brochmann et al., 2003). In the absence of stress, *S. longii* reproduction is purely clonal with shoots arising from rhizomes in an outwardly extending, circular pattern (Schuyler, 1963a, 1963b; Hill & Johansson, 1992; Figure 1c,d). Clone size indicates age, with rhizomes growing at a rate of 1.5–2.4 cm/year (Hill, 1994). The largest reported clones have a diameter in excess of 50 m (Hill & Johansson, 1992). Thus, undisturbed clones may live for hundreds of years (Hill, 1994; MacKay, Reid, William, & Hill, 2010). Reports differ on what induces culm production. On the one hand, Schuyler (1963b) suggested that excessive summer-drying induces flowering, while Rawinski (2001) posited that prolonged flooding might be responsible. Sweeney and Ogilvie (1993) reported that muskrat feeding on the bases of vegetative shoots causes flowering. Fire seems to be the primary stimulant of culm production, with multiple reported instances of massive flowering following sweeping fires (Hill & Johansson, 1992; Rawinski, 2001; Schuyler, 1963b; Schuyler & Stazs, 1985). In historical terms, culm production induced by hydrological stress or herbivory has probably been negligible relative to that induced by fire. Certainly, culms are very rare in the field and most populations are entirely of vegetative shoots. The ability of *S. longii* to tolerate low nutrient levels (Hill & Johansson, 1992) and the fact that flowering is fire-induced make

this species constitutively stress-tolerant and facultatively ruderal or weedy (Grime, 1979).

Scirpus longii exhibits many of the characteristics of extinction susceptibility and provides a useful case study to assess the vulnerability of the northern ACPF to climate change. The limited distribution of *S. longii* consists of disjunct and probably genetically isolated populations in wetlands scattered throughout the Atlantic Coastal Plain (Schuyler, 1963a). Furthermore, its sexual reproduction is restricted and infrequent, thus limiting gene flow by transport of seed (Rawinski, 2001; Schuyler, 1963b; Schuyler & Stazs, 1985).

This study has two aims: (a) to investigate the vulnerability of the ACPF to climate change and predict the climate change-fate of the ACPF in north-eastern North America; and (b) to use *S. longii* to determine whether a suite of phylogeographical, population genetic and modelling approaches are useful for assessing vulnerability of the ACPF to climate change, and if so, to use these analyses to inform conservation strategies for ACPF species. With regard to the general fate of the North American ACPF under conditions of rapid climate change, we apply composite species distribution modelling techniques to estimate past (post-glacial) and near future distributions of 18 representative northern ACPF species. Given the geography of north-eastern North America, especially the absence of substantial low-elevation coastal plain north of Nova Scotia and the

Appalachian barrier to westward migration, we predict that northern ACPF species face extinction unless they are already present in, or otherwise disperse to, Nova Scotia.

With regard to *S. longii*, we first infer the relatedness of extant populations and reconstruct a history of post-glacial migration using phylogeographical analysis and species distribution modelling. The concentration of populations in eastern Massachusetts suggests that this region is the ancestral, post-glacial source from which extant populations of *S. longii* have descended. We test the alternative hypothesis that the northern populations are derived from ancestral populations that inhabited what is now southern New Jersey. Second, we quantify the extent and distribution of genetic diversity of *S. longii* throughout its range. Under the expectation that extant populations have diverged since the Last Glacial Maximum (LGM) c. 26.5 ka, and given the extensive habitat fragmentation and fire suppression that has recently occurred throughout the range of *S. longii*, we hypothesize that genetic diversity within, and differentiation among, populations will be low. Third, we determine which populations of *S. longii* may be at risk of extirpation as climate changes, and quantify potential changes in heterozygosity throughout its range. Finally, we discuss the conservation implications of our findings for the entire northern ACPF and propose strategies for the mitigation of loss of populations.

2 | MATERIAL AND METHODS

2.1 | Distribution modelling of the Northern Atlantic Coastal Plain flora

To model the potential location of the North Atlantic Coastal Plain Flora through time, we developed species distribution models (SDMs) for *Scirpus longii* and 17 other northern ACPF species representing 14 families and including ferns, monocots and dicots (Supporting Information Table S1). These species are found in various habitats in the northern ACP, such as coastal barrens, brackish marshes, acidic bogs and fens, wooded swamps, grass and sedge meadows, and the shores and shallows of lakes and rivers. We developed SDMs using MAXENT version 3.3.3k (Phillips, Anderson, & Schapire, 2006). For each species, we compiled a data set of occurrences by combining our field observations with records from the Global Biodiversity Information Facility (GBIF; www.gbif.org), which were downloaded using the R package RGBIF (Chamberlain, Barve, Mcglinn, & Oldoni, 2018). These records were manually examined, and we removed all records that were outside the documented ranges of each species. We then obtained 19 bioclimatic raster layers from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) for each of four dates: the LGM (c. 22 ka), the mid-Holocene near the peak of the Hypsithermal Maximum (c. 6 ka; Deevey & Flint, 1957), the present and 2070. We used the MIRCO-ESM 2010 global climate model (Watanabe et al., 2011) for historical and future projections. The prediction of future climates varies with the greenhouse gas Representative

Concentration Pathway (RCP; Meinshausen et al., 2011) model used. RCPs can be optimistic (i.e., RCP26: greenhouse gas concentrations are currently at their peak, or are declining) or pessimistic (i.e., RCP85: greenhouse gas concentrations will continue to increase until 2070). We created models using four RCPs that span these extremes.

For model building, we cropped the present-day bioclimatic raster layers to include only the region of interest for the northern ACPF (82–53°W, 32–52°N). This increased computational efficiency and reduced the area from which pseudo-absences could be randomly selected, which is essential for discriminating between hospitable and inhospitable areas (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012). Thus, pseudo-absences were selected only from regions close to occurrences of ACPF species. To prevent over-fitting, we eliminated correlated bioclimatic raster layers from the analysis (Braunisch et al., 2013). To do this, we created an SDM using all variables, recorded the independent contribution of each layer, and identified which of the 19 variables were strongly correlated ($r > 0.80$). Of the latter, we eliminated those variables that contributed the least to the model, retaining eight relatively uncorrelated, informative variables: elevation, mean annual temperature, annual temperature range, mean temperature of the wettest quarter, mean temperature of the coldest quarter, precipitation of the driest month, precipitation of the driest quarter and precipitation of the warmest quarter. We also incorporated soil texture layers, including per cent clay, gravel, sand and silt. Soil data were obtained from the Harmonized World Soil Database (Food & Agricultural Organization of the United Nations, 2012). We used area under the curve (AUC) to evaluate model fits, and transformed logistic probabilities of species occurrence to a binary presence/absence matrix for each model. We then tallied the species richness in each raster cell (at 30 arc-second resolution), and calculated the change in richness comparing present-day models to models projected to 2070 under each of the emissions scenarios.

2.2 | Sampling of *Scirpus longii*

We collected *S. longii* from 20 populations throughout its range and throughout the extent of each population during the summers of 2010, 2011, 2012 and 2013 (Figure 2). We attempted to obtain at least 24 specimens from each population, but were limited when population sizes were small (<100 clones). In these cases, we collected specimens from no more than 10% of the clones. As individual clones are usually distinct due to their circular nature, we were able to avoid collecting more than a single specimen from any clone. To prevent accidental duplicate sampling of a clone, we did not collect specimens from neighbouring or overlapping clones. In instances when circular clones were not identifiable, we enforced a minimum distance of 20 m between samples. Voucher specimens are preserved at Mount Saint Vincent University (MSVU), Academy of Natural Sciences Philadelphia Herbarium (PH) and Wisconsin State Herbarium (WIS).

2.3 | DNA preparation and sequencing

We prepared DNA libraries for 230 individuals for genotyping-by-sequencing (GBS; Davey et al., 2011; Elshire et al., 2011). GBS is effective in identifying genome-wide variations among closely related individuals when reference genomes are not available (Emerson et al., 2010; Narum, Buerkle, Davey, Miller, & Hohenlohe, 2013). We extracted total genomic DNA from silica-dried leaf tissue using a DNeasy Plant Mini Kit (Qiagen). DNA was quantified with Quant-iT PicoGreen dsDNA assay kits and cleaned and concentrated with AxyPrep Mag PCR Clean-Up beads (Axygen Scientific). DNA preparations were submitted to the University of Wisconsin-Madison Biotechnology Center, where libraries were prepared using the restriction enzyme *EcoRI*. All samples were sequenced using the Illumina HiSeq 2000 Sequencing System (Illumina).

2.4 | Processing of sequence data

Raw sequence reads were subjected to a series of filtering steps. Illumina adapter sequences were removed with *CUTADAPT* version 1.3 (Martin, 2011). Filtering and assembly steps were conducted with *STACKS* version 1.21 (Catchen, Hohenlohe, Bassham, Amores, & Cresko, 2013). The *PROCESS_RADTAGS* program, which removes reads with uncalled bases (*-c* option) or that do not meet the minimum 90% probability of being correct (*-q* option), truncated all reads to 93 bases and demultiplexed the sequences.

To identify the optimal parameters for assembling loci in *STACKS*, we followed the parameter-testing pipeline established by Paris, Stevens, and Catchen (2017). Two parameters in particular can have significant impacts on the number and heterozygosity of recovered loci. These include the *ustacks -M* parameter, which determines the maximum allowable number of nucleotide differences within loci of individual samples, and the *cstacks -n* parameter, which determines the allowable number of nucleotide differences when merging sample-specific loci into catalogue loci. We first ran the *STACKS* pipeline on a subset of 36 randomly selected samples, increasing *-M* sequentially from 1 to 8 while keep *-n* constant at 1. Following Paris et al. (2017), we identified the minimum value of *-M* that maximized the number of recovered polymorphic catalogue loci, whereby no significant increase in polymorphic loci would be recovered by another increase to *-M*. In this data set, the optimal value for *-M* was 2. We then held *-M* constant at 2, and iteratively varied the *-n* parameter to determine whether this made an appreciable difference to the number and heterozygosity of recovered loci. We found no significant increase after *n* = 2.

We then ran the *STACKS* pipeline on the entire data set with *-M* and *-n* both allowing two nucleotide mismatches. Following assembly, we ran *rxstacks*, which makes corrections to the insignificant genotype models for individual samples, given the population-wide data set. We concluded assembly with the program *POPULATIONS*, eliminating loci that fell below a minimum log-likelihood limit of *-50* and treating all individuals as though they belonged to a single population.

Following assembly, we conducted a series of additional filtering steps. First, to eliminate putative chloroplast DNA loci, we removed loci that showed no variation among all individuals and across all populations. Second, we eliminated samples with over 25% missing data, which also tended to have substantially lower sequencing depths for loci. Third, we eliminated loci that were missing from more than 25% of individuals of any single population. These filtering steps were conducted using the packages “*HIERFSTAT*” (Goudet & Jombart, 2017) and “*ADEGENET*” (Jombart & Ahmed, 2011) in R version 3.1.2 (R Core Development Team, 2018).

2.5 | Molecular dating and phylogeography

We reconstructed the evolutionary relationships and timing of divergence of *S. longii* populations using *SNAPP* version 2.4.8 (Bouckaert et al., 2014; Heled & Drummond, 2010). *SNAPP* is a Bayesian coalescent model that simultaneously estimates evolutionary relationships and timing of divergence of populations, and is specifically designed for biallelic and randomly distributed single nucleotide polymorphisms (SNPs). *SNAPP* is computationally intensive and does not allow for missing data. We therefore reduced our data set, first by eliminating all samples with more than 10% missing data and second by removing loci from this reduced data set with any missing data. Only polymorphic loci were included in the data set, and mutations rates were sampled during the *SNAPP* analysis. We used the default Yule tree prior, and ran the analysis for 1 million generations. Effective sampling was assessed using *TRACER* version 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014). We constructed a maximum clade credibility tree using *TREEANNOTATOR* version 2.4.8 (Bouckaert et al., 2014; Heled & Drummond, 2010). We performed a second phylogenetic analysis with *BEAST* to determine if phylogenetic resolution was improved using all identified SNPs, with missing data included. We used the GTR model of molecular evolution for this second analysis, which identified as the best-fitting model using *JMODELTEST* version 2.1.10 (Darriba, Taboada, Doallo, & Posada, 2012).

We estimated the phylogeographical history of *S. longii* using *RASE* (Quintero, Keil, Jetz, & Crawford, 2015), a Bayesian method that produces area reconstructions, with migration conditioned on the *SNAPP* chronogram, using continuous species distribution data. We produced spatial polygons outlining each population, based on our specimen collections, and used these as the input localities for the reconstruction of ancestral ranges. We ran *RASE* for 10,000 generations and assessed effective sampling using the R package *CODA* (Plummer, Best, Cowles, & Vines, 2006).

2.6 | Population genetics

We determined the extent of genetic differentiation among populations by calculating global heterozygosity, inbreeding coefficients and global and pairwise F_{ST} values (Nei, 1978; Nei & Li, 1979; Ritland, 1996; Weir & Cockerham, 1984) using the “*HIERFSTAT*” package (Goudet & Jombart, 2017). We conducted isolation-by-distance Mantel (1967) tests to determine whether

significant relationships exist between genetic distances (D ; Nei, 1972) and the Euclidean geographical distances between populations. Pairwise measurements, permutation tests of inbreeding coefficients, and Mantel tests were all conducted with SPAGeDI version 1.5 (Hardy & Vekemans, 2002). We performed principal components analysis (PCO) of genotypes using the package "ADEGENET" (Jombart & Ahmed, 2011). We next integrated species distribution models of *S. longii* with patterns of projected heterozygosity. Following Espíndola et al. (2012), we tabulated the presence and absence of all alleles in each population, where an allele was counted as present if it was represented in at least one individual, and as absent if it was not present in at least one individual. We then used an inverse distance-weighted interpolation of both presences and absences with a decay power weight of 1. For each raster pixel, we classified a locus as heterozygous if presences and absences were projected with a score of at least 0.4, and then calculated mean heterozygosity in each pixel. We then overlaid this interpolation onto the present and future SDMs of *S. longii* (see above).

3 | RESULTS

3.1 | Species distribution modelling and extrapolation

We constructed a database with 2,462 locality records of the 18 northern ACPF species chosen for this study (Supporting Information Table S1). The initial models trained with present-day bioclimatic data had AUC scores from 0.973 to 0.990, suggesting a strong ability to discriminate between climatically suitable and unsuitable habitat areas. Visual inspection of the distributions indicated that the models reflected actual species distributions with high fidelity, suggesting that a composite model of species richness would serve as a strong proxy for the location of the northern ACPF (Figure 3a). Climatically suitable areas for the 18 species during the LGM included much of the eastern United States south of the Laurentide Ice Sheet. (Figure 3b). Patterns of species richness during the mid-Holocene (6 ka) are comparable with modern patterns, but with decreased diversity in southern New Jersey and increased diversity throughout Nova Scotia (Figure 3c). Projections for the future distribution of the northern ACPF vary depending on the RCP emissions scenario (Figure 3d–g). In all scenarios, northern ACPF diversity is projected to decrease in New Jersey and throughout the New England region, but increase along the Maine and adjoining New Brunswick Atlantic coast, throughout Nova Scotia (at present a centre of ACPF diversity), and especially in Newfoundland, relative to modern ACPF diversity. The models also predict climatic suitability of more inland areas west of the Appalachian Mountains and along the St. Lawrence River Valley. Models of present and future distributions of *Scirpus longii* in particular indicate a northward shift in climatically suitable areas (Figure 4). Suitable habitat increases throughout Maine, New Brunswick, Quebec and Nova Scotia.

(a) Present Distributions

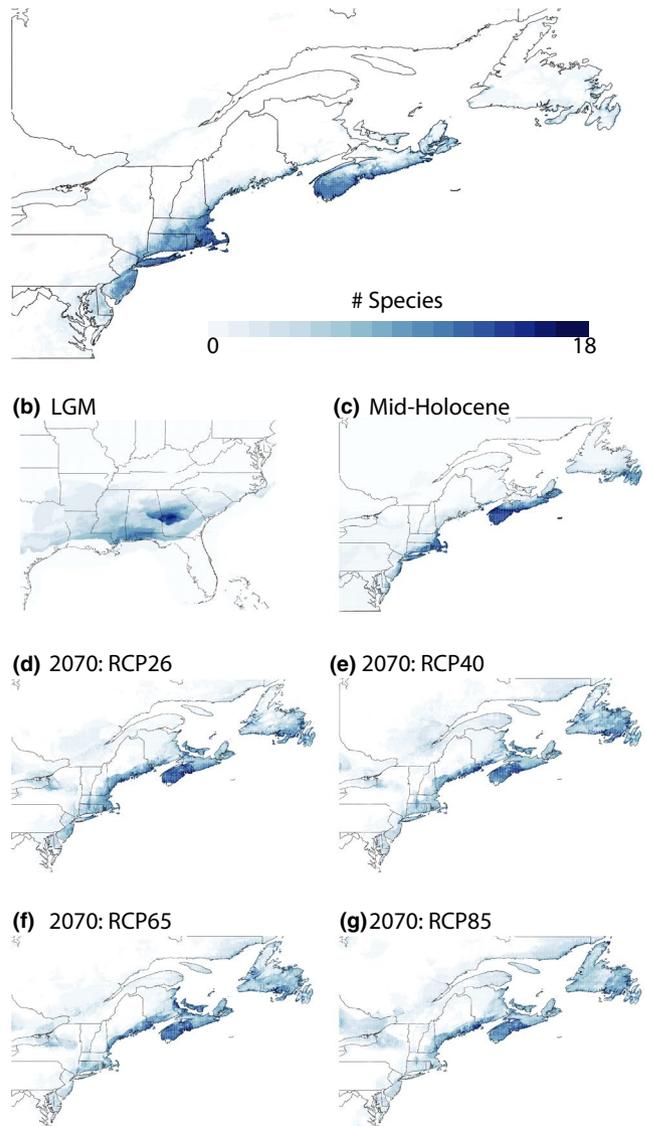
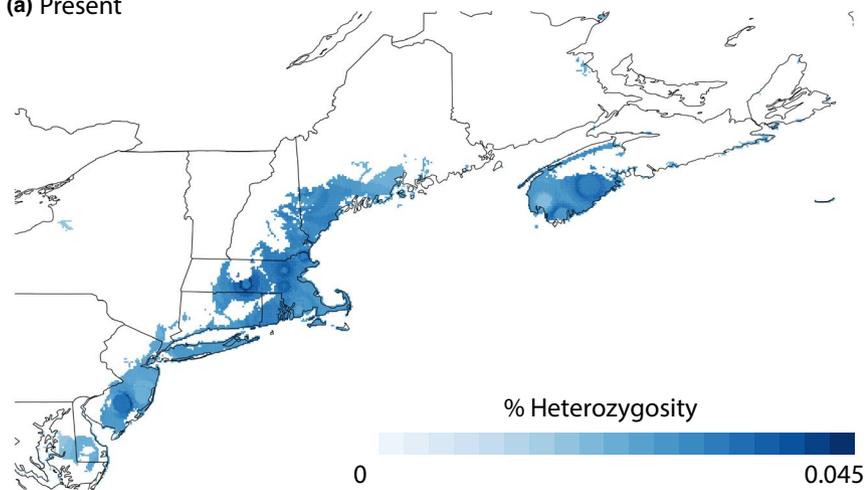


FIGURE 3 Composite model of distributions of 18 northern Atlantic Coastal Plain Flora (ACPF) species. Predicted species richness is indicated in blue. (a) Composite model based on present-day distributions and climates. (b) Model projected to the Last Glacial Maximum (LGM). (c) Model projected to the mid-Holocene (c. 6 ka). (d–g) Model projected to 2070 under four increasingly pessimistic greenhouse emissions scenarios. Representative Concentration Pathway (RCP) models reflect varying expectations of future carbon emissions, ranging from most optimistic (RCP26) to most pessimistic (RCP80) [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Genotyping by sequencing

Illumina yielded 72 billion base pairs of sequence data for 230 samples. These were parsed into over 560 million stacks with an average depth of 14.7 sequences. Stacks were assembled into 7,314 polymorphic loci, with an average depth of 15.9 reads. We eliminated 42 individuals that had more than 25% missing data, and then removed 6,217 loci that were missing in more than 25% of the remaining individuals. Our final data set consisted of 1,097 loci of 142 individuals.

(a) Present



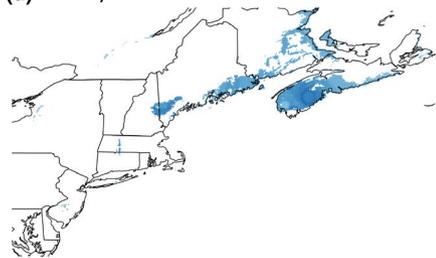
(b) 2070, RCP26



(c) 2070, RCP60



(d) 2070, RCP45



(e) 2070, RCP85



FIGURE 4 Genetic diversity of *Scirpus longii* in the present and under four models of climate change. In all images, every blue pixel represents an area that is climatically suitable for *S. longii*. The degree of intensity of blue of represents the projected heterozygosity of the pixel. (a) SDM (species distribution model) based on present-day occurrences and climates. (b–e) SDM projected to 2070 under the RCP26, RCP40, RCP60 and RCP85 emissions scenarios, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

3.3 | Molecular dating and phylogeography

For molecular dating, we reduced our data set to 71 individuals representing all populations and 107 SNPs, with no missing data. SNAPP analysis reached convergence and achieved effective sample sizes in excess of 200 after 1 million generations. A maximum clade credibility chronogram (Figure 5a) was recovered with low support, indicating low molecular divergence amongst most populations. However, several clades were recovered with strong to moderate support. The Kezar and Pleasant Pond populations in Maine (Figure 2) formed a well-supported clade. Great Meadows and Common Pasture, the two northernmost Massachusetts populations, formed a clade with moderate support, as did the two New Jersey populations (Wharton and Greenwood). The common ancestor of all sampled populations was estimated to have lived 26.2 ka, immediately after the LGM c. 26.5 ka. Subsequent divergence was initiated soon after the initial glacial retreat. The BEAST tree, estimated using an alignment of 7,314 SNPs across 137 samples of *S. longii*, was recovered with strong support (Supporting Information Figure S1). In this phylogeny, the Maine populations formed a clade sister to all remaining populations,

followed by a clade of Nova Scotia populations sister to the populations in New Hampshire, Massachusetts, Rhode Island and New Jersey.

Phylogeographical estimations using the SNAPP tree suggest that the common ancestor of all populations was widespread, encompassing both northern US and Nova Scotian populations (Figure 5). Geographical divergence among these populations did not begin until 13–10 ka, when Nova Scotian populations became isolated. In the context of the SMD, this phylogeographical reconstruction should be interpreted as a southerly population that migrated north and subsequently dispersed into Nova Scotia. Either subsequent migration, or vicariance of a once more-widespread population, occurred both northward towards eastern Maine and southwards towards Massachusetts and Rhode Island. A clear instance of dispersal occurred c. 4–2 ka to New Jersey from Massachusetts.

3.4 | Population genetics

The number of *S. longii* individuals per population considered in this analysis varied from one to 24 with a mean of 7.47 (Table 1). Both

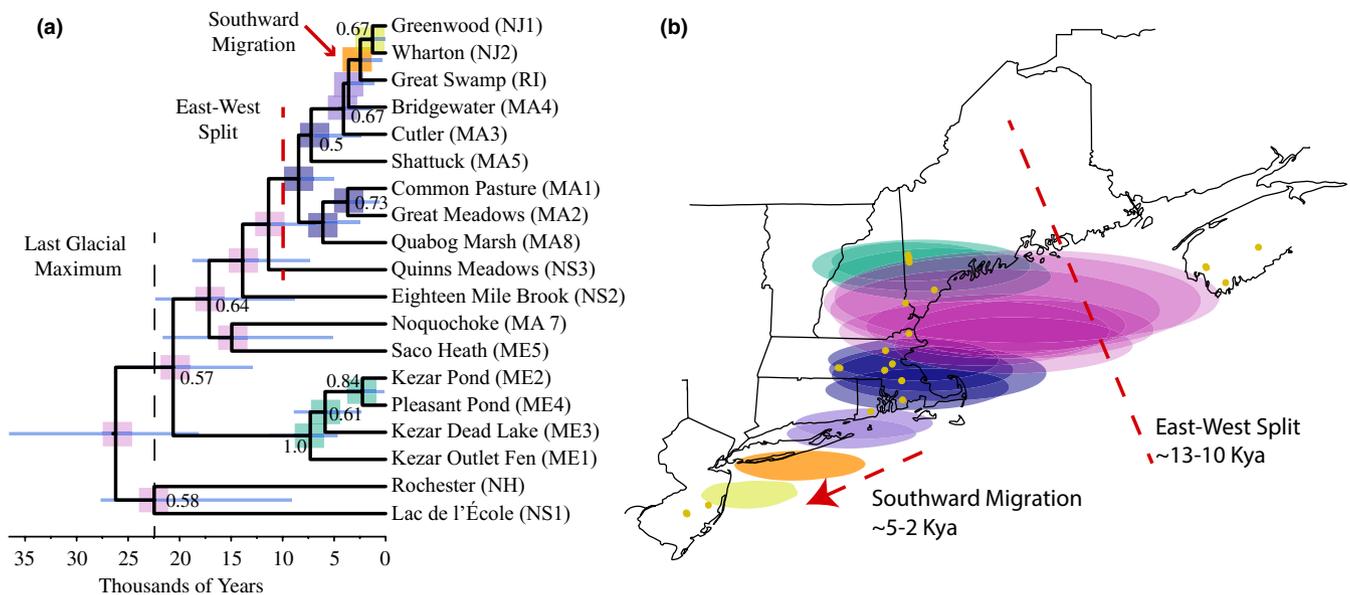


FIGURE 5 SNAPP estimate of phylogenetic relationships and divergence times and RASE estimation of historical phylogeography of *Scirpus longii* populations. (a) Chronogram of *S. longii* populations with time scale in thousands of years. Posterior probabilities are listed by nodes with >0.5 Bayesian posterior probability, and blue error bars denote the 95% confidence interval of ancestral ages. Coloured node labels correspond to ancestral areas in (b). The time of the Last Glacial Maximum (LGM) is indicated by the vertical black dotted line. Phylogenetic location of significant biographical events, including the split between Nova Scotian and US populations and the southward migration to New Jersey, are indicated with the red dotted line and arrow, respectively. (b) Ancestral ranges estimated using RASE. Coloured ovals indicate the estimated ancestral areas, with colours corresponding to the node labels in (a) [Colour figure can be viewed at wileyonlinelibrary.com]

observed and expected heterozygosity (H_O and H_E , respectively) were low, averaging 0.20 and 0.19 across populations, respectively (Table 1). Significant departure from Hardy-Weinberg expectations was observed in most populations (average $F_{IS} = 0.03$; Table 1) and among all individuals ($F_{IT} = 0.24$). Only 13% of the total genetic variance was partitioned among populations (F_{ST}). Pairwise F_{ST} comparisons of populations ranged from 0.03 to 0.44 (Table 2). Isolation-by-distance Mantel tests found no significant correlation between geographical and genetic distance for populations ($R^2 = 0.0208$, $p = 0.2$). PCO revealed genetic segregation of the Kezar and Pleasant Pond populations (Maine), the Noquochoke (southeastern Massachusetts) population, and Nova Scotian populations (Figure 6). All other populations overlapped substantially.

Our predictions of change in heterozygosity under models of climate change revealed a slight decline in genetic diversity for each of the models (Figure 4b–e). Based on SDM, current heterozygosity throughout the present range of *S. longii* is 0.029 (as compared to 0.020 as calculated directly from the genetic data). This heterozygosity is projected to decline to 0.027 under the RCP26 and RCP45 scenarios and to 0.025 under both the RCP65 and the RCP80 scenarios.

4 | DISCUSSION

4.1 | Phylogeography of the northern elements of the Atlantic Coastal Plain Flora

The Wisconsin Glacial Episode, which began to decline 16 ka, is the most recent in a series of Pleistocene glaciation events. At its

maximum, the Laurentide ice sheet was composed of nearly 16 million km^3 of ice extending over 12 million km^2 of North America, reaching as far as southern Indiana and Ohio, and northern Pennsylvania and New Jersey (Dyke et al., 2002; Russell, Rich, Schneider, & Lynch-Stieglitz, 2009). Sea levels fell 135 m below preglacial levels (Marshall, James, & Clarke, 2002; Mix, Bard, & Schneider, 2001), exposing over 1 million km^2 of continental shelf in the southeastern United States alone (Russell et al., 2009). The region south of the ice sheet exhibited particularly high species richness, as northern boreal and mixed deciduous forests co-occurred with wetlands, prairies and taigas (Hewitt, 2004; Jackson et al., 2000; Russell et al., 2009).

The Laurentide ice sheet covered nearly all areas currently occupied by the northern elements of the ACPF until about 16 ka (Brochmann et al., 2003). The consensus is that the northern ACPF would therefore have had to migrate southward to survive as the ice advanced, although northern glacial refugia are occasionally invoked despite a lack of fossil evidence (Brochmann et al., 2003; Godbout, Beaulieu, & Bousquet, 2010). Our composite species distribution model (Figure 3b) suggests that climatically suitable regions for the northern ACPF during the LGM extended from what is now the western Mississippi basin to at least what is now the coast of the Atlantic Ocean and probably the exposed continental shelf adjacent to Georgia and the Carolinas, and from the latitude of northern Florida to that of North Carolina with species richness increasing eastwards. ACPF species richness may have been greatest in northern Georgia, immediately south of the Appalachian Mountains. While the entire region identified by our models may have been climatically suitable for ACPF species, additional evidence leads us

TABLE 1 Population genetics statistics for *Scirpus longii*. The number of individuals examined per population, observed and expected heterozygosity (H_O and H_E respectively), and inbreeding coefficients (F_{IS}) are provided. Asterisks denote inbreeding coefficients that are significantly different from zero

Population name	No. of individuals	H_O	H_E	F_{IS}
Bridgewater	1	0.25	NA	NA
Common Pasture	9	0.21	0.23	0.06*
Cutler	2	0.24	0.26	-0.05
Eighteen Mile Brook	23	0.19	0.21	0.07*
Great Meadows	6	0.18	0.24	0.21*
Great Swamp	3	0.24	0.24	-0.02
Greenwood	3	0.16	0.22	0.17*
Kezar Dead Lake	6	0.14	0.14	0.04*
Kezar Outlet Fen	8	0.13	0.14	0.07*
Kezar Pond	4	0.19	0.18	-0.07
Lac de l'École	10	0.19	0.15	-0.21*
Noquochoke	9	0.20	0.19	-0.03*
Pleasant Pond	5	0.18	0.19	0.04*
Quabog Marsh	9	0.21	0.24	0.12
Quinns Meadow	24	0.21	0.20	-0.04
Rochester	5	0.17	0.17	-0.04
Saco Heath	1	0.14	NA	NA
Shattuck	5	0.21	0.22	0.01
Wharton	9	0.15	0.24	0.32
Average	7.47	0.19	0.20	0.03

Note. NA: not applicable.

to believe that their ranges were probably more restricted during the LGM. First, palynology indicates that most of this region consisted of cool or warm deciduous forest and open conifer woodlands (Jackson et al., 2000). Disjunct populations of ACPF species nested within these ecosystems would be perfectly consistent with their current distributions. However, palynological evidence indicates that Cyperaceae pollen is only abundant within 500 km of the ice margin (Jackson et al., 2000), which would have included northern but not central Georgia. This suggests that the habitat of many ACPF species, which often prefer the same habitat as the sedges, was not available beyond this limit. Consistent with this palynology, peatlands were uncommon in the southeast United States during the LGM (Gajewski, Viau, Sawada, Atkinson, & Wilson, 2001) and were generally restricted to the northeastern-most portion of the area identified by our analysis (Figure 3b) to be climatically suitable for the ACPF. Finally, nearly all extant populations of the species included in this study are within 130 km of the Atlantic Ocean and occupy elevations no >280 m. We therefore suggest that the ACPF during the LGM probably occupied only the climatically suitable

regions of North and South Carolina east of the Appalachians and the adjacent exposed continental shelf.

Our phylogeographical reconstruction of *S. longii* is based on a phylogeny with low resolution (Figure 5). Given the very low genetic differentiation among most extant populations ($F_{ST} = 0.13$; Figure 6), this low phylogenetic resolution is expected. The model indicates that the ancestor of extant populations of *S. longii* occupied a wide range at the peak of the LGM c. 26 ka, encompassing both Nova Scotian and northern US populations from about 27 to 13 ka, at which point the Nova Scotian, eastern Maine and Massachusetts populations became isolated from each other. The Laurentide ice sheet began to recede by 14 ka, and by 12 ka was gone in essentially all of the northeastern United States and southeastern Canada (Jacobson, Webb, & Grimm, 1987). At this time, the ACPF would have begun migrating to the north and inhabiting the recently exposed coastal plain. At least a single migration to Nova Scotia from a mainland source would have been necessary. While the phylogeographical model (Figure 5) indicates a widespread ancestral population occupying areas in both Nova Scotia and the eastern US, interpreting this model in the context of the SDMs (Figure 3) suggests that a southerly population migrated north and then dispersed to Nova Scotia. This interpretation is consistent with palynological evidence, which indicates that Cyperaceae pollen was abundant in 13-ka deposits as far north as southern coastal Labrador (Jacobson et al., 1987). Given the low resolution of the phylogeny along the backbone (Figure 5), it is impossible to determine whether a single migration or multiple migrations to Nova Scotia occurred. However, a single migration to Nova Scotia is supported by the high-resolution BEAST phylogeny (Supporting Information Figure S1), which shows a clade of Nova Scotia populations nested between the Maine populations and populations in the more southern states.

Our phylogeographical analysis of *S. longii* (Figure 5a, Supporting Information Figure S1) clearly suggests that the New Jersey populations are derived from a more northern source, and that the common ancestor of these populations and those of Massachusetts occurred only 5–2 ka. Projected diversity of the 18 ACPF species included in this study was much lower at the southern extent of the ACPF range (e.g., southern New Jersey) 6 ka than for the present (Figure 3a,c). As recently as 13 ka, southern New Jersey experienced multiple rounds of severe and localized permafrost generation following the glacial recession (French, Demitroff, Forman, & Newell, 2007; French, Demitroff, & Newell, 2009; French & Millar, 2014), thereby rendering the area unsuitable for ACPF species. Following these rounds of permafrost generation, southern New Jersey would probably have been too warm for many ACPF species until after the Hypsithermal Maximum at about 5 ka (Deevey & Flint, 1957; Delcourt & Delcourt, 1984; Gajewski et al., 2000; Terasmae & Anderson, 1970; Viau, Gajewski, Sawada, & Fines, 2006). Thus, the delayed arrival of *S. longii* in New Jersey until after the permafrost cycles and Hypsithermal Maximum indicates that our species distribution and phylogeographical models are consistent with each other and with palaeoclimatological records. The recolonization of habitat by the northern ACPF after recession of the Wisconsin Glacier was

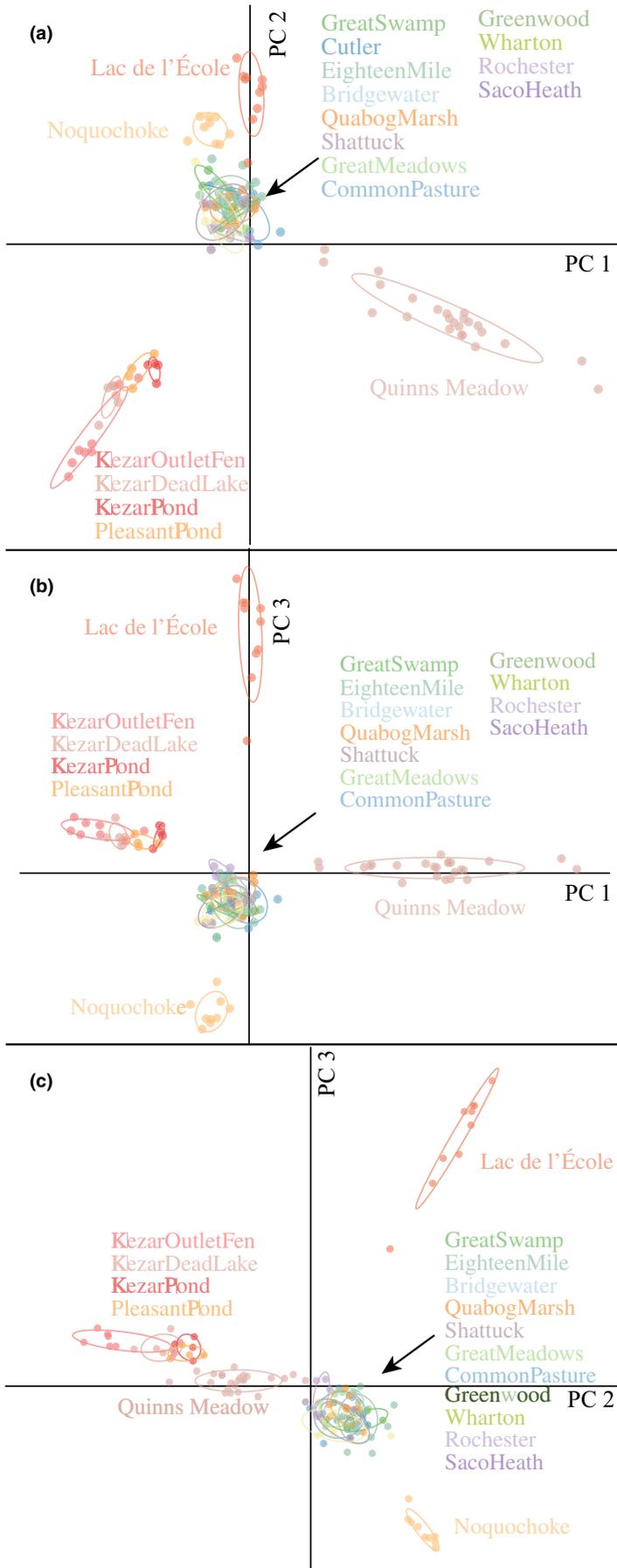


FIGURE 6 Principal components analysis (PCO) of *Scirpus longii* genotypes with populations defined a priori. Colours correspond to those in Figures 2 and 5. Ellipses represent 75% of the genetic variance associated with the population. Quinns Meadow and Lac de l'École (Nova Scotia), Pleasant Pond and the Kezar populations (all in Maine) and Noquochoke (Massachusetts) occupy a unique space in this ordination. All other populations are clustered together and overlap substantially. a–c display pairs of the three major principal components of variance [Colour figure can be viewed at wileyonlinelibrary.com]

not simply a matter of migration to the north, as temperatures and glaciation allowed.

From our models, we can make the following broad conclusions with some degree of confidence. (a) The ACPF (including *S. longii*) has come to inhabit its current distribution within the past 26 ka after migrating northwards from a glacial refugium in what is now the southeastern United States and/or the immediately adjacent exposed continental shelf. (b) The exact location of the common ancestor of extant populations of *S. longii* and the pattern of subsequent migration among populations is difficult to determine with our current information. However, a scenario consistent with our models is that Nova Scotian populations are derived from a Massachusetts source and/or the adjacent continental shelf. (c) The western Maine populations of *S. longii* (Kezar and Pleasant Pond) have remained isolated for at least 8 kyr. (d) The dispersal of *S. longii* to New Jersey is recent and can be tracked to a single dispersal event, and dispersal to Nova Scotia occurred at least once.

4.2 | Current status of *Scirpus longii*

This phylogeographical history provides context for the current structure of genetic diversity in *S. longii*. The heterozygosity (H_O) among and within extant populations is low (Table 1), these populations are slightly inbred (mean population $F_{IS} = 0.03$; mean individual $F_{IT} = 0.24$), and they exhibit little genetic differentiation ($F_{ST} = 0.13$; Table 2). We found no correlation between geographical distance between *S. longii* populations and pairwise measures of genetic differentiation. Overall, the differentiation of *S. longii* into genetically distinct populations is weak. Essentially, the genetic diversity of *S. longii* could be captured by selecting individuals from Quinns Meadow (Nova Scotia), Lac de l'École (Nova Scotia), Noquochoke (Massachusetts), the Kezar or Pleasant Pond populations (Maine), and any one of the remaining 13 populations sampled in this study (Massachusetts, New Jersey and New Hampshire; Figure 6). These measures of genetic diversity indicate that the ancestral population of *S. longii* that first inhabited deglaciated coastal plains of north-eastern North America was not genetically diverse and descendent populations did not diversify as the extant range of the species was established.

4.3 | The future of the northern ACPF

Recent estimates suggest that the northern ACPF has lost over 70% of habitat due to development (Noss *et al.* 2015). In an analysis of *S. longii*, Rawinski (2001) outlined a series of threats to the long-term survival of the species in New England, nearly all of which were anthropogenic. He listed habitat destruction above all, with specific threats including the development of cranberry farms in the coastal plain peatlands, ditching and channel-making for irrigation and roads, and the construction of waterfowl impoundments. Rawinski (2001) also suggested that eutrophication of peatlands would render them inhospitable to stress-tolerant *S. longii*. Disturbance and eutrophication will facilitate the invasion of *S. longii* habitat by ruderal (weedy)

and competitive herbaceous species, respectively (Grime 1979) and then, ultimately, woody vegetation (Rawinski, 2001). The authors have observed *S. longii* reduced to a small number of struggling clones in wetlands made eutrophic as indicated by the dominance of *Typha latifolia*. These anthropogenic threats are surely an issue for the entire regional ACPF.

Our results (Figure 3) suggest that climate change may also pose a threat to many of the northern ACPF species. Even the most optimistic greenhouse gas emissions scenario indicates a decline in ACPF species richness throughout most of the region. On the other hand, our model indicates that a wide range of climatically suitable area not currently occupied by the ACPF may be available for future colonization and serve as refugia for ACPF species (Figure 3). These areas include Maine and New Brunswick on the northern Bay of Fundy coast, eastern Nova Scotia, the St. Lawrence River lowlands in the vicinity of Quebec City and Montreal, and eastern Newfoundland. Despite climatic suitability, we believe most of these areas would be inhospitable or inaccessible to the flora. For example, migration of these species over the Appalachians into the St. Lawrence River valley is improbable. Furthermore, as nearly all extant ACPF populations remain close to the Atlantic coast, the climatic, elevational and edaphic suitable areas in inland Maine, New Brunswick and Newfoundland would also probably pose challenges for these species. Even the coastal regions of northern Maine and New Brunswick on the north shore of the Bay of Fundy appear to be unlikely habitats for ACPF species given the paucity of these species today along this coast despite the richness of ACPF species nearby in Nova Scotia and New England (with 98 ACPF species). Finally, while our projections suggest that Newfoundland may be climatically suitable for many species in the northern ACPF, migration to this region would require transport of seeds or fragments of vegetative propagules across at least 115 km of the Gulf of St. Lawrence from the northeast terminus of Nova Scotia. Our phylogeographical models suggest that the productive dispersal of *S. longii* across the comparable distance between Massachusetts and Nova Scotia has not occurred for 10,000 years. The same may also be true for other ACPF species. Of all the areas that would appear to be climatically suitable in the future but are currently uninhabited or nearly so by ACPF species, we believe that eastern coastal Nova Scotia is the most promising.

At least for those species not presently in Nova Scotia, this discussion of probable suitable habitat in the future for the northern ACPF species is based on the assumption that they will be able to disperse. Given the high level of development and habitat fragmentation in this region of North America, this should not be taken for granted. In the case of *S. longii*, the advantages it enjoys by virtue of its tolerance to low nutrient levels will probably be compromised by continuing eutrophication (Rawinski, 2001) and changes to the hydrology of its habitat. The successful conservation of the limited diversity of this species, at least insofar as this requires migration, may depend on its facultative ruderal or weedy character (Grime, 1979), that is by inducing copious seed production upon disturbance. Natural flowering of *S. longii* is very infrequent and thus the species'

potential to migrate via transport of seed is extremely limited. Historically, fire has been the primary stimulant for culm production (MacKay et al., 2010; Rawinski 2001; Schuyler & Stazs, 1985) and probably facilitated post-glacial migration. In an analysis of charcoal deposited since the LGM, Power et al. (2008) demonstrated that the frequency of fire in eastern North America peaked at about 12 ka and began to decline after about 9 ka. However, rates of fire were still higher 9a, 6 and 3 ka than they are today (Power et al., 2008). Furthermore, native Americans have occupied these regions for at least 12,900 years (Lathrop, Newby, Spiess, & Bradley, 2011) and initiated fires frequently for at least the last several thousand years (Cronon, 1983; Foster & Motzkin, 1999). This period of frequent fires corresponds with the history of *S. longii* migration as described above, raising the possibility that the post-glacial frequency and magnitude of fire could have contributed to the extant distribution of populations.

Second only to the preservation of ACPF habitat in southwest Nova Scotia, widespread disturbance in all populations of *S. longii* by means of regular controlled burns may be the single most effective strategy for conservation of this species. First, regular fire would secure the survival of current populations by stimulating the production of seedlings and by preventing invasive and woody species from encroaching on the peatland habitats of *S. longii*. Second, a strategy of induction of flowering by burning would enhance gene flow within and among populations, potentially avoiding the loss of genetic diversity expected upon migration while facilitating the increase of heterozygosity throughout the species' range. Third, long-distance dispersal of *S. longii* is unlikely without the production of seeds. The same is true for other members of the ACPF, which produce seeds or spores infrequently.

With particular regard to the conservation of *S. longii*, we recommend that the Noquochoke population in southeastern Massachusetts receive particular attention. This population has a unique genotype and is in the zone that may be climatically unsuitable by 2070. We recommend that development in this populous region of Massachusetts take extra care to maintain the current hydrology at Noquochoke, that beaver dams are dismantled as needed, and that eutrophication of the wetland and the encroachment of weedy and woody species be prevented. It is particularly important that disturbance be avoided as *Scirpus cyperinus*, the weedy relative of *S. longii*, is known to hybridize with and introgress *S. longii* populations (MacKay et al., 2010). As funds for conservation are limited, it would be advisable to focus on maintaining the genetic diversity harboured within this Noquochoke population.

The data that we present here should serve as baseline for testing the efficacy of conservation efforts. Surveying and genetic resampling after implementing these conservation strategies will be essential to determine the effects on the maintenance or potential increase of individuals or populations, their migration, displacement, and changes in genetic diversity. For example, resampling at the population level after several years of regular burning should prove an effective means to determine whether gene

flow among populations increases as a result of the induction of flowering.

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DATA ACCESSIBILITY

DNA sequences: full SNP alignments are deposited in Dryad (<https://doi.org/10.5061/dryad.b4dn0mn>). MAXENT input files are deposited in Dryad (<https://doi.org/10.5061/dryad.b4dn0mn>). Herbarium records are deposited at WIS, MSVU and PH.

AUTHOR CONTRIBUTIONS

D.S., R.M. and K.J.S. conceived and undertook the project. D.S. and R.M. conducted fieldwork, D.S. performed the laboratory work, analysed the data, and led the writing with contributions from the other authors.

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