A decade of expansion of the invasive plant *Carex kobomugi* in a coastal foredune

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ABSTRACT: Many plants show capacity for selective spatial and temporal expansion or foraging despite being sessile. In biogeomorphic coastal foredunes, the plant species that inhabit or colonize an area post-storm will affect habitat stability and thus future storm response. Along the mid-Atlantic US, invasive Asiatic sand sedge (*Carex kobomugi*) has come to dominate foredunes since its introduction in 1929 at Island Beach State Park, New Jersey. To understand controls on foredune invasive expansion, we mapped stand expanses along 3-km of foredune here since 2008, relative to shifting habitat features such as the location of the foredune crest and denuded areas ripe for colonization. Invasive stands have been laterally expanding from pre-existing stands with temporal variation in stand size and density. Stand area loss only occurred due to Hurricane Sandy, but the level of burial from Sandy did not impact stand area loss. Hurricane Sandy fragmented and destroyed stands, but these stands recovered by coalescing during periods of recovery, and then expanded further. The invasive sedge shows some directionality in growth, expanding more into areas further from the crest which experience less salt spray, but not consistently across time. *Carex kobomugi* also spread more extensively into adjacent vegetation than into bare areas, suggesting that replacement of natives is more likely than recolonization of open habitat space. Plants are the foundation of coastal foredune systems. Understanding where invasive species are expanding and the underlying controls on invasion is key to predicting current and future impacts related to climate change and future storm response.

KEYWORDS: Biogeographic System • Colonization • GIS • Disturbance • Hurricane Sandy • Storm • Vulnerable

ACKNOWLEDGEMENTS
This research was conducted in part with United States Government support under and awarded by the Department of Defense, Air Force Office of Scientific Research, National Defense Science and Engineering Graduate (NDSEG) Fellowship, 32 CRF 168a. We thank the Villanova Geography and Environment Department for allowing us to use their GIS and Trimble mapping capabilities, and specifically, we thank Guillaume Turcotte and Eric Wagner. We also thank Dr. Michael Posner of Villanova for his statistical help. We thank Colleen Cochran for aiding in salt spray transect data collection. We thank the NJ Fish & Wildlife service and Island Beach State Park's Jennifer Clayton, Kelly Scott, and Ray Bukowski for their supporting conducting this research. We thank Brenda Casper for her support.

INTRODUCTION

Habitat conditions, biotic and abiotic, dictate species dispersal and establishment, with evolutionary, life-history, and demographic implications (Bazzaz 1991; Morris 2003). The modular structure of plants and plant communities makes them capable of exploiting spatially and temporally heterogenous resources, despite their immobility (Bazzaz 1991). Plants can effectively disperse into favorable habitats and away from unfavorable ones (Janzen 1970), selectively place foraging organs in less-contested areas, and are capable of sharing resources among individuals in clonal integration (Hartnett and Bazzaz 1983; Hutchings and de Kroon 1994; Oborny 1994; Hodge 2004; Roiloa and Retuerto 2006; Liu et al. 2016). Plants are thus capable of plasticity (De Kroon et al. 2005). Responses to cues can ultimately result in the preferential colonization of more favorable patches in a heterogenous environment (Salzman 1985; Fransen et al. 1998), differential resource allocation across a landscape (de Kroon and Schieving 1991), and increased environmental heterogeneity with biological and geomorphological implications in some habitats (Stallins 2006; Hacker et al. 2019).

In biogeomorphic habitats, plants can have a strong effect on habitat structure where a change in vegetation can have cascading effects on topography (Fei et al. 2014; Balke et al. 2014; Corenblit et al. 2015; Hacker et al. 2019). Biogeomorphic habitats, are categorized by a strong reciprocal coupling of geomorphic processes, shaping the spatial and temporal distribution of biota, and biological processes, which modify geomorphic processes and topography (Corenblit et al. 2011). The timing of disturbances and recovery can dictate spatial variability in these habitats (Corenblit et al. 2015) where vegetation shifts may alter system state and response to future events (Durán Vinent and Moore 2014). Examples of biogeomorphic systems include rivers, mangroves, marshes, and coastal foredunes (Jones et al. 1997; Xiao et al. 2011; Angelini et al. 2015; Corenblit et al. 2015; Zarnetske et al. 2015). Dominant plants in these habitats are ecosystem engineers (Jones et al. 1997; Angelini et al. 2015, Corenblit et al. 2015; Hacker et al. 2019), such that replacement of native species by invasive species can change system structure and function and thus impact their ability to adapt and respond to future disturbances (Crooks 2002; Schirmel et al. 2010; Day et al. 2015; Fei et al. 2014; Day et al. 2015; Goldstein et al. 2017; Charbonneau et al. 2017) .

Coastal foredunes are biogeomorphic habitats that are particularly susceptible to the effects of invasive species (Alpert et al. 2000; Maun 2009; Fei et al. 2014; Zarnetske et al. 2015). Episodic disturbances can open up previously occupied niches frequently by denuding patches within a vegetated landscape (Hesp 2002; Durán Vinent and Moore 2014; Fei et al. 2014; Zarnetske et al. 2015). Disturbances can act as invasive species immigration and emigration opportunities, with longshore transport and storm surge transporting seeds and individual plants to new

areas within and among systems (Yang et al. 2012; Zhou et al. 2017). Human disturbances can also set the stage for a native to become invasive (Nielsen et al. 2011) and open up previously inhabited habitat spaces for non-native plants to invade (Sobrino et al. 2002). The effects of invasive establishment in biogeomorphic systems may not be manifested immediately given that biological and geomorphological time scales are not equal (Corenblit et al. 2011) and not all foredune invasive species have purely negative effects; they can create shaded fertility islands that increase native biomass (Vallés et al. 2015) and offer stability (Charbonneau et al. 2017). Negative effects of invasive establishment can include nesting bird habitat reduction (Zarnetske et al. 2010) and shifts in belowground microbial communities (Hughes et al. 2009). However, of most concern, foredune morphology and stability may be altered by invasive establishment, thus affecting storm and sea-level rise response in these habitats and affecting the vulnerability of inland areas that these land-sea interface habitats buffer such as developed infrastructure and other habitats like marshes and maritime forests. (Wootton et al. 2005; Hilton et al. 2006; Hacker et al. 2011). Disturbances, natural or anthropogenic, can thus alter species composition, richness and biomass (Brunbjerg et al. 2015) and favor invasive settlement with biogeomorphic consequences (Kim 2005).

Foredunes are generally harsh habitats, where native responses to habitat stressors have been well-studied, but controls on invasive species establishment are lacking. Sandblasting, dynamic substrate, low organic matter, burial events, low nutrients and water availability, temperature extremes, lack of shade, and salt spray make foredunes harsh (Oosting 1954; Maun 2009). Stressful abiotic conditions related to substrate movement and salt spray decrease with increasing distance from the ocean, while organic matter, nutrients, water availability, and shade increase across the same gradient (Wells 1939; Cartica and Quinn 1980; Gares 1992; Yura and Ogura 2006; Miller et al. 2009; Tackett and Craft 2010; Miller 2015; Vallés et al. 2015; Di Palo and Fornara 2017), with density and diversity among plants and edaphic microorganisms increasing as well (Çakan and Karataş 2005; Ciccarelli 2015; Roy-Bolduc et al. 2015). Species may respond differently to stresses such as burial and salt spray, and this can offer competitive advantages or disadvantages in different scenarios (Maun 1998; Morais et al. 2012), selecting for stress tolerant species closer to the crest (Moreno-Casasola 1986). As such, native and invasive stands success may vary across a foredune system relative to the magnitude of the aforementioned abiotic stressors. Despite abiotic stressors, over five years, native *Carex arenaria* went from 18 to 25% cover on grey and green dunes in Denmark, while in inland heathlands, *Ammophila arenaria* doubled in percent cover to 25% (Nielsen et al. 2011). Invasive species can spread disproportionately compared to natives (Wootton et al. 2005) such that their distributions and controls on

colonization might not be explained by stress gradients alone (Wiedemann and Pickart 1996; Maun 1998; Alpert et al. 2000; Callaway and Aschehoug 2000; Morais et al. 2012; D'Antonio and Jackson 2004), but we lack an understanding of the spatial and temporal patterns underlying the spread of invasive species in biogeomorphic systems.

Understanding the controls on invasive expansion in foredunes is key to predicting where they may expand in the future and the first step to understanding biogeomorphic impacts of invasives to target vulnerable areas for management efforts. To understand controls on foredune invasive expansion, for 10 years, we tested how populations of the foredune invasive *Carex kobomugi* shift in time and space relative to stand position in the foredune and in response to Hurricane Sandy (2012) at the site of the invasive's immigration in 1929 (Small 1954). *C. kobomugi* is an aggressive US mid-Atlantic coast invasive and can thus serve as an extreme example of a foredune invasive, similar to *Phragmites australis* in marshes (Silliman and Bertness 2004). For example, *C. kobomugi* can occupy >20% of a foredune (Charbonneau et al. 2017) and increase by 300% in 20 years (Wootton et al. 2005) compared to invasive *Rosa rugosa*, which may expand 12-27% a year in European dunes, but occupies <1% of the foredune despite decades of establishment (Jørgensen and Kollmann 2009). The species is found from North Carolina to Massachusetts, was recently reported in the Pacific Northwest in Oregon, and is listed on the US State Noxious Weed Lists for 46 states (USDA 2018). By censusing *C. kobomugi* distribution and other characteristics of the foredune habitat, we tested if: (1) *C. kobomugi* spreads mainly by expansion of existing stands or by establishment of new stands; (2) stands recover beyond a pre-disturbance distribution five years post-disturbance by examining the effects of and recovery from Hurricane Sandy 2012; (3) localized stand growth varies spatially relative to the predominant wind direction that would impose salt spray and substrate movement stress; and (4) invasive expansion is spatially random or related to stand position regarding distance to habitat features. Understanding where invasive species are expanding and the underlying controls on invasion is key to predicting current and future impacts and then appropriately evaluating management priorities.

MATERIALS & METHODS

Study Site

Island Beach State Park (IBSP), Barnegat Bay Peninsula, Berkeley Township, Ocean County, New Jersey, is a micro-tidal (tidal range < 0-2 m) ~17 km long undeveloped barrier island. IBSP is a natural high barrier island

system (Durán Vinent and Moore 2014). The foredunes are dominated by native *Ammophila breviligulata* or invasive *Carex kobomugi* with minor exceptions where *Toxicodendron radicans* is prevalent. Invasive *C. kobomugi* arrived in the US in 1929 at IBSP such that stands here are the oldest in the country (Small 1954). There are 24 beach access paths through the dune system perpendicular to the coast and there is a northeast facing vehicle access path at the southern tip of the study area. Precipitation and wind speeds are lowest seasonally April to August with prevailing southeast winds. Northwest winds prevail in winter, but episodic northeastern storm winds in fall and winter, have the greatest potential to cause coastal erosion and sand flux and as such, northeast and southwest quadrants of stands, and eastern stand halves, may have greater local abiotic stressors (Gares 1992). The most recent major storm to impact the area was Hurricane Sandy (October 2012), though smaller storms like Hurricane Joaquin (October 2015) and Winter Storm Jonas (January 22-24, 2016) have affected the park more recently (Dohner et al. 2017). Prior to Hurricane Sandy, the foredunes at IBSP were largely continuous. Hurricane Sandy had variable impact, with increasing erosion south to north (Charbonneau et al. 2017). Where we collected data, along a 3-km stretch in the southern half of IBSP between beach accesses A15-A24, the foredunes faces were eroded in collision erosion with minimal overwash by Hurricane Sandy. Here, localized areas were devegetated, but not overwashed or inundated and destroyed, as was the case north of A15 (Sallenger 2000; Charbonneau et al. 2017).

Study Species

Carex kobomugi is a C_3 clonal sedge, family Cyperaceae, with sympodially branching rhizomes and a monocarpic shoot (Voronkova et al. 2011). The shoot is a low-growing semirosette 15-30 cm tall with small petiole angles and blades touching or very close to the surface (Min 2006). A relatively thick cuticle (Charbonneau and Balsamo 2015) and short stature (Yura and Ogura 2006) resist sand blasting. Any rhizomes and shoots >60 cm sand depth are likely dead (Ishikawa and Kachi 1998). However, *C. kobomugi* roots may extend >60 cm, which is deeper than its native counterpart *A. breviligulata*, to about 40 cm (Ishikawa and Kachi 1998; Charbonneau et al. 2016). *Carex kobomugi* can reproduce sexually via seed or asexually via rhizomes, but the latter predominates (Ishikawa et al. 1993; Ohsako 2010). As a result, it is effective at spreading rapidly via lateral rhizome expansion, producing a guerilla growth form, where existing stands can expand two meters in diameter per year as a conservative estimate of known expansion rates (Halsey et al. 2006). Buoyant seeds facilitate longshore transport to new habitats (Yang et al. 2012). Though it is found in the most stressful habitat, in the foredune, as an invasive, as a native in China,

Russia, Japan, and Korea it is categorized as a stress-evading species with lower water use efficiency than other native dune plants *Ischaemum anthephoroides* and *Calystegia soldanella* (Ishikawa et al. 1990).

As an invasive in the US Mid-Atlantic, *C. kobomugi* can be considered a stress-tolerating species, found on the foredune slope, in the foredune, and in secondary and tertiary dunes, reducing native foredune plant species density and diversity (Wootton et al. 2005; Burkitt and Wootton 2011). The species creates low-lying monospecific mats of approximately 140 individuals m^2 (Wootton et al. 2005; Charbonneau et al. 2016). In 1960, *C. kobomugi* was endorsed and sold as a dune-stabilizer, and by the mid-1970s, planted all along the Mid-Atlantic Coast (Woodward and Quinn 2011). Its invasive qualities were only recognized in the 1980s and 1990s, and quantified in 2005 (Wootton et al. 2005). Subsequent to that, efforts were made to curb the spread of *C. kobomugi*, and to remove stands from foredunes in a number of coastal regions. These removal efforts typically reduced the population of the species, but did not eliminate the species (McGough et al. 2003). While removal is justified by the negative effects on native species abundance and diversity (Wootton et al. 2005), *C. kobomugi* is an effective dune stabilizer, likely resisting collision erosion (Sallenger 2000) as a function of its high root investment over shoot (Charbonneau et al. 2016) as well as resisting wind erosion due to high surface cover (Wootton et al. 2005; Charbonneau et al. 2016). Similarly, the sand that it traps as an ecosystem engineer may be better retained compared to natives of taller stature and lower density per unit area (Charbonneau et al. 2017).

Foredune Field Mapping Censuses & Data Extraction

To quantify the expansion of *C. kobomugi* in the context of a shifting foredune habitat we mapped its population and pertinent foredune features over time. Specifically, we mapped the (1) foredune crest, (2) *C. kobomugi* stands, (3) blowouts, and (4) the foredune heel as the beginning of the secondary dune sere. We mapped dune features with ArcPad vertex mapping on a Trimble® GeoXT™ GeoExplorer® (≤0.8m +/- accuracy 95%) post-processed to account for any error. We defined dune features in the field as follows: (1) *foredune crest* – polyline, a connected sequence of line segments, where the plateaued foredune habitat drops as the most landward part of the seaward foredune slope; (2) *C. kobomugi stands* – polygon with plants ≤1 m apart considered part of the same stand and patch area indicative of age (Jørgensen and Kollmann 2009); (3) *blowouts* – polygons marking depressions devoid of vegetation formed by erosion (Hesp 2002) their boundary intersecting of the vegetated foredune; and (4) *foredune heel* – polyline of the topographic low landward of the foredune crest where vegetation community

assemblages shift to that of secondary dune communities (Maun 2009; Zarnetske et al. 2015). We did not quantify *C. kobomugi* stands on the foredune slope, as to do so we would have damaged this sensitive area. Blowouts were predominantly wind-created, whereas (≤5%) may have been initiated by both wind and waves.

Census timing varied by the feature being mapped. We determined crest location pre- and post-Sandy by manually analyzing aerial photos to delineate crest position in ArcGIS based on shadows and shading. The pre-Sandy aerial survey was flown March 2012 by the NJ Office of Information and Technology and Office of GIS and the first post-Sandy aerial was flown November 1, 2012, by the National Oceanic Atmospheric Administration. We assumed that any differences observed between these two aerials can be attributed to Hurricane Sandy (Charbonneau et al. 2017). After 2012, we physically mapped crest position, with Trimble GPS, in the field in January 2016 and September 2018, after Winter Storm Jonas and 2017/18 Nor'easters. The foredune heel did not shift in position during this study from its mapping in 2014. The foredune habitat is the area bounded by the crest and heel. We mapped blowouts and *C. kobomugi* stands at the end of the growing season yearly for the former and in 2008, 2013, 2016, and 2018 for the latter. We mapped the total extent of barren areas, even if the features extended into the secondary dune. For *C. kobomugi,* we mapped full stands extending into the secondary dune if the edge was within 30 m of the foredune habitat, otherwise, we mapped the stand to the secondary dune.

GIS Spatial Data Extraction & Salt Traps

We applied a variety of tools in ArcGIS 10.3.1 to understand spatial relationships in the context of where, how, and why *C. kobomugi* extents have changed over time. Specifically, we tested if (1) *C. kobomugi* spreads mainly by radial expansion of existing stands or by establishment of new stands. To do so, we determined the reduction in blowout area (m^2) across successive census mappings due to *C. kobomugi* expansion using the Intersect Tool. We then measured the distance of blowouts that were either colonized (fully or partially) or not colonized at all from the nearest *C. kobomugi* stand in the previous census. We identified new (not present in previous censuses), pre-existing (present in the previous census), fragmented, and coalesced stands across time. We defined fragments as separate stands located within the boundaries of a stand existing the previous census and coalesced stands were distinct those that were previously distinct but merged (Fig. 1). By comparing the area of each stand between successive censuses, we determined if stand growth or loss occurred and quantified the proportion of change for each. We determined mean lateral stand radius expansion, by measuring stand differences in radius from 2013,

2016, and 2018 in ten random spots along the stand edges in ten stands that never fragmented or merged across the 10 years. With the above information, we determined if (2) stands recovered beyond a pre-disturbance distribution five years post-disturbance by examining the size of stands pre- and post- Hurricane Sandy.

We tested if (3) localized stand growth varies spatially, directionally by compass direction, relative to the predominant wind direction and if (4) total stand growth is related to a stand's distance to habitat features. We defined the centroid (i.e. center of mass) of stands that never fragmented (n = 18) in the census in which each stand was first observed. We then split these stands in that same location in successive years, into quadrants (northeast (NE) 0-90°, southeast (SE) 90-180°, southwest (SW) 180-270°, and northwest (NW) 270-0°). To determine if distance to beach accesses and beach width impacted expansion, we used the Near Tool to measure: (1) centroid distance to the southern extreme of our census area which is a car access, (2) centroid distance to the nearest beach access path, and (3) centroid distance to the ocean, defined as elevation 0m above sea level as determined from publicly available USGS topobathymetric data.

We measured salt spray to ensure it decreased with distance from the crest (Cartica and Quinn 1980). On July 6, 2015 we established six linear transects perpendicular to the ocean. Along each transect we installed suspended and taut traps 30.5 cm from the sand surface. The first trap was at the crest, and we installed another trap every 25 m westward, for 200 m in length or to the maritime forest boundary depending on dune width (Online Resource 1). Traps were a single piece of 30.5 cm x 30.5 cm 100% cotton unbleached grade 50 28 x 24 weave cheese cloth left in the field for 24 hours, 08:00 to 08:00. Following Rajaniemi and Allison (2009), we cut a 10 cm x 10 cm section from center of each trap, immersed in 100 ml deionized water, and measured the salinity of the water as conductivity using a Delta-T HH2 Moisture Meter.

Lastly, we determined if burial induced by Hurricane Sandy affected changes in *C. kobomugi* stand sizes from 2008 to 2013. We used the Extract by Mask Tool on publicly available Light Detection and Ranging (LIDAR) data (Wright et al. 2014), pre- (flown April 2012 by NJOIT) and post- (flown November 1, 2016) Hurricane Sandy using the 2008 *C. kobomugi* stand extents to define areas to extract. Using the Raster Calculator, we subtracted the post-Sandy LIDAR masks from pre-Sandy LIDAR mask and then multiplied by cell size (0.75 m x 0.75 m) to calculate volumetric change summed across each *C. kobomugi* stand using the Zonal Statistics as Table Tool.

Statistical Analyses:

We used JMP Pro 14.0 to perform all statistical analyses. All tests are two-tailed with means reported ± SE.

We used Matched-Pairs t-Tests to compare stand sizes across time. Specifically, (1) we compared stand area 2008-2018, excluded one stand that fragmented (n = 18); (2) examined stand area between successive censuses, where we combined the area of any fragmented stands; and (3) quantify the effect of Hurricane Sandy by examining stand area only in stands that did not fragment 2008-2013 (n =11). We calculated the percent change of each stand and compared percent change between the period 2013-2016 and 2016-2018, when Sandy did not impact stand sizes, with Wilcoxon Rank Sum test; the percent change data were not normally distributed, and were skewed towards positive values, but continuous beyond 100%. We determined which stands expanded into blowouts and used ANCOVA to analyze how colonization area varied in blowouts compared to surrounding vegetation areas, controlling for stand size the previous year as a covariate. Lastly, we used Student's t-tests to compare how the distance to a *C. kobomugi* stand affected whether or not blowouts were colonized and to compare stand area in stands that had and had never fragmented 2008-2018.

We quantified the spatial distribution of *C. kobomugi* stand area using inverse distance with Moran's Index. In these analyses, neighboring stands have a larger influence than features further away and distances are calculated as Euclidean (i.e. straight line) between features. To ensure any non-random spatial results are meaningful, we examined them further with Hot Spot Analysis. Hot Spot Analysis identifies statistically significant hot and cold spots using the Getis-Ord Gi* statistic and False Discovery Rate Correction to account for multiple tests.

We compared percent change in localized stand growth within stands (by compass direction) only during the latter two periods (2013-2016 and 2016 -2018) to examine stand growth in the absence of a major disturbance, knowing that Hurricane Sandy had reduced the projected growth of *C. kobomugi* stand area (Charbonneau et al. 2017). We compare percent change in *C. kobomugi* area in east and west stand halves and quadrant 2013-2016 and 2016-2018 with matched pairs t-test. We examined if variation in salt spray is predicted, by distance from the crest and transect latitude with regression. We also used regression to examine if beach width predicted percent stand area change. To examine how the location of a stand may impact expansion 2013-2018, we performed a Standard Least Square Regression with the independent variables distance to the closest beach access point and to the car access, including only stands that existed all 10 years and never fragmented (n = 25).

Lastly, we examined if Hurricane Sandy burial impacted stand erosion from 2008-2013 using regression. We tested if variation in volumetric change from Sandy predicted changes in *C. kobomugi* stand sizes from 2008-

2013. We examined this relationship at three levels at which we postulated that burial might impact stands, specifically examining changes in stand area, absolute value of area change, and examining stands that eroded. In these analyses, we excluded stands that fragmented or coalesced from 2008-2013.

RESULTS

Invasive stand sizes, density, and foredune habitat occupied by *C. kobomugi* varied across time, expanding between all successive censuses except 2008-2013 (Table 1). After Hurricane Sandy (2012) *C. kobomugi* was reduced to 82% of its 2008 extent and stand area was significantly reduced in 2013 relative to 2008 ($t_{21} = -2.15$, $P < 0.05$). This stand reduction was associated with fragmentation and was the only fragmentation occurred, as 11 stands (37% of 2008 stands) split into 37 fragments, with each stand splitting into a maximum of six fragments (minimum 2, 3.7 ± 0.5). Stands present 2008 not fragmenting and still existing 2013, did not change in area ($P > 0.05$), but population reduction occurred as 2008 stand sizes (1342 ± 275 m^2) were larger than the area of remaining stands 2013 (955 ± 218 m^2) after combining related fragmented stands ($t_{10} = -3.08$, $P < 0.01$). Stands were only ever lost, five (67.4 ± 29.6 m^2) 2008-2013. Fragments remaining in 2013 post-Sandy were a maximum 90% of their original 2008 area (18.7 ± 4.1%), but did not have less percent change in area by 2018 than those that never fragmented.

After Sandy, stands recovered and grew to occupy more foredune habitat space (Table 1 Invasive in Foredune). Stands were larger 2013 than they were 2016 ($t_{23} = 3.62$, $P < 0.005$), expanding 43% in area and 3.4 ± 0.18 m in radius laterally over this three-year period 2013-2016. Stands continued to expand 2016-2018 ($t_{24} = 2.84$, $P < 0.01$), and grew 17% from the 2016 extent and expanded 2.8 ± 0.14 m in radius. Mean stand area percent increase was greater 2013-2016 (137.9 ± 36.8%) than (39.2 ± 11.3%) 2016-2018 ($Z = 2.04$, $P < 0.05$). By 2016, six of the 37 fragments created by Hurricane Sandy remained distinct, and by 2018 two of these six remained. Five years post-Sandy, the area *C. kobomugi* occupied in the foredune expanded by 68%. After 2013, *C. kobomugi* consistently occupied 20+% of the total foredune area, and more of the vegetated foredune after accounting for blowout space (Table 1).

Over ten years stand area grew by 170% ($t_{18} = 4.38$, $P < 0.001$) and the total area that *C. kobomugi* encompassed in the foredune expanded to 34% in 2018, from 14% in 2008 (Table 1). Growth was primarily from existing stands expanding, 2008-2013 nine new stands established (65.6 ± 58.9 m^2), 2013-2016 five new stands established (26.5 ± 20.7 m^2), and 2016-2018 four new stands established (34.2 ± 12.8 m^2). There was a negative

linear relationship between the change in area that stands underwent 2008-2013, and subsequent growth 2013-2018 ($F_{1,17} = 4.89$, $R^2 = 0.23$, $P < 0.05$, Fig. 2).

Table 1: *C. kobomugi* foredune distribution across time relative to changes in the size the foredune habitat and the size of blowouts within it. All areas are reported as m^2.

Year	*Stands*	*Mean Stand Area*	*Maximum Stand Area*	*Invasive Area in Foredune*	*Foredune Habitat Area*	*Foredune Blowout Area*	*Invasive Foredune Habitat*	*Invasive in Vegetated Foredune*
2008	30	725 ± 147	2,829	21,734	152,125	-	14.3%	-
2013	58	309 ± 67	2,539	17,925	97,432	27,857	18.4%	25.8%
2016	33	906 ± 175	3,102	25,690	92,856	16,204	27.7%	33.5%
2018	31	1238 ± 249	6,112	30,142	88,158	14,062	34.2%	40.7%

Both *C. kobomugi* and *A. breviligulata* colonized previously unvegetated blowout areas during the study. From 2013-2016, 11,167m^2 or 42% unvegetated blowout area was colonized by vegetation. *Carex kobomugi* accounted for 2,537 m^2 or 23% of this colonization and the remaining 77% was colonized by *A. breviligulata*. In this same period, *C. kobomugi* fully colonized four of 55 blowouts that existed in 2013 and partially vegetated 20 (39.3 ± 8.1%). *Carex kobomugi* expanded into vegetated areas more than into blowouts (ANCOVA, $F_{2,39} = 3.80$, $P < 0.03$) and stand size was not a significant covariate affecting this relationship. From 2016-2018, unvegetated blowout area remained more consistent than 2013-2016 (Table 1), and *C. kobomugi* colonized 822 m^2, 5.2%. *Carex kobomugi* completely vegetated nine of 78 blowouts that existed in 2016 and partially vegetated 30 (48.1 ± 7.5%). Blowouts that were fully colonized (40.9 ± 13.0 m^2) were smaller than those partially colonized (1058 ± 259 m^2, $t_{40} = -3.92$, $P < 0.001$). All areas colonized fully or partially (0.51 ± 0.33 m), were closer to *C. kobomugi* stands than those that were not colonized (11.1 ± 1.14 m, $t_{91} = -8.91$, $P < 0.0001$). There was up to 5,228 m^2 of habitat conversion from *A. breviligulata* to *C. kobomugi* 2013-2016 and an additional conversion of 3,570 m^2 2016-2018 (Table 1).

Carex kobomugi stand sizes were randomly spatially distributed with no significant hot or cold spatial clusters in the data (Moran I and Hot Spot Analysis*;* $P > 0.05$), but growth varied within stands by compass direction and as a function of stand location. West (landward) halves of *C. kobomugi* had greater percent increase than east (seaward) stand halves 2016-2018 ($t_{14} = 2.97$, $P < 0.01$, Fig. 3), halves did not differ 2013-2016 ($P > 0.05$, Fig. 3). From 2016-2018 NW=SW ($P > 0.05$) and NE=SE ($P > 0.05$), and the NW quadrant expanded more than both eastern quadrants (NW > NE, $t_{14} = 2.31$, $P < 0.04$; NW > SE, $t_{14} = 2.37$, $P < 0.04$) as did the SW quadrant (SW > NE, $t_{14} = 2.13$, $P = 0.04$; SW > SE, $t_{14} = 2.18$, $P < 0.05$). Salt spray may explain these results as it decreased with distance from the crest ($R^2 = 0.29$, $F_{1,42} = 16.98$, $P < 0.001$) and similarly, there was a positive relationship between

percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between percent stand area change and beach width ($R^2 = 0.17$, $F_{1,21} = 4.17$, $P = 0.05$). and similarly, there was a positive relationship between

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The amount of burial caused by Hurricane Sandy (2012) did not impact changes in *C. kobomugi* stand area 2008-2013 examining an effect on stand area, absolute value of area change, and then only examining eroded stands (all $R^2 > 0.00$, all $P > 0.05$). Change in elevation in the stands was 0.18 ± 0.03 m, with maximum burial 2.4 m and mean maximum burial 0.95 ± 0.13 m.

DISCUSSION

Despite the occurrence of multiple storms with the potential to reduce *C. kobomugi* extent, the invasive sedge has spread considerably over 10 years. Hurricane Sandy reduced the invasive distribution and eliminated some stands, but by 2016 the sedge recovered and grew 68% beyond its pre-storm state in five years 2013- 2018, despite the occurrence of other lesser storms (Dohner et al. 2017). This spread is by expansion of existing stands with limited new stand establishment. Localized stand growth varies spatially, spreading into vegetated areas overtaking *A. breviligulata* with more success inland, potentially due to salt stress, compared to closer to the crest and into barren blowout areas. Expansion rates were unrelated to stand position relative to distance to beach and walking beach access paths that could act as vectors. These combined results suggest that in dune habitats, *C. kobomugi* can be considered an aggressive invader whereby less stressful native vegetated habitat space may be more vulnerable to future invasion than storm impacted barren blowouts.

Carex kobomugi appears to be more aggressive or successful than many other foredune invasives. For comparison to *C. kobomugi*, *A. saligna* invaded <2% of dune habitat over 8-9 year periods in Israel (Kutiel et al. 2004) and *R. rugosa* expanded 12-27% a year in European dunes, but occupies less than 1% of the foredune despite decades of establishment (Jørgensen and Kollmann 2009). Similarly, stands of multiple invaders have been found to occupy less habitat space (<20%) along a coastal strip than just *C. kobomugi* alone, which occupied 14-41% of IBSP

foredunes over the ten years (Sobrino et al. 2002). In Europe, *D. flexuosa* has recently come to be a predominant dune invader, and has been documented as occupying 20% of habitat space, but not changing in distribution over five years (Nielsen et al. 2011) whereas *C. kobomugi* expanded 68% and invaded an addition 15% of the vegetated foredune in five years. To compare to native dune species, in five years *C. arenaria* in Denmark went from 18 to 25% cover on grey and green dunes, while inland, *A. arenaria* doubled in percent cover to 25% (Nielsen et al. 2011). This native growth may have been greater in the absence of the invasive *D. flexuosa* as when invasive *A. arenaria* was removed from dunes in the American Northwest, native growth drastically increased from 2.7% to 38% over two years (Wiedemann and Pickart 1996). The greatest documented dune invasion to date that we are aware of is *A. arenaria* invading Humboldt Bay, CA, with extent doubling in 22 years and nearly quadrupling in about 50 years across foredune and inland dunes (Buell 1992). If we consider the expansion 2016-2018 as 'business as usual' expansion, ≈5,000 m^2 every two years, then with this trajectory, *C. kobomugi* in theory could double in extent within ≈15 years from 2008 to 2023, rivaling or exceeding *A. arenaria* expansion. Given the negative effect of the sedge on native plant diversity (Wootton et al. 2005), and the uniqueness of coastal dune plant communities , this finding suggests the need for discussion on the appropriate management strategies for this species, and implementation of measures to limit expansion to protect remaining native communities (French et al. 2011).

Lateral expansion of *C. kobomugi* rivals that of *A. breviligulata* and surpass other natives. *Uniola paniculata* can spread 0.6-1 m per year via the rhizomes whereas *A. breviligulata* can expand 1-3 m per year (Woodhouse et al. 1977; Maun 1985; Hacker et al. 2019). Unequal colonization rates result in one species outcompeting another over time, as occurs with *Uniola paniculata* and *A. breviligulata* (Woodhouse et al. 1977). Lateral expansion of *C. kobomugi* was 2.8 to 3.4 m, such that *A. breviligulata* appears capable of 'keeping pace' with the invasive though we found the native being invaded at stand interfaces. This could suggest that the invasive may negatively alter belowground competition with secondary metabolites like *Carex distachya* (Fiorentino et al. 2006) whereas natives may facilitate establishment and diversity with more favorable belowground environments (Franks 2003). To compare *C. kobomugi* lateral expansion to another foredune invader, *A. arenaria* will expand 50% within 1-m of existing patches and 85% within 2-m (Keijsers et al. 2015). Lateral expansion may indirectly control dune shape (Stallins 2006; Goldstein et al. 2017; Hacker et al. 2019) and as such indirectly impact buffering ecosystem services while directly impacting recovery time (Cheplick 2016; Charbonneau et al. 2017).

It is not surprising that few new *C. kobomugi* stands arose, as seed viability is typically low both in this species (Ishikawa et al. 1993), other invasives, and among native foredune plants (Noble and Weiss 1989; Franks 2003; French et al. 2011). For example, dispersal is 4% versus 85% sexual and asexual respectively in *A. breviligulata* (Maun 1994). It is important to note that new stands could have been connected to older nearby stands, as we did not dig up individuals to assess rhizome connections. However, this seems unlikely because *C. kobomugi* typically has low internodal space (Small 1954) that can increase with burial (Maun 1994). Regardless, new stands were much smaller than existing stands, supporting smaller stands being younger as has been found with invasive *R. rugosa* (Jørgensen and Kollmann 2009). *Carex kobomugi* has spread, and it has largely done so radially, nucleating from existing established stands (Yarranton and Morrison 1974).

In blowouts, there is a lack of competition, but *C. kobomugi* colonized less than 10% of this space 2013-2018, suggesting *C. kobomugi* may be a stronger competitor in more substrate stable vegetated microenvironments with 6x more colonization here than into blowouts. Invasive *Acacia saligna* has also been documented at having ow colonization rates, <2%, into bare sand compared to vegetation (Kutiel et al. 2004). Clonal integration could allow ramets to expand into and survive in blowouts despite low resources and substrate mobility (Alpert and Mooney 1986). However, invaded blowouts being closer to invasive stands than uninvaded blowouts supports dispersal limitation as a key determinant of new habitat colonization, which has been suggested of other disturbance tolerant native and invasives (French et al. 2011). These results highlight the importance of clonal growth. If connected ramets colonize blowouts with low success, then isolated seedlings will have even lower survival. Nucleation provides the best explanation for blowout colonization with adult ramets facilitating colonization by younger ramets.

Beach accesses and burial do not appear to impact *C. kobomugi* invasion. These results do not suggest that *C. kobomugi* establishment is unaffected by anthropogenic affects, as higher-trafficked areas tend to create conditions that favor invasive settlement (Kim et al. 2008), but that controls on expansion following establishment are dependent more on biological or abiotic controls. However, burial does not appear to be one of those controls. Wind and or wave forces can be accelerated in a funneling process of fluid dynamics in narrow openings, such as paths cut in dunes (Gares 1990), thereby causing more erosion and instability in these areas (Barone et al. 2014). A lack of expansion being affected by distance to vehicle and foot access paths and a lack of burial from Hurricane Sandy impacting stands suggests that unlike, *A. breviligulata*, which is known to increase vertical growth vigor when buried (Maun 1998; Maun 1998), *C. kobomugi* may be less affected by burial positively or negatively.

Greater spread of *C. kobomugi* west is colonization towards more favorable habitat and away from less favorable ones (Bazzaz 1991). Sand movement and blasting (Moreno-Casasola 1986; Yura and Ogura 2006) and salt spray (Rajaniemi and Allison 2009) are stressful conditions that have been suggested as key controls on the distribution of species on foredunes, with their stress decreasing with distance from the ocean and crest (Oosting 1945; Oosting 1954). Salt can stunt growth and seed production (Xiao et al. 2011) such that roots can preferentially grow into non-saline soils with the intensity of salinity discrimination varying among individuals (Salzman 1985). Greater colonization westward 2016-2018 and greater expansion in areas with wider beaches support this. The impact of salt spray may with time, due to wind strength and direction, foredune height relative to sea level, and rainfall occurrence (Noe and Zedler 2001). Such variations may account for the different expansion rates seen in this study, with greater westward expansion being observed 2016-2018, but not 2013-2016. Colonization rates seaward of the crest, for comparison, could confirm salt stress or substrate flux limiting expansion.

Though *C. kobomugi* may spread inland more than seaward, these inland habitats may later become the forefront of the dune when a major erosional event occurs, a potential eventuality that should be considered by managers. Wide expanses of foredunes can be eroded away in wave or wind erosion from storms as was the case at IBSP during Hurricane Sandy when 3.6 m of foredune transect were lost (Charbonneau et al. 2017). This is an issue because plants are believed to build dunes morphologically similar to their own stature (Wootton et al. 2005; Hilton et al. 2006; Zarnetske et al. 2012). As such, foredunes fronted by dunes colonized by relatively low-growing *C. kobomugi* could be less capable of keeping pace with sea level rise than those fronted by dunes stabilized by the much taller *A. breviligulata* (IPCC 2014). The transition between native and invasive plant communities within coastal foredunes thus has implications for dune stability as a result of biogeomorphic feedbacks that may take years or decades to become apparent (Corenblit et al. 2011). The finding that stands that lost more area from Sandy expanded more in subsequent years, while those that lost less expanded less (Fig. 2) suggests that the most effective way to slow expansion post-storm may be to target eradication efforts on stands that experienced the greatest reduction in area such as by targeting the lost areas with tillering to remove invasive biomass.

Understanding the factors underpinning species distributions is especially necessary in biogeomorphic habitats where distributions will affect storm response and recovery for future shoreline stability. This research adds to the body of examples of plant colonization and adds to the relatively small number of population-level, studies of the factors affecting invasive species distributions, as opposed to smaller censuses among quadrants or transects.

The effects of climate change, specifically, greater storm severity, unpredictability, and frequency, (IPCC 2014) and range shifts (Goldstein et al. 2018) including species invasions, will add to global coastal instability. Understanding the factors that influence where populations of invasive species are expanding and the underlying controls on invasion are key to predicting current and future impacts and then appropriately evaluating management priorities.

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FIGURES

Fig. 1 Aerial photos showing fragmentation and coalescence of two *C. kobomugi* stands 2008 to 2016. Solid line denotes foredune crest. The dark grey polygons are the distribution of *C. kobomugi* in 2008 and progressing in time, the lighter grey polygons in 2013 are the fragmented remains of the two stands after Hurricane Sandy (2012) overlaid on top of the past 2008 stand distribution to highlight stand loss. By 2016, the 2013 fragments all coalesced.

Fig. 2 Stands of *C. kobomugi* stands that lost more in Hurricane Sandy (2012) recovered stronger 2013 to 2018, while stands that lost less also gained less.

Fig. 3 Percent change in *C. kobomugi* stands was greater landward (west) than oceanward (east) 2016 to 2018.

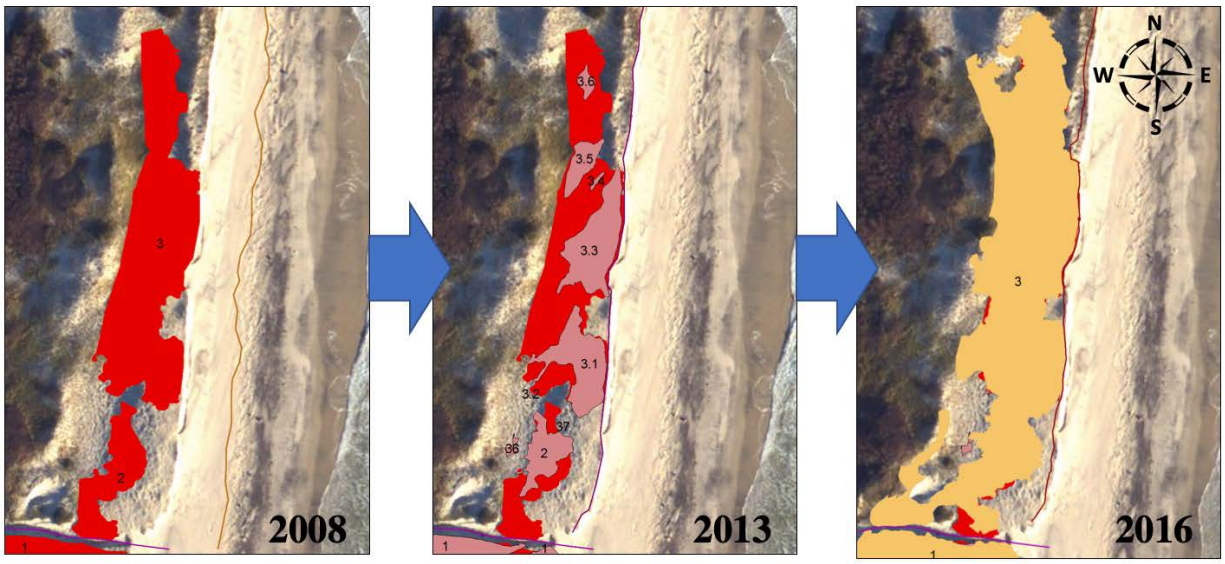

Figure I: By giving the 2008 stands UIDs that carry over in 2013, 2016, and 2018 we can determine the fate of each stand as having been fragmented or melding with other stands as well as locate and define new and lost stands. The trajectory of stand UID2 and UID3, which were both one stand in 2008 are shown. By 2013, UID2 shrunk, and UID3 fragmented into six stands. By 2018, stand UID2 and all of the fragments of UID3 expanded such that they became one continuous stand denoted in the case of melding as the UID of the largest of the melded stands. Note the changing location of the crest. All images to the same spatial extent.

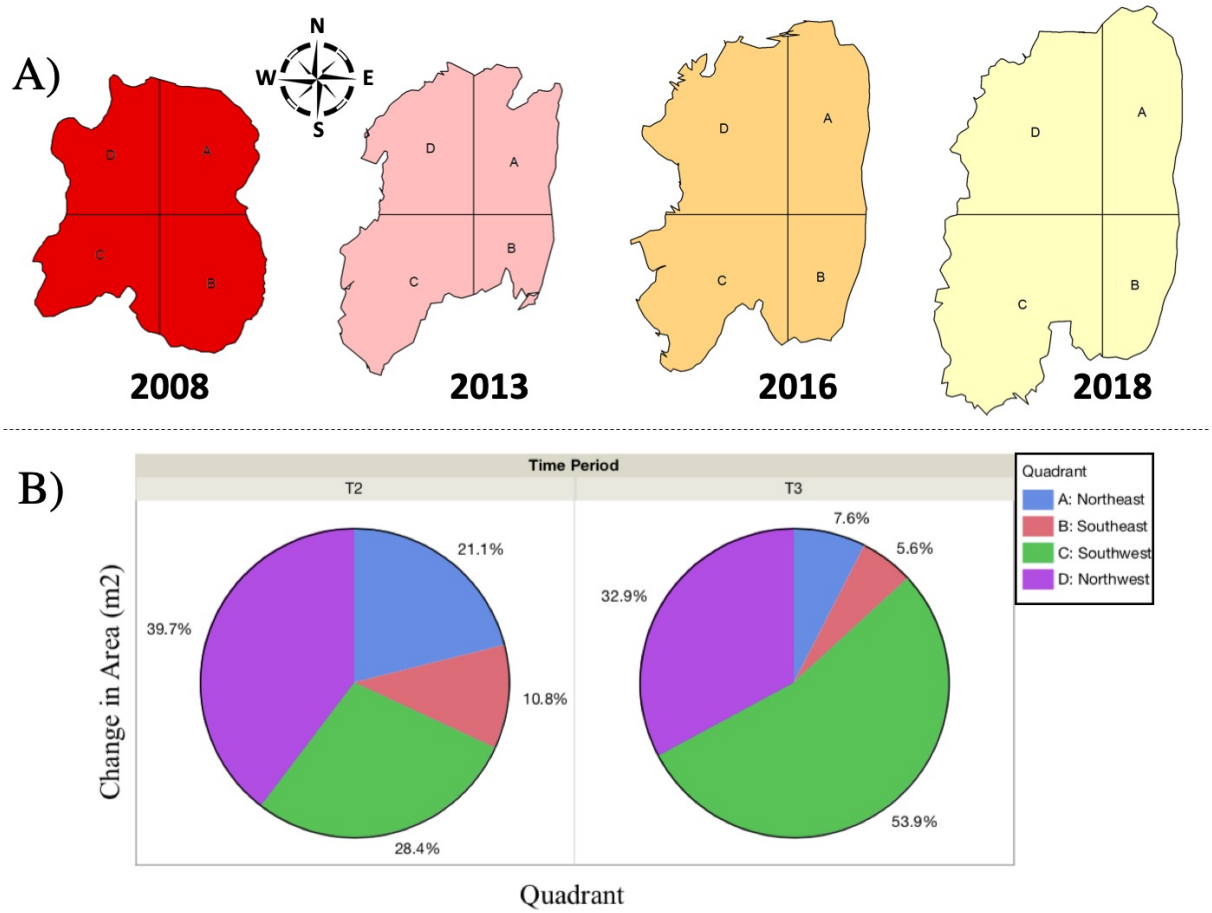

Figure II: A) We split stands that were never fragmented over the 10 years into NE, SE, SW, and NW (A, B, C, and D) quadrants from the centroid of the stand in 2008 to compare how stands spatially changed across time. All images to the same spatial extent. B) All tests are done on raw stand area, but here we show percentages for ease of digestion. T1, 2008 to 2013, there were no difference in the growth of quadrants. However, T2, 2013 to 2016 the growth in all quadrants was significantly greater than in B and a trend of growth in D being greater than A. T3, 2016 to 2018, C > A ($t_{14} = 2.13$; $P < 0.03$; one-tailed), C > B ($t_{14} = 2.18$; $P < 0.03$; one-tailed), D > A ($t_{14} = 2.31$; $P < 0.02$; one-tailed), D > B.

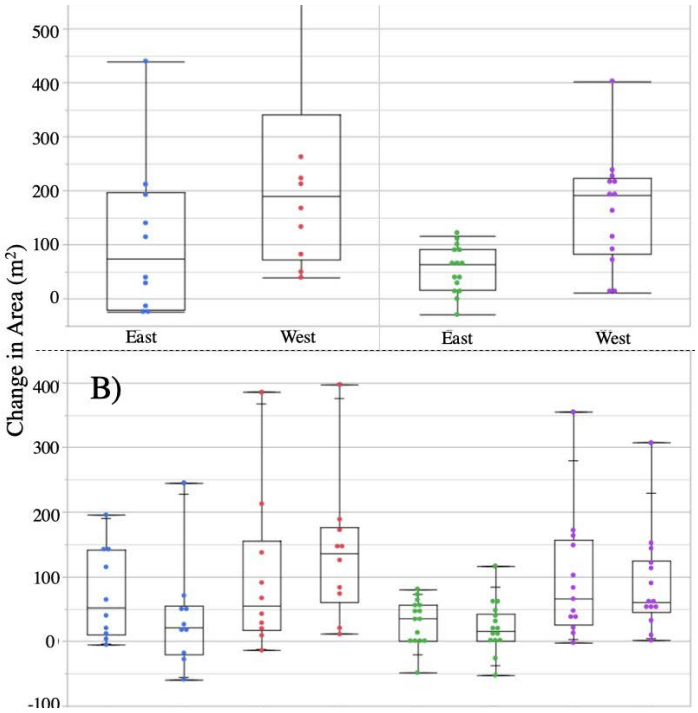

Figure III: dfds