

Literature-based latitudinal distribution and possible range shifts of two US east coast dune grass species (*Uniola paniculata* and *Ammophila breviligulata*)

Evan B Goldstein $^{Corresp.,\ 1}$, Elsemarie V Mullins 1 , Reuben G Biel 1 , Joseph K Brown 2 , Sally D Hacker 3 , Katya R Jay 3 , Rebecca S Mostow 3 , Peter Ruggiero 4 , Julie C Zinnert 2 , Laura J Moore 1

Corresponding Author: Evan B Goldstein Email address: evan.goldstein@unc.edu

Previous work on the US Atlantic coast has generally shown that coastal foredunes are dominated by two dune grass species, *Ammophila breviligulata* (American beachgrass) and Uniola paniculata (sea oats). From Virginia northward, A. breviligulata dominates, while *U. paniculata* is the dominant grass south of Virginia. Previous work suggests that these grasses influence the shape of coastal foredunes in species-specific ways, and that they respond differently to environmental stressors; thus, it is important to know which species dominates a given dune system. The range boundaries of these two species remains unclear given the lack of comprehensive surveys. In an attempt to determine these boundaries, we conducted a literature survey of 97 studies that either stated the range limits and/or included field-based studies/observations of the two grass species. We then produced an interactive map that summarizes the locations addressed in the published papers, books, and other records included in our survey. The literature review suggests that the current southern range limit for A. breviligulata is Cape Fear, NC, and the northern range limit for *U. paniculata* is Assateague Island, on the Maryland and Virginia border. In addition, our data suggests a northward expansion of *U. paniculata*, possibly associated with warming trends, while the data for A. breviligulata remain inconclusive. We intend this map to aid coastal researchers who are interested in the dynamics of these two species and the potential for their ranges to shift as a result of climate change.

¹ Department of Geological Sciences, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, United States

² Department of Biology, Virginia Commonwealth University, Richmond, Virginia, United States

 $^{^{3}\,}$ Department of Integrative Biology, Oregon State University, Corvallis, Oregon, United States

⁴ College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, United States



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- 2 species (*Uniola paniculata* and *Ammophila breviligulata*)
- 3 Evan B. Goldstein^{1*}, Elsemarie V. Mullins¹, Reuben G. Biel¹⁺, Joseph K. Brown²⁺, Sally D.
- 4 Hacker³⁺, Katya R. Jay³⁺, Rebecca S. Mostow³⁺, Peter Ruggiero⁴⁺, Julie C. Zinnert²⁺, Laura J.
- 5 Moore¹⁺
- 6 Department of Geological Sciences, University of North Carolina at Chapel Hill, 104 South Rd,
- 7 Mitchell Hall, Chapel Hill, NC 27599 USA
- 8 ²Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284, USA
- 9 ³Department of Integrative Biology, Oregon State University, 3029 Cordley Hall, Corvallis,
- 10 Oregon 97331 USA
- 11 ⁴College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, 104 CEOAS
- 12 Administration Building, 101 SW 26th Street, Corvallis, Oregon 97331 USA
- 13 *Corresponding author: evan.goldstein@unc.edu (email); @ebgoldstein (Twitter)
- 14 ⁺Denotes equal contribution



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33	change.

Introduction

35	Coastal foredunes are often the first line of protection against elevated water levels,
36	protecting habitat and infrastructure from flooding and storm impacts (Sallenger, 2000). Coastal
37	dunes are the result of ecomorphodynamic feedbacks — the presence of vegetation leads to
38	localized sand deposition (e.g., Arens, 1996; Kuriyama et al., 2005), and this burial stimulates
39	plant growth, (e.g., Maun and Perumal, 1999; Gilbert and Ripley, 2010) resulting in further sand
40	deposition and the eventual development of a vegetated coastal dune (e.g., Hesp, 1989; Arens,
41	1996; Arens et al., 2001; Hesp, 2002; McLean and Shen, 2006; Zarnetske et al., 2012; de Vries et
42	al., 2012; Durán and Moore, 2013).
43	Along the northern portion of the US Atlantic coastline, Ammophila breviligulata Fernald
44	(American beachgrass; perennial C ₃ plant) is the dominant grass in dune development. In
45	contrast, along the southern coastline, <i>Uniola paniculata</i> L. (sea oats; perennial C ₄ plant) is the

46	dominant dune-building grass. Other vegetation also contributes to the growth of US east coast
47	dunes, including Spartina patens (saltmeadow cordgrass; Lonard et al., 2010), Iva imbricata
48	(dune-marsh elder; Colosi and McCormick, 1978), Schizachyrium littorale (shore little bluestem;
49	Oosting and Billings, 1942; Lonard and Judd, 2010), Carex kobomugi (Asiatic sand sedge; Small
50	et al., 1954; Wooton et al., 2005; Burkitt and Wootton, 2011), and Panicum amarum (bitter
51	panicgrass; Woodhouse et al., 1977; Lonard and Judd, 2011). These species can be locally
52	abundant and play a secc y role in dune development.
53	Work in the 1970s by Godfrey and coworkers (Godfrey, 1977; Godfrey and Godfrey,
54	1973; Godfrey et al., 1979) attributed the morphological differences in coastal dunes to a
55	combination of factors such as forcing conditions (wind, waves, tide), dominant grain size, and
56	vegetative controls. Godfrey (1977) hypothesized that <i>U. paniculata</i> and <i>A. breviligulata</i> differed
57	in their growth form, setting the pace of dune growth as well as defining dune shape and size
58	(i.e., hummocky dunes of <i>U. paniculata</i> vs. continuous dunes of <i>A. breviligulata</i>). The effects of
59	grass morphology and growth form on dune shape has also been shown on the US west coast,
60	where two non-native grass species with distinct morphologies produce differing dune shapes
61	(Hacker et al., 2012; Zarnetske et al., 2012
62	Regional analysis of the factors important to the geomorphology, coastal protection
63	services, and restoration dynamics of east coast dunes could be improved by an increased
64	understanding of the range limits of the two dominant dune grasses. Broadly, authors have stated
65	that the northern range limit of U . paniculata is in $\forall A$, and the southern limit for A . breviligulata
66	is in NC, with both species occurring in each of the states (e.g., Duncan and Duncan, 1987;
67	Silberhorn, 1999). Our overall objective in this study is to provide a review and synthesis of
68	previous work on the range limits of <i>U. paniculata</i> and <i>A. breviligulata</i> along the US Mid-
69	Atlantic coast as a baseline for future investigations of possible shifts. To achieve this, we
70	conducted a literature search of papers that contain range limits and occurrences of one or both of
71	the two species at or beyond the generally accepted geographic limits. Our specific goals were to
72	1) determine the range boundaries of <i>U. paniculata</i> and <i>A. breviligulata</i> from an extensive
73	literature survey and assess the zone of overlap between the two species; 2) investigate, through
74	temperature trends, whether climate may be playing a role in the boundaries and potential range
75	shifts, and 3) provide a map-based literature review (Tobias, 2014; Tobias and Mandel, 2015) to
76	aid researchers studying the dynamics of the two grass species across their range and within their
77	zone of overlap.



Materials & Methods

We performed a literature search on December 19 th , 2017 for published studies in botany, ecology, and coastal geomorphology that specifically include four types of information, which we then collated: 1) statements regarding the northern range limit of <i>U. paniculata</i> ; 2) statements regarding the southern range limit of <i>A. breviligulata</i> ; 3) studies focusing on these species and their occurrences (in a coastal dune context) at the limits of the stated range, with an emphasis on examples of <i>A. breviligulata</i> in NC and southward and <i>U. paniculata</i> in VA and northward; 4) greenhouse and laboratory studies focusing on <i>U. paniculata</i> and <i>A. breviligulata</i> that may relate
to their ranges. E.B. Goldstein and E.V. Mullins wrote the search protocol with guidance fro
L.J. Moore to determine inclusion/exclusion criteria. All the authors participated in the search.
All relevant range data were noted in a spreadsheet shared among the co-authors along
with the following information: the author designated place name (e.g., 'Cape Hatteras'), the year
published, citation information (e.g., book title, journal, DOI), species ('A' or 'U'), if the stated
species was part of an explicit planting experiment, and where in the text the comment on
occurrence was made (e.g., 'third column, second paragraph, page three'). Lastly, latitude and
longitude were included; either those given in the text, or if not explicitly given, as estimated
based on place names provided in the text.
We placed all papers that referenced <i>U. paniculata</i> and <i>A. breviligulata</i> from NC to NJ in
a shared folder. We used a version of 'snowball' sampling to find new publications by conducting
forward and backward searches ('cited by' and 'citing') in Web of Science and Google Scholar to discover new documents, We also searched for previous taxonomic names of <i>U. paniculata</i> —
Briza caroliniana J. Lamark, Nevroctola paniculata C. Rafinesque-Schmaltz. ex Jackson,
Trisiola paniculata C. Rafinesque-Schmaltz, Nevroctola maritima C. Rafinesque-Schmaltz ex
Jackson, Uniola floridana M. Gandoger, Uniola heterochroa M. Gandoger, Uniola macrostachys
M. Gandoger; sea oats (Yates, 1966, Lonard et al., 2011) — and A. breviligulata — Ammophila
arenaria var. breviligulata (Fernald), though A. breviligulata has been a stable species name since
the 1920s (Maun and Baye, 1989). Data collection was performed as a 'sprint' during which time
authors worked contemporaneously (see Supplemental S1). We then used the `Leaflet` Javascript
library (Agafonkin, 2017) via an R package (Cheng et al., 2017) in R version 3.4.1 (R Core
Team, 2017) to create an interactive map from the collected data.
In addition to literature searches, we used the GBIF (The Global Biodiversity Information
Facility; GBIF, 2017a) database to extract occurrence records of <i>U. paniculata</i> (GBIF, 2017b;
2018b) and A. breviligulata (GBIF, 2018a) on the US east coast, including data from digitized



occurences from GBIF contains data from queries for "U. paniculata L." (GBIF, 2018b) and "U. 112 113 paniculata Roth." (GBIF 2017b). Only GBIF records with latitude and longitude were used. 114 **Results** In total, we found 97 unique papers/books/chapters (Table 1) that provided 102 and 158 115 116 mentions (specific to the statements we were searching for) of A. breviligulata and U. paniculata, respectively, from 1900 to 2017 (260 total mentions; Figure 1; Supplemental S2). Of the 260 total 117 mentions in our dataset, 31 refer to range boundaries specific enough to place on a map. Of these 118 31 mentions spanning 1946 to 2013, 14 are mentions of *U. paniculata* and 17 mentions for *A.* 119 120 breviligulata (Table 2; Supplemental S3). Because each mention of a range limit is tied to a 121 citation, we were able to collect temporal information on the northern range limit of U. 122 paniculata and the southern range limit of A. breviligulata (Figure 2). Many mentions of range limits give general geographic information, for instance limiting *U. paniculata* to the 'Virginia 123 Capes', or A. breviligulata to the 'Outer Banks' — this geospatial imprecision prohibits a 124 125 thorough regression analysis; however, the data in Figure 2 is at least qualitatively suggestive of a slight northward trend in the stated northern range limit of *U. paniculata*. The data do not allow 126 us to draw conclusions about temporal range shifts for A. breviligulata. 127 128 We compiled mentions of each species in geographic space by placing them on an 129 interactive map (Figure 3; Supplemental S4). The full interactive html map enables users to examine specific observations in greater detail by changing the scale, selecting individual 130 observations of interest, and navigating to linked primary literature via DOIs or stable URLs. The 131 most southerly studies of A. breviligulata in our dataset are Bright et al. (2011) at Kure Beach, 132 NC and Hosier and Eaton (1980) at Bald Head Beach, NC. The sparsity of references to A. 133 134 breviligulata in southern NC stands in contrast to the many references of A. breviligulata farthe 135 north in NC (e.g., Bogue Banks and Cape Lookout). Our literature review suggests that A. 136 breviligulata becomes sparse south of Cape Lookout, NC, with no mentions in the literature of its 137 presence south of Cape Fear, NC. 138 North of the Chesapeake Bay mouth, *U. paniculata* has been observed along the 139 uninhabited islands of the VA eastern shore (Zinnert et al 2011; Boulé, 1976; Stalter and Lamont, 2000; Bachmann et al., 2002; McCaffrey and Dueser, 1990; Mullins and Moore, 2017). Farther 140 141 north, *U. paniculata* appears along Assateague Island (Stalter and Lamont 1990; Hill, 1986; 142 Subudhi et al., 2005). We can find reports of only a single stand of *U. paniculata* north of

herbarium specimens and licensed, research-grade iNaturalist observations. The *U. paniculata*

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Assateague Island: In Avalon NJ, *U. paniculata* was planted by the US Department of Agriculture as a trial (Nordstrom, 2008). This experimental stand still exists, but reports in 2013 suggest that no natural recruitment has occurred (USDA, 2013). Our literature review therefore suggests that *U. paniculata* becomes sparse north of the Chesapeake Bay mouth, with only a single (human-planted) stand described north of Assateague Island.

Discussion

Thermal tolerances are often implicated in limiting the range of these two species. Godfrey (1977) and Lonard et al. (2011) suggest wintertime temperatures limit U. paniculata growth in more northern settings. Seneca (1969, 1972) noted that germination below 29°C was rare for U. paniculata and growth was significantly reduced at low temperatures. We used long-term climate data from a NOAA meteorological station in Painter, VA, to examine annual and seasonal trends in temperature between 1956-2016, near the northern range limit of U. paniculata. Data from 2003 is excluded due to missing observations for the month of July. Data are presented as annual mean maximum and minimum temperature and winter (Dec 21 - March 20) mean temperature. There was a general warming trend in annual maximum (1 °C, $r^2 = 0.24$, p < 0.0001) and minimum temperature (2 °C, $r^2 = 0.52$, p < 0.0001), as well as winter minimum temperature (3.6 °C, $r^2 = 0.33$, p < 0.0001) since 1956 (Figure 4) This increased warming in winter may result in temperatures at or near a threshold limit for successful germination an

along the Virginia barrier islands, populations planted experimentally in 2013 have thrived (Mullins et al., in review). Experimentally planted *U. paniculata* in the higher latitudes of NJ show no natural recruitment (USDA, 2013).

We found no indication of temporal trends in the stated range limit for *A. breviligulata* in

vegetative propagation of *U. paniculata*. Although there are few observations of *U. paniculata*

the literature. However, early studies indicate a sparsity of *A. breviligulata* in southern NC before a history of extensive plantings. Lewis (1918) remarks on the lack of availability of *A. breviligulata* in Beaufort, NC for planting 'barrier dunes' — suggesting instead the use of *U.*

169 paniculata. Ammophila breviligulata is also missing from a Bogue Banks survey by Burk (1962).

170 In contrast to Lewis (1918), van der Valk (1975) notes that the NC Outer Banks were planted

with *A. breviligulata* instead of *U. paniculata* during campaigns in the 1930s and 1950s.

172 Schroeder et al. (1976) and Godfrey (1977) also mention plantings of *A. breviligulata* along the

NC coastline and Outer Banks. Godfrey (1977), Travis (1977), as well as Maun and Baye (1989)

note that *A. breviligulata* plantings occur beyond the probable 'natural' range (i.e., too far south).





175 Seneca (1969, 1972) found that A. breviligulata had higher germination rates at low temperatures 176 of 18°C. In addition to thermal constraints, Woodhouse (1977) and Singer (1973) discuss pest and 177 disease pressure in southern populations of A. breviligulata, as does Seliskar and Huettel (1993) 178 for mid Atlantic A. breviligulata populations. 179 Several studies that are not included in the map (because they describe greenhouse 180 experiments) are relevant to understanding shifting range limits of these species and interactions 181 that contribute to present-day range limits. These recent experiments focused on species interactions between A. breviligulata and U. paniculata (Harris et al., 2017; Brown et al., 2017), 182 183 which are likely to be most important in their zone of overlap from NC to VA. Harris et al. (2017) 184 found that *U. paniculata* reduces growth of *A. breviligulata* by altering physiological 185 performance at temperatures consistent with summertime on the Virginia barrier islands. Brown 186 et al. (2017) built upon these results by showing that leaf elongation and root length of A. breviligulata are reduced through interactions with *U. paniculata*. This reduction in performance 187 188 may explain the lack of a clear southern range shift and observations of species replacement, in 189 which A. breviligulata plantings were replaced within 6-10 years by native U. paniculata along Core Banks, NC (Woodhouse et al., 1968). Woodhouse et al. (1977) notes that A. breviligulata 190 191 tends to grow faster than *U. paniculata* and spread more rapidly. These differences in growth rate 192 have implications for dune morphology, which have been observed in the field (Woodhouse et al., 1977) and explored in numerical models of coastal dune growth (Goldstein et al., 2017). These 193 194 studies suggest that dunes dominated by A. breviligulata coalesce faster than those formed by U. 195 paniculata, resulting in high, continuous dune ridges compared to hummocky dune formations 196 associated with *U. paniculata*. Further exploration of species interactions in the zone of overlap 197 are needed to fully understand the implications of potential changes in species composition for 198 dune building as climate changes in the future. 199 Although the focus of our study is on cataloging and mapping literature data, absences of 200 A. breviligulata or U. paniculata in particular areas are also worth noting. For example, we found 201 no reference to A. breviligulata south of Cape Fear, NC. However, there are suggestions in the 202 literature that A. breviligulata has been planted further south — Woodhouse and Hanes (1967) advise that A. breviligulata can survive when planted for dune restoration purposes as far south as 203 204 the South Carolina border with North Carolina. Maun and Baye (1989) discuss the presence of 205 planted, ephemeral populations in South Carolina, Georgia, and Florida, but only cite personal 206 communications (with E.D. Seneca) and provide no specific locations. However comprehensive 207 works by Stalter (1974; 1975) also did not mention the occurrence of A. breviligulata in at



208 several sites in coastal SC. Paired surveys by Stallins (2002; 2005) and Stallins and Parker (2003) 209 also do not record the presence of A. breviligulata in Georgia locations (as compared to NC sites 210 in the same study). 211 Our results can be compared to the GBIF dataset extracted for this study (GBIF 2017a; 212 2017b; 2018a; 2018b). We use GBIF data associated with a known latitude and longitude (636 213 points), which leads to a zone of overlap from Kitty Hawk, NC (southernmost observation of A. 214 breviligulata) to Cape Henry, VA (northernmost observation of *U. paniculata*; Figure 5). Our 215 study yields a larger zone of overlap (from Cape Fear, NC to southern NJ), and records many 216 observations from within the zone of overlap (Figure 4). 217 **Conclusion:** 218 Our literature review suggest the current southern range limit for A. breviligulata is Cape 219 Fear, NC, and the northern range limit for *U. paniculata* is Assateague Island, at the border of 220 Maryland and Virginia. The range for these two species overlap between Virginia and North 221 Carolina. Results suggest a northward expansion of *U. paniculata*, possibly associated with 222 warming trends, while the data for A. breviligulata remain inconclusive. 223 We acknowledge that there may be additional information in theses and local guides (e.g., 224 Denslow et al., 2010). These sources — as well as scanned herbarium sheets from museum 225 collections — constitute 'dark data', data not discoverable because of problems in indexing, 226 storage, and retreival (Heidorn, 2008). For this reason a more complete picture of range limits 227 and species abundances should come from contemporaneous, modern, synoptic field surveys of 228 U. paniculata and A. breviligulata throughout the zone of overlap — from NC to NJ. Given the 229 recently burgeoning interest in the construction of dunes as a means for providing storm shaifn cof in 230 protection, it may also be useful to explore how the vigor and survival of natural vs. planted 231 stands of these two grasses vary across their ranges as well as how their interactions with each 232 other are affected by species composition and geographic location. 233 234 **Acknowledgements:** Financial support was provided by NOAA (EESLR NA15NOS4780172), NSF-GLD (EAR-235 236 1324973), and the Virginia Coast Reserve Long-Term Ecological Research Program (NSF DEB-237 123773). Support for EVM was also provided by the NSF GRFP (DGE-1650116). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the 238



239	author(s) and do not necessarily reflect the views of the National Science Foundation. Map data
240	$copyrighted\ OpenStreetMap\ contributors\ and\ available\ from\ \underline{https://www.openstreetmap.org}.$
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242	Code and Data availability:
243	All data, code, and and the interactive map will be made available on Figshare with a citable
244	DOLIn the interim, the datasets are attached as Supplemental S2 and S3
245	The interactive .html map is attached as Supplemental S4
246	The code to render html map from Supplemental S2 data is available as a github repository
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Table 1 (on next page)

References used in construction of the interactive map



Species	Citation
A. breviligulata	Brantley et al., 2014; Conaway and Wells, 2005; Conn and Day, 1993; Day et al., 2004; Dilustro and Day, 1997; Harvil, 1979; Heyel and Day, 2006; Klotz, 1986; Koske and Polson, 1984; Martin, 1959; Roman and Nordstrom, 1988; Schroeder et al., 1979; Seliskar, 1994; Seliskar, 1995; Seliskar, 2003; Seliskar and Huettel, 1993; Seneca and Cooper, 1971; Singer et al., 1973; Wolner et al., 2013; Woodhouse and Hanes, 1967; Young et al., 2011; Yousefi Lalimi et al., 2017
U. paniculata	Burgess et al., 2005; Burk, 1961; Cleary and Hosier, 1979; Franks et al., 2004; Godfrey and Godfrey, 1974; Godfrey and Godfrey, 1976; Godfrey, 1979; Harper and Seneca, 1974; Hitchcock, 1935; Hodel and Gonzales, 2013; Hosier and Cleary, 1977; Lewis, 1918; Long et al., 2013a; Long et al., 2013b; Mullins and Moore, 2017; Oosting, 1945; Oosting and Billings, 1942; Purvis et al., 2015; Seneca, 1972; Silander and Antonovics, 1982; Stallins, 2002; Stalter, 1975; Subudhi et al., 2005; Tatnall, 1946; Tyndall et al., 1986; Tyndall et al., 1987; USDA, 2013; Wagner, 1964; Wells, 1928; Zinnert et al., 2011
A. breviligulata and U. paniculata	Andrews, 2002; Bachmann et al., 2002; Boulé, 1979; Boyce, 1954; Bright et al., 2011; Brown, 1959; Burk, 1962; Godfrey, 1977; Godfrey and Godfrey, 1973; Hill, 1986; Hosier and Eaton, 1980; Kearney, 1900; Kearney, 1901; Levy, 1976; McCaffrey and Dueser, 1990; Odum et al., 1987; Seneca, 1969; Shafer, 2003; Stallins, 2005; Stallins and Parker, 2003; Stalter and Lamont, 1990; Stalter and Lamont, 1997; Stalter and Lamont, 1999; Stalter and Lamont, 2000; Travis, 1977; van der Valk, 1974; van der Valk, 1975; van der Valk, 1977; Woodhouse et al., 1968; Woodhouse et al., 1977

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Table 2(on next page)

References with mentions to range limits



Species	Citation
A. breviligulata	Brown, 1959; Burk, 1968; Frankenberg, 2012; Godfrey and Godfrey, 1973; Godfrey and Godfrey, 1976; Godfrey et al., 1979; Pilkey et al., 2004; Rogers and Nash, 2003; Thornhill et al., 2013
U. paniculata	Hodel and Gonzales, 2013; Liang, 1958; Lonard et al., 2011; Wagner, 1964; Woodhouse, 1982; Yates, 1966
A. breviligulata and U. paniculata	Duncan and Duncan, 1987; Godfrey, 1977; Hitchcock and Chase, 1950; Krause, 1988; Overlease, 1991; Seneca, 1972; Silberhorn, 1999; Woodhouse and Hanes, 1967



Dataset composition

Dates for all referenced work for each species in our dataset, binned every 5 years.

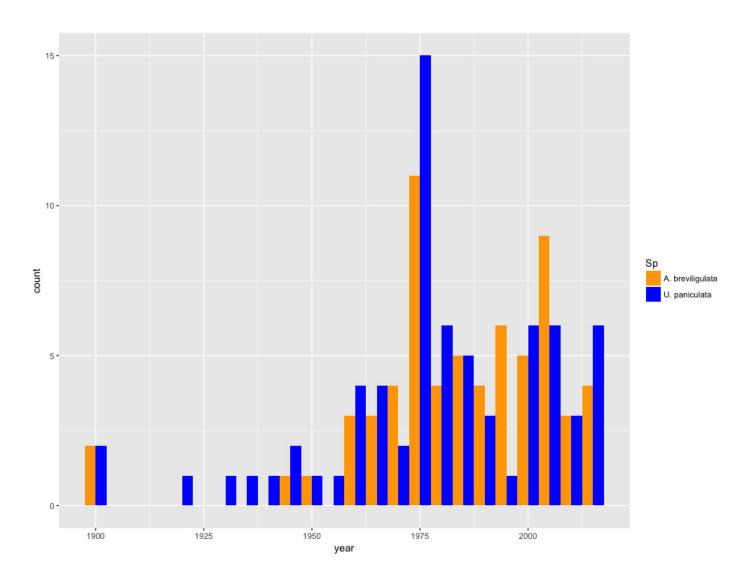
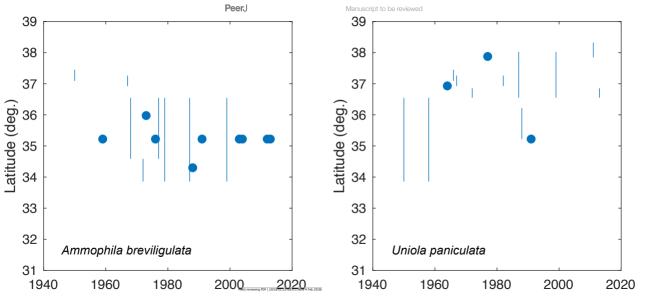




Figure 2(on next page)

Range Limits

Southern range limit for *A. breviligulat*a (left) and northern range limit *U. paniculata* (right), extracted from literature sources of various age. Points are specific geographic mentions, while lines are ambiguous geographical references (e.g., 'Southern North Carolina, 'Virginia Capes').

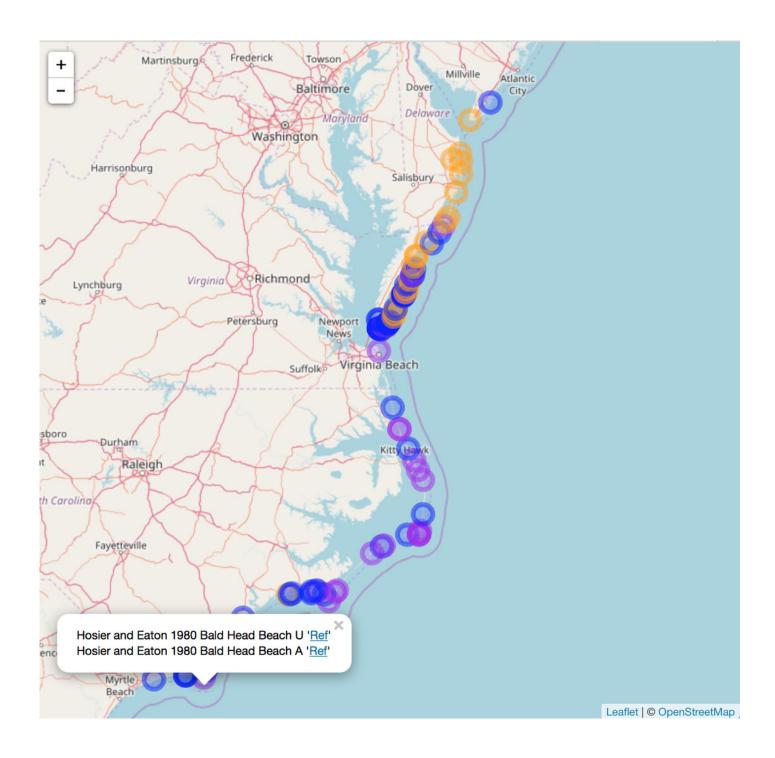




Static snapshot of interactive map

Each circle marker corresponds to a literature mention of a given species (orange for *A. breviligulata*, blue for *U. paniculata*, purple for both). Mentions can be seen within the pop-up label, as well as the corresponding species label ('A' or 'U'), a location name ('Bald Head Beach') and an active link via the a DOI or stable URL to primary source. The map background is OpenStreetMap data (https://www.openstreetmap.org).



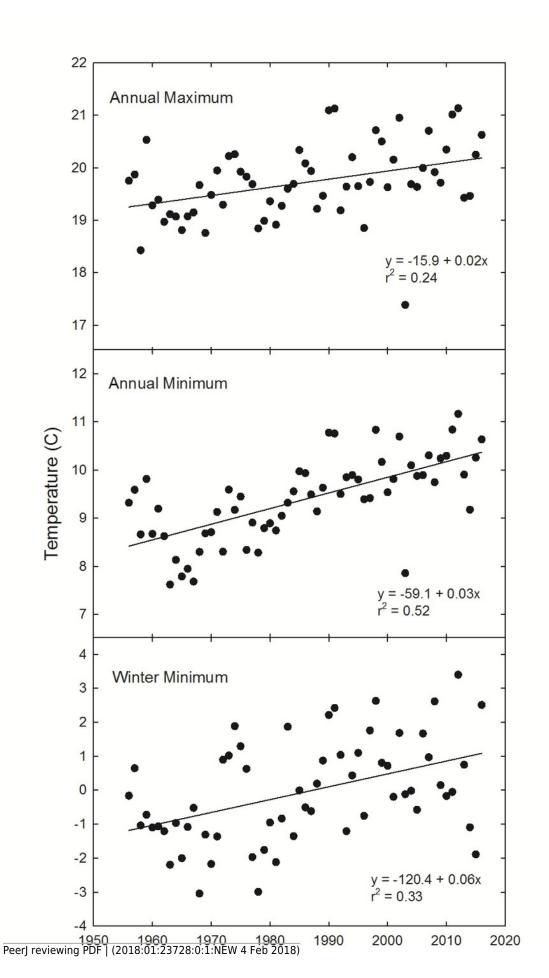




Painter, VA temperature trends

Observations and trends of increasing annual maximum temperature (top), annual minimum temperature (middle) and winter minimum temperature (bottom) at Painter, VA, near the northern range limit of *U. paniculata*.





GBIF data

Map of A. breviligulata (yellow) and U. paniculata (blue) occurences from the GBIF database.

