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Extending the observational record to provide new insights into invasive alien species in a coastal dune environment of New Zealand

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ABSTRACT

Coastal habitats are regarded to be highly vulnerable to the impacts of invasive alien species. These impacts can be particularly visible in areas of national cultural and heritage significance, raising public awareness of a growing global trend and often requiring urgent changes to management practices. New Zealand has a relatively long history of invasive alien species with the introduction of non-native marram grass (*Ammophila arenaria*) for sand stabilisation and erosion control since the mid-nineteenth century. Of national importance, the sand dunes of the Hokianga Harbour are considered to be the spiritual birthplace of Māori culture in New Zealand and have experienced substantial vegetation change over the last century. Here we report a multi-disciplinary study combining palaeoecology with historic and contemporary observations to better characterise the changing distribution and mechanisms of spread of invasive alien species on the Hokianga headland. Our analysis indicates the vegetation established on the headland is primarily linked to late Pleistocene water-retaining, lignite deposits. We find, however, an abrupt increase in the area colonised by invasive alien species during the late twentieth century, most probably linked to reduced sediment supply in the Hokianga Harbour. Urgent management strategies may be required if the present dune headland is to be conserved, particularly against a backdrop of rising sea level which will most probably limit sediment resupply.

1. Introduction

Habitat and biodiversity fragmentation and losses are of increasing global concern, with greater public awareness of these issues leading to renewed attention on ecological management policies (Early et al., 2016; Haddad et al., 2015; Tucker et al., 2018). Land use changes, climatic changes, anthropogenic activities, and invasive alien species and pathogens are increasing threats to ecosystems (Nentwig, 2007), the impacts of which can be far-reaching and unpredictable, due to highly complex ecosystem and species interactions (Conser & Connor, 2009; Dawson, Jackson, House, Prentice, & Mace, 2011; Thuiller et al., 2008). Invasive alien species are typically recognized as non-native species that once introduced (either accidentally or on purpose), can spread beyond any control efforts (Westbrooks, Manning, & Waugh, 2014). Impacts of invasive alien species are now recognized as a major risk for changes in ecosystem composition and the survival of less competitive (threatened) native species (Liu, Sheppard, Kriticos, & Cook, 2011; Pardini, Vickstrom, & Knight, 2015; Vilà et al., 2011); failure to manage key invasive alien species threats can therefore lead to local/national extinction of native species, and the permanent degradation of native communities (Jay & Morad, 2006). A major challenge for determining the threshold for widespread expansion of invasive species is the limited temporal nature of the observational record (Dakos & Hastings, 2013; Thomas, 2016). Assessing data from different time scales improves understanding of invasive species spread by helping to determine changing baselines of vegetation extent, particularly when the date of initial invasive alien species introduction is unknown. This in turn helps to quantify the resilience of ecological systems.

The combination of increasing human activity in the landscape, exposure to aerial and ocean transportation, climate change and increasing sea level make coastal areas particularly susceptible to the introduction and spread of species (Gregory, 2009; Macdiarmid et al., 2012; Muhlfeld et al., 2014; Stachowicz, Terwin, Whitlatch, & Osman, 2002; Walther et al., 2009). Sand dune communities are particularly vulnerable to invasive species due to the widespread nature of the

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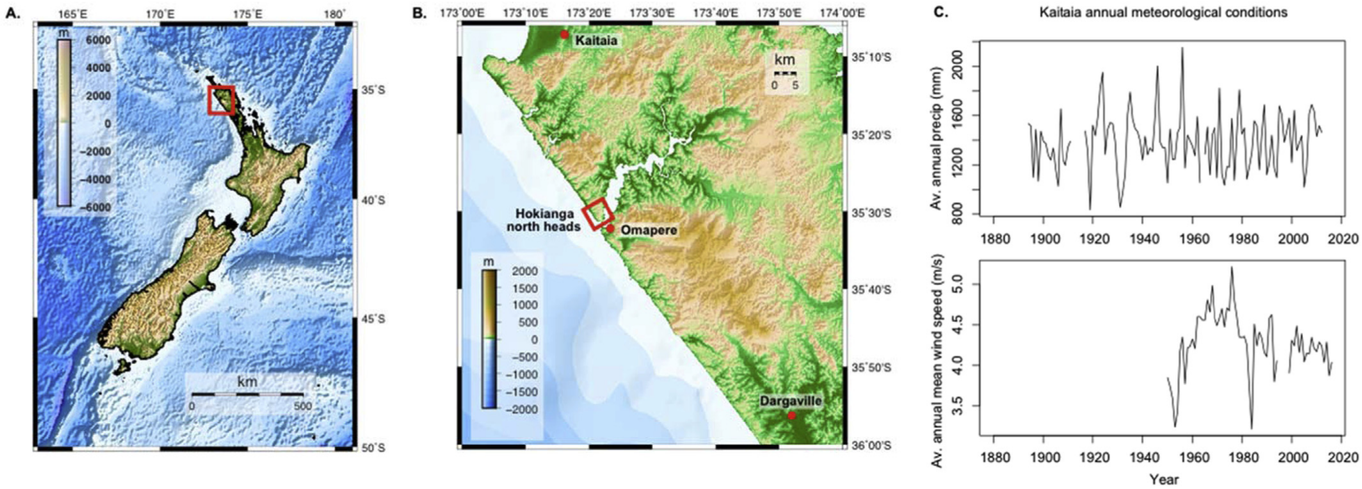

Fig. 1. **A.** Location of study area within New Zealand (red box); **B.** West Coast of Northland, New Zealand, showing the Hokianga estuary, and the towns of Omapere, Kaitaia and Dargaville (red dots). **C.** Kaitaia average annual rainfall and wind speed (source: New Zealand National Climate Database at http://cliflo.niwa.co.nz/). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

invasive plants and low levels of competition (Baker, 1986; Brown & McLachlan, 2002; Defeo et al., 2009); non-native plants on foredunes, especially invasive grasses, often out-compete indigenous sand binding species and reduce or prevent natural dune form and function. In particular, the expansion of invasive sand-stabilising species is becoming an important ecological problem in coastal dunes in many parts of the world (Barrows, Allen, Brooks, & Allen, 2009; Hilton, 2006; Kutiel, Cohen, Shoshany, & Shub, 2004; Marchante, Kjøller, Struwe, & Freitas, 2008). Dune fixation and stabilisation techniques to convert the land for forestry, farming, and even urban areas have included planting rapid-growth herbaceous and/or woody species; however, over time, these species may exhibit invasive behaviour, causing serious problems for the conservation of the coastal dune ecosystems (French, Mason, & Sullivan, 2011; Seabloom, Ruggiero, Hacker, Mull, & Zarnetske, 2013).

New Zealand is experiencing increasing pressure from invasive alien species, a trend that has been exacerbated since the arrival of Europeans (Goldson et al., 2015; Owens, 2017). The ecology and distribution of many invasive species is relatively unknown with important management implications (Giera & Bell, 2009; Goldson, 2011; Goldson et al., 2015; Peltzer, 2013). An excellent example in this regard is marram grass (*Ammophila arenaria)* which was originally planted throughout New Zealand in the mid 19th century for sand stabilisation purposes and erosion control, primarily to prepare dunes for afforestation with North American conifers, particularly *Pinus radiata* (Hilton, 2006). Several studies from coastal areas of New Zealand have detailed the invasive behaviour of marram grass at the expense of native species such as pingao (*Ficinia spiralis*) and spinifex (*Spinifex hirsutus*) (Dixon, Hilton, & Bannister, 2004; Hilton, 2006; Hilton, Duncan, & Jul, 2005). However, marram grass was not the only non-native plant that was planted on coastal dune areas for back dune stabilisation to support forestry; yellow tree lupin (*Lupinus arboreus*) was also used, in part due to its legume properties of nitrogen fixation (McQueen, 1993). The typical plant community found on coastal dunes of Northland, NZ, include a selection of both native and non-native species. The native species include spinifex, the main dune forming indigenous plant in New Zealand, and pingao, an indigenous sand-binder. In addition to marram grass and lupin, other common invasive alien species in coastal dune communities include pampas grass *(Cortaderia selloana),* and kikuyu (*Pennisetum clandestinum*).

Whilst the distribution of non-native species in New Zealand are relatively well documented (Atkinson & Cameron, 1993; https://www.landcareresearch.co.nz/resources/identification/plants/weeds-key), few long-term (centennial length) records are available, limiting our understanding of the driver(s) of change through the twentieth century. Of particular concern is the time window available to contain the threat of expansion. Once a species has become well established and relatively widespread, eradication or containment is rarely feasible or economic (Westbrooks et al., 2014). Decisions with regards eradication (the permanent removal of all individuals of a species with little or no risk of reinvasion) or containment (ongoing control to prevent spread beyond a defined distribution, including preventing invasion) depends on the timeframes of available action (Simberloff, 2003). Fortunately, for the purposes of monitoring past vegetation changes and impacts, sand dunes provide excellent natural archives on centennial and longer timescales as they are able to preserve macro and microfossils, including tree stumps (Grimm, 2001; Hesse, Telfer, & Farebrother, 2017; Telfer, Thomas, & Breman, 2012).

The Hokianga is located on the west coast of Northland (North Island, New Zealand) and is a coastal area with an extensive dune system on its northern headlands that is also under threat from invasive alien species (Hilton, 2006). The importance of preserving the dunes of the Hokianga Harbour encompasses three main aspects: cultural/historical, tourism/local economy related, and conservation. The Hokianga (full name "Hokianga-nui-o-Kupe", meaning "the final departing place of Kupe") is considered to be the spiritual birthplace of Māori culture in New Zealand, and refers to the place where Kupe, the first Māori to discover New Zealand, embarked on his return to Hawaiki after exploring the northern New Zealand coast. The area has particular cultural significance to Māori iwi, with approximately 40 archaeological sites recorded including shell middens, terraces and pits found on the northern headlands, primarily focused around the open and harbour coastlines and related flanks (Northland Regional Landscape Assessment, 2014). As a result, one of the areas local iwi recognise as a priority for preservation is the Kahakaharoa, an area on the northern headlands of the Hokianga Harbour, as the site Kupe's final departure (Fig. 1). In terms of wider local and economic interest, the sand dunes of the Hokianga heads are a central component of the identity of the outer Hokianga and one of the chief scenic attractions of the tourist resorts at Omapere and neighbouring Opononi; with the view from the southern shore of the harbour considered in itself worthy of preservation (Hicks, 1975). As part of a wider ecological area, the sand dunes are noted as a representative site for six ecological units, and location of four species of threatened flora and five species of threatened fauna (Northland Regional Landscape Assessment, 2014). In spite of the significance of the Hokianga, there has been no short- or long-term vegetation-monitoring programme in place. Recent anecdotal evidence suggests that invasive alien species have spread downwind of forested areas (Hokianga Historical Society, pers. comm.) but no quantified estimates are available.

In order to determine the causes of and therefore provide possible insights into the options for invasive alien species control, it is first necessary to establish the timing, pattern, rate and extent of invasion. Analysis of historical invasions, spreading rates and patterns can contribute to an understanding of how changes in the structure and functioning of dune ecosystems occur, which can subsequently be used to model future spread, and determine the potential effectiveness of differing management practices. Previous studies have shown historic photographs are an efficient method of assessing invasive alien species cover (Kollmann, Jørgensen, Roelsgaard, & Skov-Petersen, 2009; Wilmshurst, Bestic, Meurk, & McGlone, 2004), particularly in the absence of vegetation records. Fortunately, a series of photographs, combined with historical reports and supplemented with aerial imagery has allowed a unique temporal perspective to examine these key questions for the sand dunes of the Hokianga Harbour. Here we exploit historic and satellite observations, in addition to *in situ* observations and palaeoecology, to better understand the non-native species invasion across the Hokianga dunes.

2. Study area

The Hokianga dunes are located on the west coast of Northland, North Island, New Zealand (35°30′S, 173°21′E; Fig. 1). The dune system on the north heads cover an area of $\sim 30\,km^2$ (Hicks, 1975) and experiences a subtropical oceanic climate with a mean annual rainfall of ~ 1400 mm (accessed from NIWA's National Climate Database, www.cliflo.niwa.co.nz). Ocean currents in the area are highly variable, but recent studies demonstrate a southeast-ward drift in mean flow offshore the west coast of Northland and a northwest-ward current closer inshore (Palmer et al., 2014; Sutton & Bowen, 2011). The primary source of the sands on the headlands are the upper reaches of the Waikato River to the south of the Hokianga, derived from unconsolidated rhyolitic and pumiceous volcanic debris from the central North Island (Hicks, 1975; Manvile, 2002) and delivered north via longshore drift and southwest swells (King et al., 2013). The prevailing westerly winds allow the deposition and remobilisation of sand, which in combination with the ocean currents results in a high-energy dissipative beach system that has led to the construction of Holocene and Pleistocene dunefields (King et al., 2013).

3. Materials and methods

A suite of approaches was taken to survey this area over different spatial and temporal scales in an effort to obtain a holistic understanding of the rate and scale of alien species invasion. To determine the current extent of vegetation (both herbs and shrubs) on the Hokianga dunes, an aerial survey using an unmanned aerial vehicle (UAV) was undertaken to provide a high-resolution image mosaic and a three-dimensional digital elevation model of the sand dunes on the north heads of the Hokianga Harbour. Using this remote-sensing technique allows the acquisition of high-resolution topography data, which is otherwise unavailable from satellite imagery. This study utilised a low altitude UAV (flying at a height of 120 m above ground level at take-off, providing an average of 7 cm spatial resolution) for the collection of data, providing sufficient detail to accurately locate vegetation boundaries. A ground survey was also undertaken where the individual species (both native and non-native) were photographed and identified, helping to ground-truth the remote sensing data. Recent and contemporary Google Earth satellite imagery was used to provide information on vegetation extent back to the beginning of the twenty-first century, with new (archived) satellite imagery available at a resolution sufficient for the purposes of this study during 2004, 2010, 2011, 2013, 2014, and 2016.

Here, we identified two major invasive alien species patches on the dune covered headland: Patch 1 which is of concern to the local Iwi due to its proximity to the traditional departure point of Kupe (i.e. special cultural significance); and Patch 2, of concern to the local residents in terms of the visual aesthetic from Omapere and Opononi, across the harbour. Using Google Earth recent and contemporary satellite imagery, we calculated the area of the vegetation patches and how these have changed over time by creating a polygon estimation of the area. To establish a baseline of vegetation cover further back in time, historic photographs and postcards sourced from the Hokianga Historical Society were used to establish vegetation baselines before the onset of satellite observations, with the earliest images available taken in 1905. Although the sporadic nature of the photographs and their location prevents a precise quantitative measurement of the vegetation change of the entire dune area, the vegetation boundaries in these areas are recognisable. The vegetated area was visually estimated by overlaying the photograph onto Google Earth satellite imagery to create a polygon estimation from which it was possible to determine the historic area of the invasive alien species patch. For both the recent satellite imagery and the historical photograph overlays the mean of five separate polygon (area) estimates was determined for each image. The standard deviation of these five area estimates was then used to provide an estimate of the measurement uncertainty. While we acknowledge that this method of measurement may have biases in terms of view angles and resolutions, the polygon estimations from 2004 onwards are determined with the same satellite imagery and therefore should allow robust comparisons. The uncertainty is inevitably larger for the historical photograph overlays. Here we have taken a conservative approach and doubled the standard deviation of the five area estimates; it is important to note that regardless of the method used to estimate the uncertainty in the historical photographs, the trend through the twentieth century is clear (as described below).

To explore evidence of past vegetation cover on much longer (millennial) time frames, samples of preserved wood and compacted organic material preserved within the sand dunes were sampled and sent for radiocarbon (^{14}C) dating to determine when the dune fields were previously vegetated. Samples from an emergent kauri (*Agathis australis*) spar from a lignite bed at the southern-most point of the North Heads (X, Fig. 2), and from *in situ* lignite deposit of compressed peat from a ravine slightly further north (Y, Fig. 2) were taken in the field and measured by the University of Waikato Radiocarbon Dating Laboratory (Hogg, Fifield, Turney, Palmer, & Galbraith, 2006). A pōhutukawa (*Metrosideros excelsa*) tree stump from the top of a ravine (Z, Fig. 2) was also sampled for dating. Surfaces were scraped clean, and the wood was chopped up into small splinters and milled, washed in demineralised water, and dried. The samples were then pre-treated to alpha-cellulose using an acid-base-acid (ABA)/acidified sodium chlorite/ABA pre-treatment regime at Waikato. The radiocarbon measurements were undertaken at the University of California at Irvine on a NEC compact Accelerator Mass Spectrometry (UCI AMS 1.5SDH) system. The pretreated samples were converted to CO_2 by combustion in sealed pre-baked quartz tubes, containing Cu and Ag wire. The CO_2 was then converted to graphite using H_2 and a Fe catalyst, and loaded into aluminium target holders for measurement at UCI. Radiocarbon ages were calibrated using SHCal13 (Hogg et al., 2013 & Reimer et al., 2013) and the probability distributions summed using OxCal 4.2 (Bronk Ramsey & Lee, 2013). Calibrated ages are expressed here as thousands of years before present, CE 1950 (ka).

4. Results and discussion

4.1. Dune vegetation and morphology

The entire Hokianga dune system mapped by a UAV provided topographical constraints to the existing satellite imagery (Figs. 2, 3a and 3b, and Table 1), and allowed contours and ridgelines to be identified.

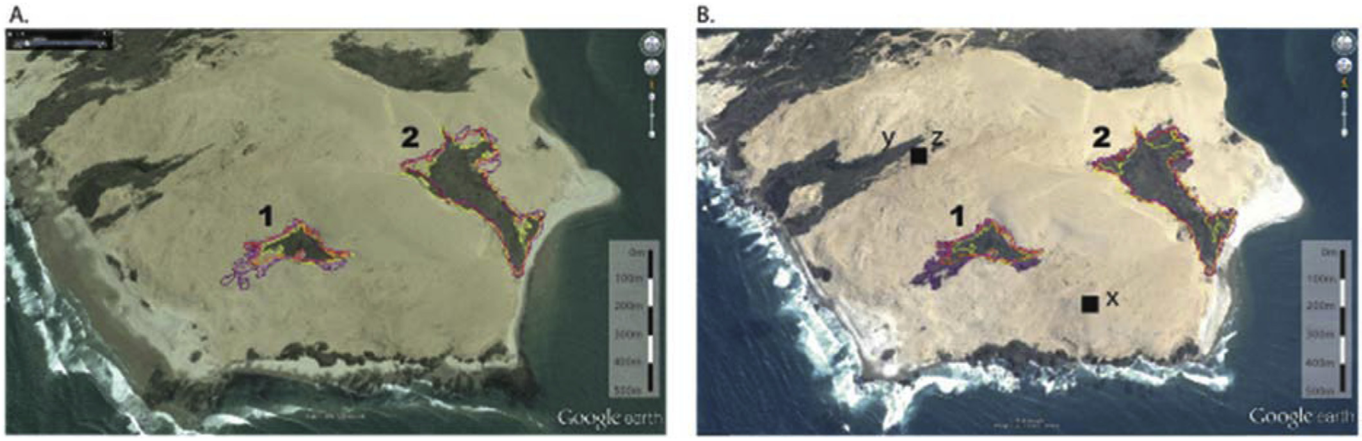

Fig. 2. Recent Google Earth satellite imagery, using DigitalGlobe's Quickbird satellite imagery from 2004 to 2007, and WorldView from 2007 onwards. **A.** 2004 and **B.** 2016, with coloured polygons overlaid showing the changing spatial extent of the two vegetation patches (yellow = 2004; orange = 2010; red = 2013; magenta = 2014; purple = 2016). Square boxes indicate the locations of the radiocarbon dates taken as shown in Table 1 (x = Kauri spar, y = Pōhutukawa stump and z = lignite (kauri) outcrop). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Importantly, the topography of the dune fields show the two prominent vegetation patches at similar elevations comprising a number of non-native species, which ground-truthing identified to include marram grass (*Ammophila arenaria*), sandplain lupin (*Lupinus digitatus*), tree lupin (*Lupinus arboreus*), gorse (*Ulex europaeus*), pampas grass (*Cortaderia selloana*), as well as native species including pingao (*Ficinia spiralis*) and spinifex (*Spinifex sericeus*) (Fig. 4a). These vegetation patches are associated with the location of lignite deposits (Fig. 3c). The geomorphological context is not unique to the Hokianga headland. The coastal area around the Hokianga (south along the 112 km-long Ripiro Beach) is part of an extensive palaeodune system containing scattered lignite beds that represent former lakes and wetlands (containing

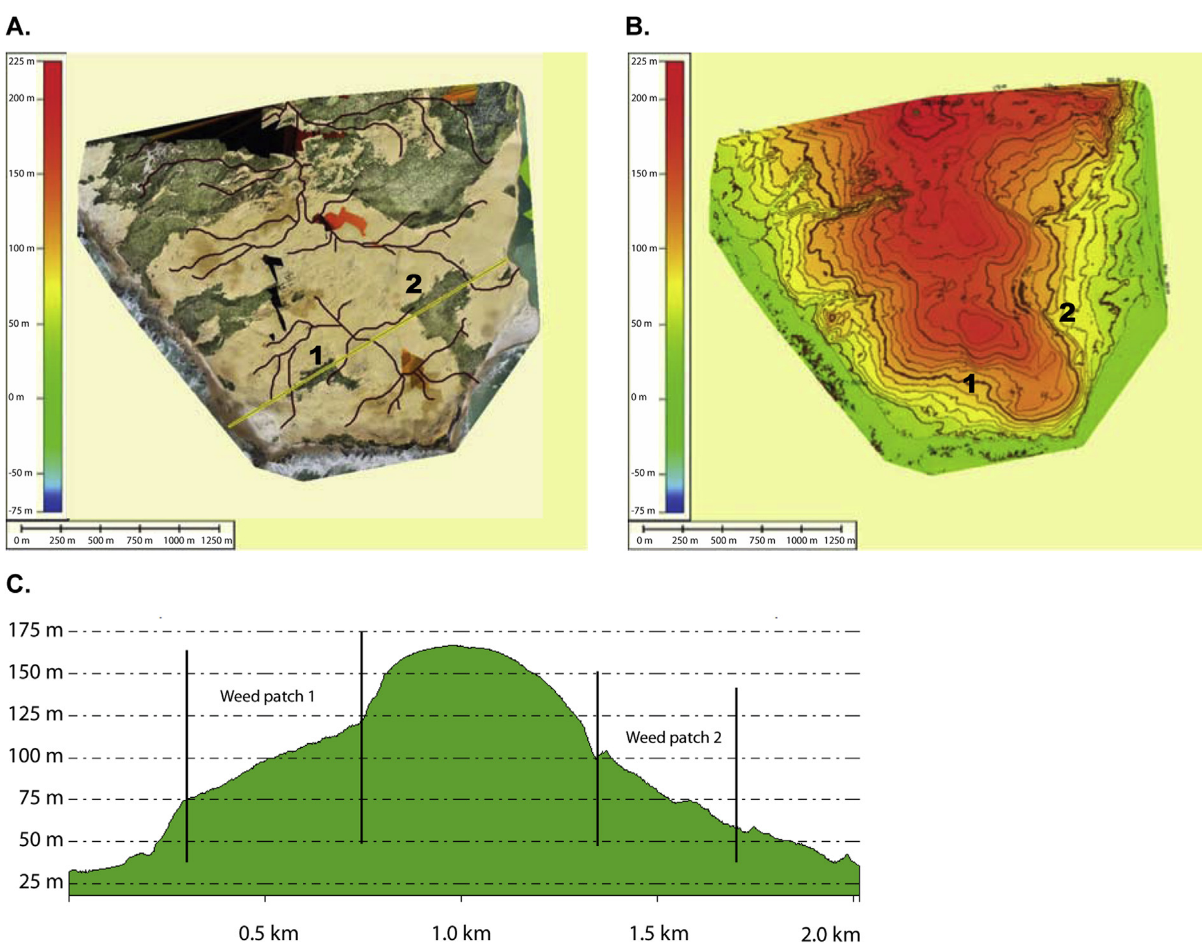

Fig. 3. A. Image mosaic derived from UAV imaging with ridgelines overplotted and a transect line running approximately southeast to northeast, Hokianga headland; **B.** 3D terrain model with contours from UAV mapping. Numbers indicate the two vegetation patches of interest. **C.** Cross section diagram of the transect line in A., with the area of the two vegetation patches marked. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Radiocarbon and calibrated ages for tree and lignite samples from the Hokianaga North Heads. 'Wk' denotes University of Waikato radiocarbon laboratory; 'UCIAMS' denotes the University of California at Irvine radiocarbon laboratory.

Lab. number	Site name	Latitude, °S	Longitude, °E	Altitude, m	^{14}C age BP (± 1σ)	Mean age (cal. BP, 1σ)
Wk 44059	Kauri spar	35.5203	173.3636	78	52,500 ± 3100	> 52,000
Wk 35546	Lignite outcrop (kauri)	35.5096	173.3553	125	> 50,000	> 50,000
UCIAMS 164050	Pōhutukawa stump	35.5084	173.3558	130	5105 ± 15	5820 ± 48

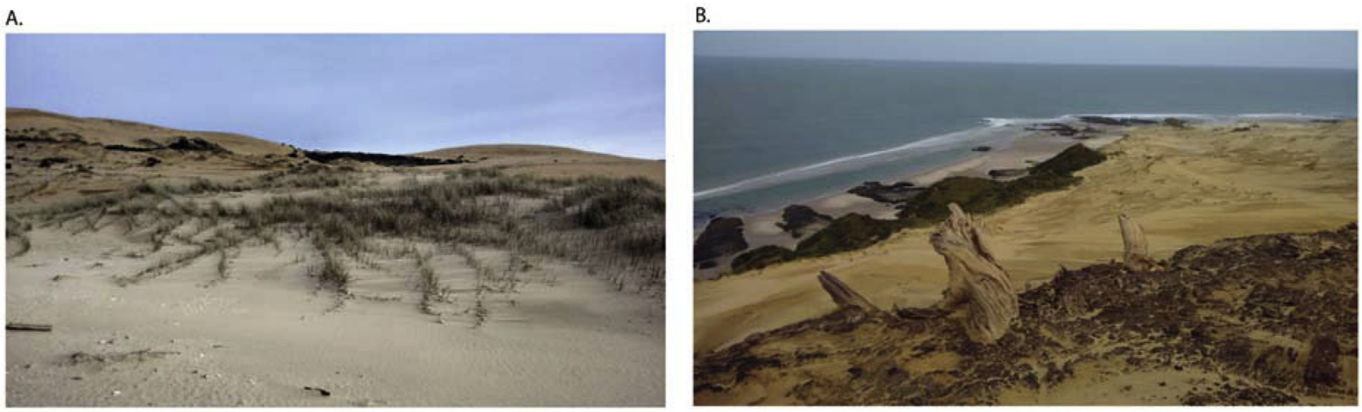

Fig. 4. A. Photograph showing native *spinifex* in the foreground with an established vegetation patch in the background, Hokianga headlands. B. Photograph showing a tree spar eroding out of the sand dunes at the North Head of the Hokianga Harbour (photo pointing approximately due west). Radiocarbon (14C) dated at 52,500 ± 3100 14C yrs BP (Wk-44059).

preserved fallen trees) and exposed along the eroding western coastal dune cliffs (Lorrey et al., 2018; Palmer et al., 2006). A kauri spar, protruding out of a lignite bed on the top of a sand dune at the southernmost tip of the North Head was radiocarbon dated to age of 52,500 ± 3100 ^{14}C BP (Fig. 4b) while a lignite sample of a separate deposit returned a ^{14}C age at > 50,000 ^{14}C BP (Table 1). These lignite deposits appear to play an important role in the establishment of vegetation on the headland and potentially the future trajectory of spread by non-native species.

The lignite beds on the Hokianga headland are buried to a considerable depth by sand dunes and the overlying weight coupled with the form of the underlying valley leads to the creation of concave beds (in profile). Their relatively high wax and oil content appears to impede percolation through the dunes. As a result, water accumulates above the concave lignite layer and then spills out from the edge of the underground bed as seepage points or 'springs', possibly via other interleaved beds, before finally emerging as small streams at the base of the dune system, creating year-round water sources near the surface that supports vegetation. Importantly, this spatial perspective highlights the importance of the geomorphology of the sand dunes: the patterns of vegetation are clearly linked to the lignite beds, where rainfall seepage points allow and/or promote establishment on the headland.

4.2. Temporal and spatial changes in dune vegetation

In addition to the presence of ancient (swamp) kauri in the dunes demonstrating former vegetation on the headland, we identified a pōhutukawa stump from the top of a ravine immediately above a lignite bed on the Hokianga Heads. Radiocarbon dating of this pōhutukawa stump produced a calendar age of 5800 ± 50 cal. BP supporting the contention that the Hokianga headland has been (at least partially) vegetated for millennia before the first human settlers in the area. This information is vital to assess the timescales of changes across the system, and suggests that the system has been resilient to major change over millennia.

By exploiting the images taken of the headland over the last century we were able to place the above vegetation observations in historical context (Fig. 5). Although the historic photographic sequences do not offer a continuous time series for the sand dunes, and in particular the north-facing slopes, they do provide important spot observations that allow an assessment of the changing vegetation coverage over the last two decades determined from Google Earth (Fig. 2). Based on the estimated areas from the historic images, we find vegetation cover was more sparse during the first half of the twentieth century than that observed in the most recent decade (Table 2). Furthermore, the accelerated rate and magnitude of spread is considerably higher than any other time in the last 110 years (Fig. 6), implying increasing occupation of the dunes of what had been limited vegetation patches. Concerningly, the foot survey also identified an extensive fine covering of marram grass and juvenile lupin, outside the identified polygons in Fig. 2, which was not visible from the UAV, satellite, or historic imagery. These areas are of considerable importance since remote monitoring methods are not sufficiently resolved to identify these areas.

4.3. Mechanisms for vegetation establishment

Invasion ecology highlights the importance of species interactions for understanding the establishment and persistence patterns of non-native species (Kuebbing & Nuñez, 2015). Notably, invasional meltdown theory suggests that invaders facilitate other invaders (Simberloff & von Holle, 1999). In this case, once an ecosystem becomes hospitable to an introduced, or non-native species, the invasive alien species will continue to successfully establish due to the existence of a suitable environment but also by profiteering from the ecological disruption caused by prior invasion. A positive invasive feedback loop thus exacerbates complexity of system and makes management more challenging. However, identifying the initial trigger for this increase in the area should consider external mechanisms, such as changes in climate and/or sediment flux. Unfortunately it is not known exactly when the invasive alien species were introduced to the Hokianga headlands. It is likely associated with the pine plantations to the north, but it is assumed to be at least after the date of the first imagery in 1905.

There are several possible climate-related aspects that may affect the rate of non-native species invasion. Climatic traits such as soil

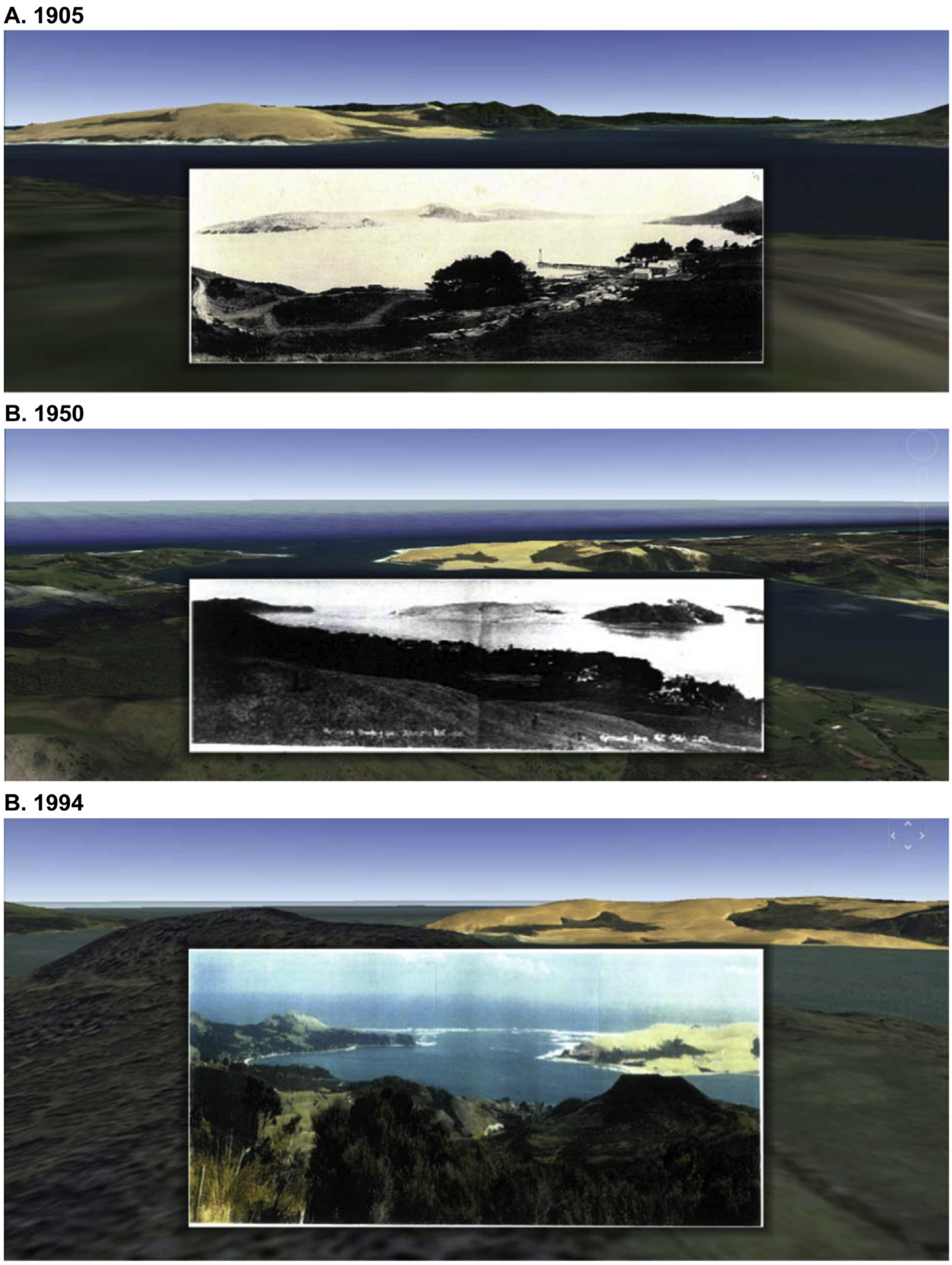

Fig. 5. Image overlays, using historical photographs from the Hokianga Heads, taken in 1905 (A.), 1950 (B.) and 1994 (C.) compared to 2016 Google Earth imagery.

temperature, soil moisture, pattern of rainfall and evaporation, and carbon dioxide concentration can all affect the floristic composition (Dukes & Mooney, 1999; Early et al., 2016; Kathiresan & Gualbert, 2016; Palmer et al., 2015). For example, a study of coastal dune communities in Australia has suggested that increased windy conditions may promote fast seed dispersal and thus a high rate of invasion (French et al., 2011). Although the annual precipitation sum and average wind speed in Kaitaia (the closest weather station with

Table 2
Calculated areas of the two identified vegetation patches on the Hokianga headland. *Hokianga Historical Society, pers comm.

Date	Vegetation patch 1 (hectares)	Uncertainty (1σ)	Vegetation patch 2 (hectares)	Uncertainty (1σ)
13/04/1905	0*		3.5 (estimated)	1.5
01/01/1950			2.5 (estimated)	1.4
01/01/1994			8.9 (estimated)	1.3
08/11/2004	21.7	1.3	133.0	0.4
21/02/2010	26.7	1.1		
04/09/2011	28.5	1	139.4	0.9
23/08/2013	36	1.4	144.3	1.8
09/03/2016	41	1.8	151.8	1.7

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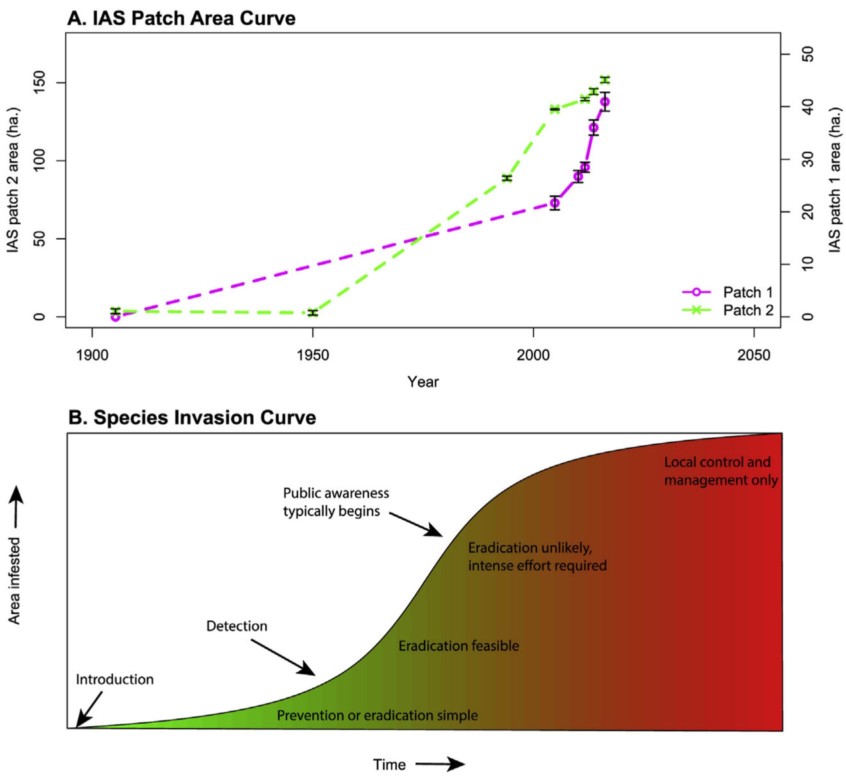

Fig. 6. A. Area (hectares) of vegetation Patch 1 and 2, measured from Google Earth Imagery (2004–2016) and comparison to historical photographs (dashed lines; 1905–1994). Error bars indicate uncertainty on measurements. **B.** Typical species invasion curve, adapted from Australian Government Department of the Environment and Water Resources (2006). During the initial phase, fewer impacts are seen to natural resources and invasive species have a high probability of eradication. As the population of invasive species enters the growth phase it begins to spread rapidly. At some point the non-native species will reach its ecological amplitude where it occupies all the space available to the species, and is very difficult to eradicate.

continuous rainfall data through the 20th century, Fig. 1c) show no discernible long-term trend, it is possible that the site-specific relationship may differ to the average annual patterns.

An alternative mechanism that may affect the rate of invasive alien species invasion is a change in the sediment flux. Observations from a coastal dune system of aeolian sediment transport indicate that transport rates and supply to the foredunes critically depend on the presence of dry sand sources, such as represented by well-drained intertidal bars (Bauer et al., 2009). Unfortunately there are no long-term measurements of sediment transport and/or flux in the Hokianga catchment. Anecdotal evidence, however, suggests that sediment supply may play a major role. As the two vegetation patches are centred on areas of lignite, a reduction in sediment flux could help to explain the expansion of the vegetated areas beyond the direct influence of the lignite. Sediment flux can be affected by a range of different factors: one of the most common causes of a change in long-term sediment flux is change in sea level, where 'offshore' sand sources are either restricted (as a consequence of sea level rise) or exposed (linked to sea level fall). Other factors influencing sediment flux include changing land use and the dredging of sand from harbours or other sand bar areas.

There is evidence from the Hokianga to support a changing sediment flux during former periods of higher sea level. During a regional high sea level stand in the mid-Holocene it is likely that there was a reduced sediment flux (Clement, Whitehouse, & Sloss, 2016; Turney et al., 2017; Dougherty, 2014), providing an opportunity for vegetation of the slopes to establish through decreased sand mobility. When sea levels fell again, exposure of sand enabled increased sand mobilisation and dune re-establishment. Support for this interpretation comes from the pōhutukawa tree stump, dated to approximately 5.8 ka BP, suggesting vegetation cover may have been more extensive during the mid-Holocene. Projected sea levels by the end of this century (IPCC, 2013) are of a comparable magnitude to the regional mid-Holocene sea level peak and will likely reduce the sediment flux onto the Hokianga headlands, further encouraging the expansion of invasive alien species. Future sea level rise should be considered in future management planning.

Although there is no historic record of extensive sand extraction from the Hokianga Harbour, there is from the Kaipara Harbour (Kanwar et al., 2015) and Port Waikato (both to the south), suggesting a decrease in coastal drift of sand (Schofield, 1970). There is also evidence for recent changing land use on the northern headlands. Since the mid-twentieth century, the dunes appear to have been stabilised by pine forest plantation, potentially starving sediment supply. The fact that the kauri spars and associated lignite bed were exposed indicates recent overlying sand removal; the spars had not previously been exposed otherwise the ancient wood would have gradually rotted away. From this we can conclude the balance between sand attrition vs. removal has changed with a decline in the amount of sand being replenished resulting in the wind eroding the overlying sand. Such a scenario provides certain invasive alien species with a competitive advantage. For example, marram grass has a more extensive rhizomatous root system to that of pingao, which gives it a competitive advantage in terms of water and nutrient uptake (Partridge, 1995), whilst also being more tolerant to sand burial, high temperatures, and moisture deficits (Dixon et al., 2004). Crucially, the rapid formation of the deep and extensive root network which binds the grains together and holds the sand firmly, turning mobile dune habitats into a more stable environment (Gadgil, 2002; Hilton et al., 2005), resulting in a positive feedback. By stabilising mobile sand, woody invasive species such as gorse and tree lupin are then able to establish, whereupon studies from other regions have shown the nitrogen-fixing properties of lupin facilitate the invasion of other non-native and native species, further decreasing sand mobility and allowing other plant species to invade (Pickart, 2004). Although dune profiles are largely dependent on the wind and sand dynamics, the interactive effects of vegetation can also play an important role (Baas, 2002). For example, the seaward facing fore dune slopes that are dominated by spinifex and pingao tend to be less tall and steep than those dominated by marram grass (Hilton et al., 2005). A regime shift in dominant plant species can thus lead to substantial changes in dune structure and stature (Zarnetske et al., 2012). These collective impacts appear to be resulting in the conversion of sparsely vegetated dune ecosystems dominated by native plant species to more densely vegetated systems dominated by non-native plant species. Whilst we do not have the data to test whether the geomorphology of the dunes has been altered, our reconstruction from historic, satellite and UAV imagery and ground surveys strongly suggests that the coverage and diversity of non-native species is increasing.

Once established, non-native species can spread quickly and become invasive. The species invasion curve (Fig. 6b) shows the relationship between the spread of invasive alien species and the time and effort needed to eradicate the threat (Australian Government Department of the Environment and Water Resources, 2006); generally, the steeper the slope of the invasion curve, the more rapidly the invasive species has spread. During the initial phase, relatively few impacts on natural vegetation are observed, and invasive species have a high probability of eradication. As the range and population of invasive species enters the growth phase they begin to spread rapidly. At some point the introduced non-native species will reach their ecological amplitude where they occupy all the space available to the species, and become extremely challenging to eradicate. The species invasion curve, as mapped by the historical photographs and satellite imagery, display a similar trajectory to the theoretical species invasion curve, with rapidly increasing coverage (Fig. 6). The spatial extent of the invasive alien species patch is a key indicator of whether an eradication attempt is likely to succeed (Moore, Runge, Webber, & Wilson, 2011), with eradication more likely with a smaller area (< 100 ha), and taking place soon after the initial invasion (Mack & Lonsdale, 2002). On the Hokianga headlands, Patch 1 is < 50 ha, while Patch 2 is ~150 ha, suggesting that eradication is feasible for Patch 1, but may be more difficult for Patch 2. It is difficult to determine exactly where on the theoretical species invasion curve the invasive alien species patches lie, but given the areas currently covered, and increase in rate within the last decade, it is likely to be between the ‘eradication feasible’ and ‘eradication unfeasible’ stages (particularly taking into account that there is already local public awareness of the invasion). Worryingly, the detection of marram grass and juvenile lupin outside the two main vegetation patches (which were not identified by remote imagery), suggests that the invasive species are close to becoming firmly established across the dune system, and swift action may be required to prevent further expansion across the dune system.

4.4. Invasive species management strategy

There are a number of possible options on the Hokianga headland. The most appropriate methods for the restoration of the natural character of coastal sand dunes and preservation of native plant species are still under debate, though the removal of invasive species is a commonly used approach in restoration projects (Lithgow et al., 2013). A critical primary aim of dune restoration is the prevention of spread of invasive species into uninvaded areas of sand dunes. However, the removal of the target species from densely invaded sites is also often necessary to reduce the ability for further spread, although species removal alone is not always sufficient to restore plant communities in sand dunes, particularly when the invading species alters the soil properties or dune profile (Emery, Doran, Legge, Kleitch, & Howard, 2013; Konlechner, Hilton, & Lord, 2015). For example, chemical removal of lupin was undertaken on a sand dune habitat in southern New Zealand, and while effective at reducing lupin cover, six years after treatment, the pre-lupin plant communities had not re-established (Konlechner et al., 2015). Secondary environmental changes can cause other long-term impacts such as further invasions by other new or non-dominant invasive alien species, or erosion and sand blowouts due to removal of species necessary for sand stability (Emery et al., 2013; Konlechner et al., 2015). At the site in southern New Zealand, increased cover of the non-native grass *Lagurus ovatus* and native sand sedge (pingao) was observed, indicating a mixed plant community response. Some studies have therefore suggested that regeneration of native coastal dune communities may require the active reintroduction of species (French et al., 2011) to replace the eradicated plant biomass and prevent further weakening of the system as a habitat and protective structure. Lessons from other New Zealand-based pest management programs should be learnt such that additional post-removal activities and long-term monitoring are likely essential to ensure the desired outcomes are achieved and to restore the native vegetation of the Hokianga headlands.

While there are many lupin shrubs established in the vegetated patches of the dune area, our foot survey revealed a substantial number of juvenile marram grass and lupin plants outside the established vegetation patches that would be suitable for manual removal, for example by community-based volunteer activities. This is a recommended strategy that should contain or at least slow down expansion. However, hand-pulling has been shown to be ineffective at removing marram grass unless carried out frequently and over a long period (Partridge, 1995) as a result of the rhizome material left in the ground (Gadgil, 2002). Strategies for lupin eradication primarily involve the prevention of further spread, followed by manual removal techniques. Selected herbicides have been used by the New Zealand Department of Conservation, such as the grass-specific herbicide haloxyfop (‘Gallant’), which can be advantageous if managing a pingao dune where marram grass has encroached (since pingao is a sedge and is not affected by the herbicide). While manual removal on the fringes of the invasive alien species patches may prevent further spread, a more concerted action, likely involving a mixture of physical, chemical and biological control might be the most likely to succeed in reducing the more established invasive alien species areas on the sand dunes of the Hokianga.

5. Summary and conclusions

Using a multiproxy approach combining palaeoecology, historic, satellite and UAV imagery, and ground surveys, we suggest that it is the combination of the complex geomorphology, the initial planting of invasive species such as marram grass, and a decreased sediment flux related to pine plantations in the north, that has allowed invasive alien species expansion to accelerate in recent decades. With sea level projected to rise over the next century, the likely reduced sediment flux could further encourage the establishment of invasive alien species on the headlands, threatening what has until recently been relatively sparsely vegetated headland of the Hokianga.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.apgeog.2018.07.006.

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