EARTH SURFACE PROCESSES AND LANDFORMS
Earth Surf. Process. Landforms **40**, 1088–1100 (2015)

(wileyonlinelibrary.com) DOI: 10.1002/esp.3691

Vegetation succession in deglaciated landscapes: implications for sediment and landscape stability

Megan J. Klaar,[1]* Chris Kidd,[2] Edward Malone,[1] Rebecca Bartlett,[1] Gilles Pinay,[3] F. Stuart Chapin[4] and Alexander Milner[1]
[1] University of Birmingham School of Geography, Earth and Environmental Sciences, Edgbaston, Birmingham B15 2TT, UK
[2] University of Maryland, Earth System Science Interxdisciplinary Center, 8082 Baltimore Avenue, College Park, Maryland 20740, USA
[3] Universite of Rennes 1, OSUR-CNRS-ECOBIO, Campus de Beaulieu. avenue general Leclerc, Rennes cedex 35042, France
[4] University of Fairbanks, Institute of Arctic Biology, Fairbanks, Alaska 99611, USA

Received 5 August 2013; Revised 24 November 2014; Accepted 25 November 2014

*Correspondence to: M. J. Klaar, University of Birmingham School of Geography, Earth and Environmental Sciences, Edgbaston, Birmingham B15 2TT, UK.
E-mail: m.j.klaar@bham.ac.uk

ESPL
Earth Surface Processes and Landforms

ABSTRACT: Landscapes exposed by glacial retreat provide an ideal natural laboratory to study the processes involved in transforming a highly disturbed, glacially influenced landscape to a stable, diverse ecosystem which supports numerous species and communities. Large-scale vegetation development and changes in sediment availability, used as a proxy for paraglacial adjustment following rapid deglaciation, were assessed using information from remote sensing. Delineation of broad successional vegetation cover types was undertaken using Landsat satellite imagery (covering a 22 year period) to document the rate and trajectory of terrestrial vegetation development. Use of a space-for-time substitution in Glacier Bay National Park, Alaska, allowed 'back-calculation' of the age and stage of development of six catchments over 206 years. The high accuracy (89.2%) of the remotely sensed information used in monitoring successional change allowed detection of a high rate of change in vegetation classes in early successional stages (bare sediment and alder). In contrast, later successional stages (spruce and spruce–hemlock dominated forest) had high vegetation class retention, and low turnover. Modelled rates of vegetation change generally confirmed the estimated rates of successional turnover previously reported. These data, when combined with the known influence of terrestrial succession on soil development and sediment availability, suggest how physical and biological processes interact over time to influence paraglacial adjustment following deglaciation. This study highlights the application of remote sensing of successional chronosequence landscapes to assess the temporal dynamics of paraglacial adjustment following rapid deglaciation and shows the importance of incorporating bio-physical interactions within landscape evolution models. © 2014 The Authors. *Earth Surface Processes and Landforms* published by John Wiley & Sons Ltd.

KEYWORDS: primary succession; biogeomorphology; physical–biological interactions; Glacier Bay; Alaska; paraglacial adjustment

Introduction

Following glacial recession, deglaciated landscapes undergo rapid geomorphic change as sedimentological, hydrological and aeolian processes begin to alter the landscape. The term 'paraglacial' refers to the unstable conditions and high geomorphic activity typically associated with recently deglaciated landscapes during this phase (Ballantyne, 2002a), when rates of landscape change and sediment output from the system are typically elevated. Physical processes that extensively rework sediments at this time are often referred to as 'paraglacial adjustment processes' and persist until catchment sediment yields return to those typical of unglaciated catchments (Benn and Evans, 2010).

Geomorphic development following glacial recession is influenced by high sediment loads originating from glacial features, such as moraines, debris flow, flow tills and outwash, and processes involved in the modification of glacier forelands, such as mass movement, frost action, fluvial processes, and slope processes (e.g. avalanches, rock slides and debris falls). Reworking and transport of these sediments are the dominant driving variables affecting landform change during this paraglacial adjustment period (Ballantyne, 2002a; Benn and Evans, 2010), as processes which drive sediment transport (e.g. fluvial transport, slope failure, debris flow, erosion) or exhaustion (e.g. bank and slope stabilisation) characterise the period in which paraglacial adjustment takes place (Church and Ryder, 1972). Due to the high availability of mobile sediments and increased fluvioglacial activity, paraglacial landscapes are particularly dynamic, and the adjustment period is deemed to have ended once the sediment yield has returned to a 'non-glacial' state where glacially conditioned sediment availability is exhausted or attains stability as a result of reworking processes (Ballantyne, 2002b). As no processes are unique to paraglacial environments (Slaymaker, 2009; Benn and Evans, 2010), a number of authors (Ballantyne, 2002b; Slaymaker, 2009; Benn and Evans, 2010) have proposed that 'paraglacial' is best defined as a *period of time* during which rapid environmental adjustment takes place following deglaciation, rather than a definition of specific processes or landforms. We adopt this definition when referring to 'paraglacial', and those 'paraglacial adjustment processes' which occur during this time. Depending on the spatial scale of observation, the dominant paraglacial processes involved, and the land system, the paraglacial adjustment period may last between 10 and 10 000 years (Ballantyne, 2002b).

Physical and biological processes that alter sediment availability and resultant sediment yield within catchments through sediment transport and stabilisation act as drivers of paraglacial adjustment, and hence determine the length of the paraglacial period (Benn and Evans, 2010). Recently, Slaymaker (2009) suggested that paraglaciation and its associated processes are better defined as a dynamic transition from glacial disturbance to a stable landscape lacking glacially influenced conditions, and hence, paraglaciation is better defined and quantified using a rate and trajectory of change from glacial to non-glacial conditions. In this manner, paraglacial adjustment processes are better classified as some of many components of large-scale development that occurs following deglaciation.

Although our understanding of geomorphic change in the paraglacial period is increasing (Ballantyne, 2002b), particularly the role and importance of physical processes such as debris flow, mass movement and fluvial transportation in creating and stabilising geomorphic features (Fitzsimons, 1996; Irvine-Fynn *et al.*, 2011; McColl, 2012), few studies have addressed the influence of biotic processes and interactions on the rates of paraglacial adjustment processes (with the exception of Eichel *et al.*, 2013). Terrestrial vegetation alters sediment availability by reducing soil erosion via rainfall interception (Quinton *et al.*, 1997), increased soil infiltration, decreased bulk density, and increased soil shear strength and cohesion (Gyssels *et al.*, 2005). These changes in turn, stabilise slopes (outlined by Marston, 2010) and river banks (Thorne, 1990), thereby influencing catchment-scale sediment yield, particularly in small catchments (Marston, 2010).

Given the influence of vegetational processes outlined above, it is evident that the colonisation and development of vegetation on deglaciated landscapes contributes to paraglacial adjustment processes by stabilising landforms (e.g. valley slopes, paraglacial debris cones and alluvial fans, and river channels) and sediment exhaustion of glacially influenced sediment sources. Indeed, vegetation colonisation has been specifically identified as a major factor contributing to the exponential sediment exhaustion component of Ballantyne's primary paraglacial activity model (Ballantyne, 2002b). However, research that quantifies the role of vegetation development on sediment availability, and the rate of change and trajectory of paraglacial adjustment and landscape development remains sparse.

Vegetation succession on newly exposed sediments following deglaciation and the process of primary succession is a central concept in ecology (Begon *et al.*, 1996). During this process, pioneer plant species colonise and stabilise land surfaces, and a succession of communities undergo a pattern of colonisation and extinction controlled by both biotic and abiotic factors over time (Matthews, 1992). During succession plant communities undergo a gradual increase in structural complexity, biomass, species diversity and ecosystem interaction (Odum, 1969; Matthews, 1992; Milner *et al.*, 2007) over a time period similar to that of paraglacial adjustment. Sediment availability and soil characteristics evolve as terrestrial succession progresses, changing from soils with a characteristically high sediment availability and simple structure to a complex soil structure with lower sediment availability, stabilised by vegetation growth at later successional stages. For example, Orwin and Smart (2004) demonstrated that sediment mobilisation and suspended sediment loads in proglacial streams following rainfall events were much higher on 'young' paraglacial surfaces than 'mature' or 'old' surfaces following the Little Ice Age maximum. These surfaces showed evidence of rapid temporal decline in surface sediment response to rainfall events due to surface armouring and sediment exhaustion, resulting in stabilising surfaces within a few decades following deglaciation. Rapid surface sediment reworking and stabilisation were also found to occur within decades of deglaciation following the Little Ice Age maximum as a result of upslope processes (Matthews, 1992; Orwin and Smart, 2004; Moreau *et al.*, 2008), and vegetative colonisation (Moreau *et al.*, 2008; Eichel *et al.*, 2013). As succession progresses, and species composition and the structural complexity of terrestrial plant communities begin to change, sediment mobilisation declines as tensile strength and sediment binding by roots and organic matter (OM) begin to increase (Crocker and Major, 1955; Milner *et al.*, 2007), resulting in increased infiltration and interception of rainfall.

Despite the synchrony of vegetation succession and paraglacial adjustment on the deglaciated landscape, and their potential interaction and facilitation, there is a paucity of research on these linkages. Increasing research on vegetation–landscape interactions including plant–sediment dynamics within riverine environments (Gurnell *et al.*, 1999; Corenblit *et al.*, 2008, 2009; Osterkamp *et al.*, 2012; Cowie *et al.*, 2014), and slope–vegetation interactions (Marston, 2010) have begun to investigate the interaction between biological/ ecological and geomorphological processes. These studies illustrate the role of biogeomorphic interactions in ecosystem functioning and recovery following geomorphological disturbances (Viles *et al.*, 2008; Rice *et al.*, 2012). However, there remains a gap in our understanding of the development and influence of biogeomorphic interactions in the development of ecosystems following large-scale, extreme disturbance caused by glacial processes.

Although previous studies have elucidated a number of interactions and processes, the lack of information on intermediate timescales (100–500 years) is likely to have omitted those processes that take longer to develop and mature, as well as those processes that operate at the landscape scale (Rossi *et al.*, 2014). For example, previous research has often been limited to either short-term (up to 100 years following deglaciation, Gurnell *et al.*, 1999; Orwin and Smart, 2004; Moreau *et al.*, 2005, 2008), or long-term (e.g. Holocene or Little Ice Age; Passmore and Waddington, 2009; Hobley *et al.*, 2010) timescales and are often limited in spatial area (e.g. 5–1200 km^2; Irvine-Fynn *et al.*, 2011; Tunnicliffe *et al.*, 2012). Given the increasing recognition of vegetation–landscape interactions, and previous difficulties in studying intermediate timescales of paraglacial adjustment, it is likely that the importance and role of these interactions in determining the timescale and processes of paraglacial adjustment is lacking.

Vegetation change in Glacier Bay National Park (GBNP) in southeast Alaska is one of the best studied examples of primary succession (Chapin and Walker, 1988; Matthews, 1992) following rapid retreat of an extensive Neoglacial icesheet within the last 250 years. During the early stages following deglaciation, vegetation development is limited to species tolerant of the harsh, constantly shifting physical habitat characteristic of proglacial areas (see below for species involved). Over time, however, unconsolidated substrates become more stable, due to changing and developing drainage networks, facilitating subsequent vegetation succession, and culminating in a diverse Sitka spruce-western hemlock forest. Space-for-time substitution in GBNP allows a 250 year chronosequence of vegetation development to be assessed on the basis of spatial differences over a relatively small distance (~120 km of linear glacial retreat).

Reinhardt *et al.*, (2010) identified remote sensing systems as an 'under-utilised toolbox' of analytical techniques to study biogeomorphic interactions. The repeat survey capabilities of the Landsat satellites were highlighted as being particularly useful to study vegetation change, as landscape dynamics and physical processes which occur over relatively short ($<10^2$ years) timescales are deemed too difficult to measure directly (Reinhardt *et al.*, 2010). These timescales are also of particular importance in the study of the interactions of biological and physical processes with one another over the long term (Rull, 2012) as physical–biological feedbacks and interactions often require significant time to develop before influencing their surroundings (Reiners *et al.*, 1971; Milner *et al.*, 2007). Given the opportunities for the space-for-time substitution available at GBNP, combined with the existence of repeat aerial Landsat satellite images in this area over a 22 year period and an extensive body of literature available regarding processes of vegetation succession, soil development and changes in sediment yield over time within GBNP, we aim to determine the rate and processes of vegetation–landscape interactions which influence sediment availability, and by proxy, paraglacial adjustment on glacier forelands over the 250 year time period since the Neoglacial maxima.

The principal objective of this study was to assess mesoscale land surface stability by measuring primary successional changes in vegetation cover and soil development over an inferred 205 year period using Landsat images from a number of catchments of different ages. This examination of the coevolution of landforms and biological communities will assist in the continued development and refinement of landscape evolution models, which hitherto have lacked the incorporation of bio-physical processes and linkages (Marston, 2010; Reinhardt *et al.*, 2010), and help to increase our understanding of the role of vegetation development in defining the processes and timescales of paraglacial development.

Methods

Study area

Glacier Bay National Park and Preserve (GBNP) is located in southeast Alaska, ~105 km west of Juneau (Figure 1). The National Park covers an area of ~11 030 km^2, most of which is dominated by a Y-shaped tidal fjord over 100 km in length and 20 km in width at its widest point. The area has undergone a number of glacial advances and recessions over time, reaching a maximum in the Pleistocene during which time an ice sheet covered the entire area, which later receded to approximately current-day glacial extent in the late Wisconsin following an increase in temperature and decrease in precipitation (Streveler and Paige, 1971). During this time, it is thought that the entire area was filled with glacial sediments (Streveler and Paige, 1971). Later, a large piedmont glacier covered the entire area of the current GBNP area during the Little Ice Age, reaching its maximum around AD 1700 near the mouth of the current fjord (Cooper, 1937). Recession of the current glacial coverage began ~250 years ago, following a change in local climatic conditions, and once initiated

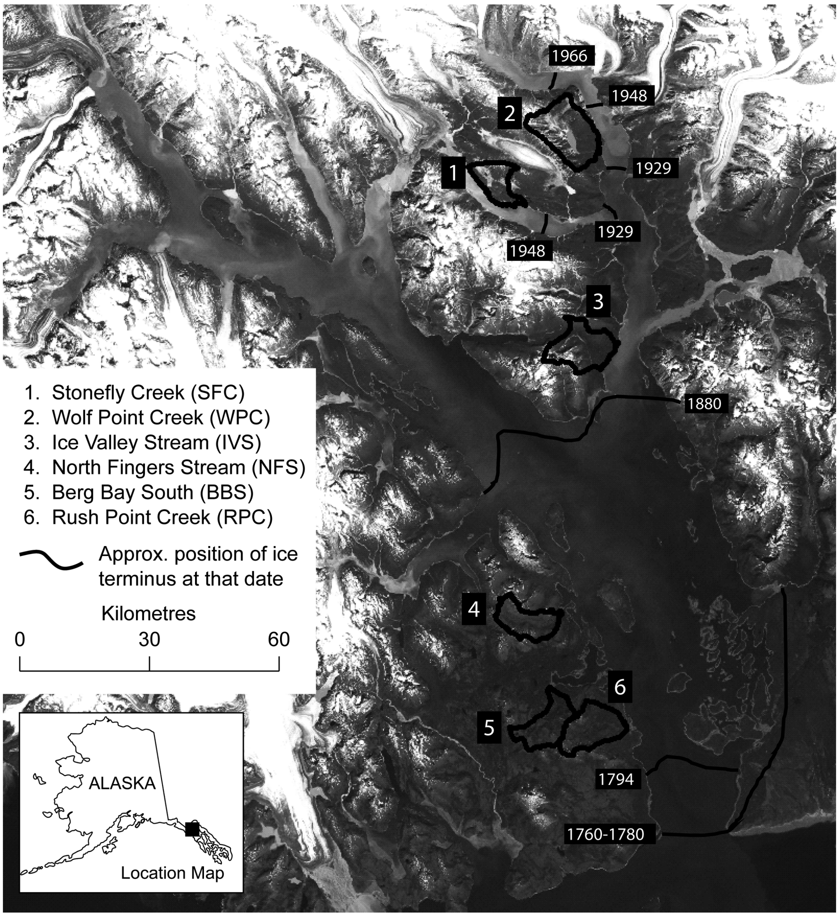

Figure 1. Glacier Bay National Park, Alaska, indicating study catchments and dates of glacial recession. Basemap courtesy of ArcGIS world imagery. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

the ice sheet retreated rapidly (Chapin *et al.*, 1994), resulting in numerous glaciated valleys separated by mountains. During these series of glacial advances, existing vegetation and landforms were scoured from the upper sections of the valleys, while the lower sections were buried under hundreds of metres of sediments deposited by glacial streams (Cooper, 1923). Exposed land surfaces are therefore dominated by glacial outwash and unconsolidated sediments, in addition to areas of bedrock, which are often shaped by fluvio-glacial processes. The deglaciated landscape is characterised by glaciated valley land-system features (Matthews, 1992), including steep sediment-mantled slopes and kame terraces which are subject to debris flow and subsequent fluvial transportation (illustrated in Figure 2). Detailed historical and geological data allow recession of the ice since the Neoglacial maximum to be accurately dated, and catchment age may be deduced from its distance from the retreating glacier termini. Modern day stream and catchment ages have been defined as the time since ice recession from the stream mouth (Milner *et al.*, 2000).

Vegetation development on the recently exposed glacier forelands within Glacier Bay follows a known succession of stages, beginning with the colonisation of barren ground by nitrogen-fixing species such as *Dryas drummondii*, *Salix* species, and Sitka alder (*Alnus sinuata*) within the first 50 years after deglaciation (Fastie, 1995). These species often form a dense thicket and persist until competition from later successional species limits their success (Crocker and Major, 1955). Cottonwood (*Populus trichocarpa*) typically follows the initial alder–willow thicket stages, peaking in abundance approximately 50–70 years following deglaciation (Reiners *et al.*, 1971). Sitka spruce (*Picea sitchensis*) begins to increase in abundance approximately 100 years following deglaciation, creating a mixed cottonwood–spruce forest before slowly being replaced by scattered western (*Tsuga heterophylla*) and mountain hemlock (*T. mertensiana*) which dominate the forest over time (Chapin *et al.*, 1994). Observation of adjacent areas that were not covered by Neoglacial ice suggests that *Sphagnum*-dominated muskeg is the climax community. This successional pattern might change through time, if historical vegetation development alters seed availability of potential colonisers (Fastie, 1995); however, as it is the *broad scale* patterns of landscape development that are of interest to this study, the exact pattern of vegetation succession is not of great importance, and hence, the possibility of multiple successional pathways (Fastie, 1995) does not impede the analysis.

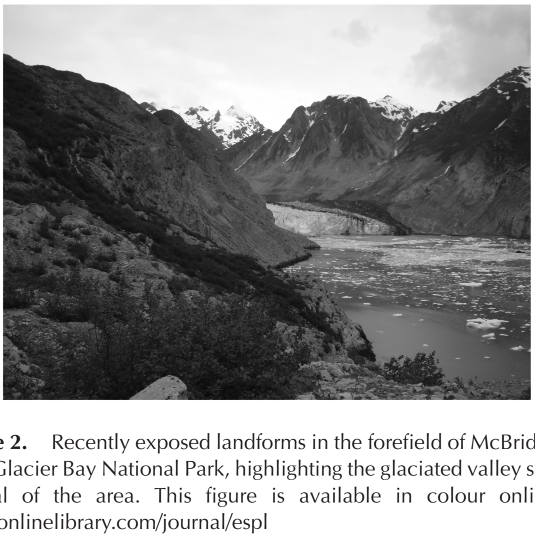

Figure 2. Recently exposed landforms in the forefield of McBride glacier, Glacier Bay National Park, highlighting the glaciated valley system typical of the area. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

Satellite image collection and processing

Changes in vegetation development from bare ground to alder–willow shrub, cottonwood, spruce and later spruce–hemlock forest may be delineated and classified using remote sensing techniques, owing to differences in spectral response related to colour and foliage density. Comparison of reflectance values in the spectral bands collected by Landsat satellite sensors distinguishes between the spectral behaviour of dominant species within a successional stage allowing a broad-scale classification over a large area of land to be generated. The method for classifying vegetation in this way is detailed below and outlined in Figure 3 (Hall *et al.*, 1991; Chambers *et al.*, 2007).

Landsat satellite images (spatial resolution 30 m) were obtained from the USGS Glovis website (www.glovis.usgs.gov) for the WRS-2 path number 59 and row 19, taken in the month of August in order to limit any differences in seasonal vegetation characteristics and solar incidence angle that might affect the inter-annual comparison of vegetation cover. Using these parameters, a total of 13 images were identified, of which six were suitable (Table I) for further use; localised cloud cover over areas of interest limited the usefulness of those images not included in the analysis. All images were acquired with L1T level of processing (geometric and terrain correction) and projected to the UTM coordinate system (WGS84). Satellite images were corrected for at-sensor spectral radiance and top-of-atmosphere reflectance as outlined by Chandler *et al.* (2009). Images were then 'normalised' to the 2010 image using a linear regression between digital number (DN) values to allow comparison between years, as detailed by Collins and Woodcock (1996). All zero (missing; DN = 0) and saturated (DN = 255) values were excluded from the calculation. Once the slope and offset for each band of the image had been calculated, these corrections were applied to the imagery to provide a new corrected image consisting of bands 1–5 and 7. As images were calibrated to the 2010 image, the 2010 image was not used further in the analyses.

Field observations and aerial photographs at a number of locations throughout GBNP were collected in summer 2010 to verify areas in which dominant land cover was identified for subsequent use as training areas for a supervised classification using ERDAS Imagine 2010 (ERDAS, 2010). From these ground-verified areas, a minimum of four areas, at least 1000 pixels in size were identified as representative for each land cover class; 10 classes were identified; 'glacier'; 'snow'; 'sea/water'; 'non-vegetated' (typically bare soil or sediment), 'alder'; 'cottonwood'; 'spruce'; 'mature' (spruce–hemlock dominated forest); 'open vegetation' (includes both muskeg and small, scrubby vegetation dominated by blueberry, crowberry and small willows) and 'mountain vegetation' (typically higher elevation, open vegetation dominated by *Epilobium latifolium, Dryas* and scattered blueberry and crowberry). The 'mountain' vegetation group may be relict nunatak vegetation communities and hence were classified separately from open vegetation. Using these groupings, a signature file was produced that determined the set of statistical parameters of pixels within the training areas, which would be used to identify similar land cover in additional satellite images. In this instance, a set of parametric statistical signatures, based on minimum distance, were used as the decision rule in determining land cover classification (Sader *et al.*, 1995).

Accuracy of the supervised classification of the 2010 image was assessed using 31 points of known vegetation cover (from aerial and field-based observations, different from those areas used in the training process) from which a confusion matrix was produced using ERDAS' accuracy assessment to compare the classification of the known points against the

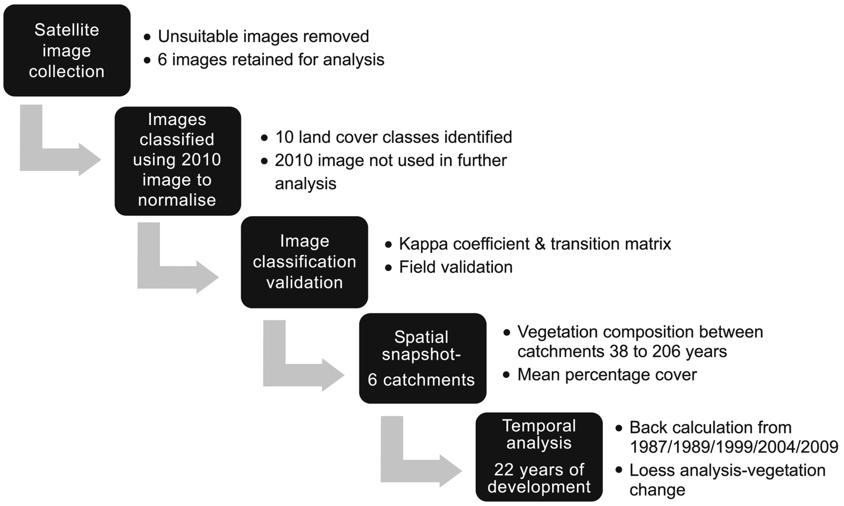

Figure 3. Workflow diagram of Landsat image processing and analysis steps.

Table I. Summary of the Landsat image characteristics utilised within the study

Year	Date	Satellite
1987	Aug 24	Landsat 5 TM
1989	Aug 13	Landsat 5 TM
1999	Aug 21	Landsat 7 ETM+
2004	Aug 14	Landsat 7 ETM+
2009	Aug 04	Landsat 5 TM
2010	Aug 15	Landsat 7 ETM+

classification produced using the signature file (ERDAS 2009). An output of the accuracy assessment is the Kappa coefficient of agreement, which expresses the proportionate reduction in error generated by the classification process compared with the error of a completely random classification (ERDAS, 2009). In essence, the Kappa coefficient of agreement is a value which indicates the percentage of the misclassification error that was avoided compared with that which is generated from a completely random classification. A value of 0.82 would therefore imply that the classification process had avoided 82% of the errors that a completely random classification would generate (Congalton, 1991; ERDAS, 2009) The remaining satellite images (1987, 1989, 1999, 2004 and 2009) were then classified using the signature file generated from the 2010 image. Classifications were further ground-truthed in July 2011 to confirm species composition within the broad land-cover classifications (i.e. determination of vegetation within 'open' and 'mature spruce–hemlock' land cover).

Pixel transition matrices were calculated to assess both classification accuracy (e.g. misclassification due to 'mixed' and/or mis-registered pixels; Hall *et al.* 1991) and rate and trajectory of landscape development. Pixel transition from one land cover class to another was assessed through the creation of a matrix table of changes in vegetation type between different classified images.

'Spatial snapshot' analysis

Six catchments, ranging in age from 38 to 206 years (Figure 1) were selected to provide detailed analysis of the successional gradient present from the upper to the lower sections of the bay, and to focus on the changes in landscape development over 206 years. Catchment boundaries of the six study catchments were obtained from Geiselman *et al.* (1997) and used as the basis for subsequent calculation of subcatchment boundaries using the ArcHydro extension within ArcGIS (version 9.3; ESRI, 2009), which identified a total of 22 subcatchments across the six stream catchments which were used as replicates in subsequent vegetation cover analysis. Catchment age was related to the distance of an area from the retreating glacier termini, and catchments were selected due to their similarity in non-age-related catchment characteristics (Table II) and temporal coverage that facilitate analysis of vegetation change over time. Assessment of the differences between these catchments therefore provides a 'spatial snapshot' of the differences in vegetation and landscape structure that occur within and across successional stages due to time since deglaciation. Differences in mean vegetation type cover were calculated in ArcGIS within subcatchments of each of the study watersheds to estimate within-catchment variability.

Table II. Characteristics of the six study catchments

Catchment	Age (in 2009[a])	Area (km^2)	Max altitude (m)	Geology
Stonefly Creek (SFC)	38	10.0	632	Qs[b], Kg
Wolf Point Creek (WPC)	65	29.8	817	Qs, Kg[b]
Ice Valley Stream (IVS)	141	19.4	732	Qs[b], Ss
North Fingers South Stream (NFS)	166	16.8	590	Qs, Sc + Ss[b], Kg
Berg Bay South Stream (BBS)	181	33.1	490	Qs, Sc + Ss[b], Tg
Rush Point Creek (RPC)	206	23.3	551	Qs, Sc + Ss, Tg[b]

Qs Quaternary surficial depostis.
Tg Tertiary intrusives (biotite granodiorite).
Kg Cretaceous intrusives (biotite-hornblende granodiorite and tonalite).
Sc Silurian-Devonian sediments and carbonates (Rendu Formation).
Ss Silurian sediments (Tidal Formation).

[a] Age in years defined relative to the time at which the mouth of the watershed was uncovered.

[b] Dominant geology.

Assessment of land cover changes over a 22 year period: 'temporal analysis'

Land cover change within GBNP over 22 years, from 1987 to 2009 was assessed using the classified satellite images. Zone statistics available within ArcGIS provided a summary of the percentage of each land cover/vegetation class within the areal extent of interest. Rate of change of land cover was calculated as the difference between the percentage of one particular vegetation type in 1987 and that in 2009. This calculation provides an indication of the permanency of each land cover class over time, the relationship of which may be described using regression analysis. A locally weighted (quadratic least squares), or loess curve, using a span of 0.75 was constructed using R (R Core Team, 2013) to illustrate the general trend of vegetation change following deglaciation. Classification maps generated in ArcGIS from the satellite images provide a visual guide to the gradual change in land cover over time, particularly the spatial differences in landscape development between the lower (older) and upper (younger) sections of the Bay.

Utilising the space-for-time substitution available in GBNP, it was possible to back-calculate approximate catchment ages from the Landsat images. This allows, for example, back calculation of vegetation development within the oldest catchment (Rush Point Creek) to be assessed at 206 years (its age in 2009), 201 years (age at the time of the 2004 image), 196 years (age in 1999), 186 (1989 age) and 184 years (1987 image). Each of the 22 subcatchments was analysed in this manner, thereby providing a total of 110 catchments in terms of development ages ranging from 16 to 206 years, and the rate and progress of vegetation and landscape successional development to be determined.

In order to differentiate this back-calculation method of assessing temporal landscape development within the watersheds from 1987 to 2009 from the more general assessment of spatial differences between landscapes within upper and lower portions of GBNP (as determined by comparing vegetation and landscape development from only the 2009 satellite image), the two analyses will be referred to as 'temporal' and 'spatial snapshot' analyses, respectively, throughout this paper.

Soil characteristics

Soil samples were collected within the identified broad scale vegetation classes to ascertain sediment characteristics which are likely to change as a result of successional processes and therefore provide information on soil properties for comparison with existing data on sediment availability and structure. Soil samples were collected from under the dominant vegetation types within each catchment, taking care to ensure that sample locations between catchments were similar in terms of slope, position and aspect. Each was a composite of three subsamples taken from within a 1 m^2 area, to a depth of *c.* 10 cm and placed in a sealable plastic bag for transportation to the laboratory. Once back in the laboratory the soils were sieved (4 mm mesh size) to remove any stones or large vegetative material. After this they were weighed (*c.* 10 g dry-weight) and dried at 80 °C for 24 h for transportation to the University of Birmingham, UK, where soil OM content (%OM) was determined by loss on ignition method where samples were heated to 450 °C for 4 h and then reweighed.

Soil bulk density ($g\,cm^{-3}$) was measured *in situ* using a PVC pipe (5 cm diameter × 15 cm length) which was driven into the soil to a depth of 10 cm and then dug out to ensure no soil was lost from the base of the sampling pipe; these soil cores were then placed in a sealable plastic bag for transport. Once back in the laboratory they were sieved and dried (80 °C) prior to weighing to obtain bulk density.

Results

Accuracy of satellite image classification and 'spatial analysis' of vegetation development

The Kappa coefficient of the satellite classification indicated a high overall accuracy (89.2%) of land cover classes (Table III). Analysis of the errors in classification suggests that it was difficult to differentiate between alder and open vegetation, which had accuracy coefficients of 0.62 and 0.64 respectively. Ground-truthing of image classification accuracy in July 2011 confirmed these inconsistencies; in particular, a large area of 'open vegetation' predicted using remote sensing within Stonefly Creek was confirmed to be alder-dominated. This error was likely due to the steep gradients on these slopes (>30°) characteristic of this area, which can result in image misclassification (Dymond and Shepherd, 1999). To correct the error for subsequent analyses, this area was reclassified by hand. No other significant misclassifications were noted.

The transition of vegetation within each classification type from the 1987 to 1999 to 2009 satellite images (Table IV) indicates a robust retention of land cover classes (diagonal elements), ranging from 40.8–79.5% retention of classified pixels. Alder had the lowest retention of the broad-scale successional land cover classifications (49.9% from 1987 to 1999, and 46.6% from 1999 to 2009) while spruce had the highest (68.5 to 79.5% retention 1987 to 1999 to 2009 images, respectively). Land cover classified as 'other' (an amalgamated group comprising of those land cover classes not used in the succession analysis, including glacier, snow, water and mountain vegetation classes) had a low retention rate, predominantly transitioning to either 'mature' or 'open' land cover (19.3 and 19.1%, respectively, from the 1987 to 1999 images, 26.2% transition from other to open from the 1999 to 2009 image). Further analysis of the high transition rate of 'other' pixels to alternative land cover classifications revealed a high turnover of pixels from 'mountain/high altitude' vegetation to 'open' vegetation. Similarities in the structure of dominant species within each of these classes (i.e. scrub and shrub cover) may explain these results.

Further analysis of the transition matrices shows that transition frequencies as a result of succession-driven changes (the upper off-diagonal elements) are highest in those vegetation classes characteristic of early successional stages, and the transition from one vegetation cover to the other follows the pathway previously documented within GBNP (e.g. 21.3% of pixels classified as non-vegetated land transitioned to alder land cover from the 1987 to 1999 image, 24.7% from 1999

Table III. Summary of classification accuracy of the land cover types

Land cover	Kappa coefficient
Glacier	1.0
Snow	1.0
Non-vegetated	1.0
Alder	0.62
Cottonwood	0.77
Spruce	1.0
Mature	1.0
Open vegetation	0.64
Mountain	1.0

Table IV. Transition matrix of pixel transition between land cover classes. The figures represent the total percentage of pixels occupying a land cover class from its original classification in the earliest satellite image (1987 in Table IV(a); 1999 in Table IV(b)) to the next satellite image. Diagonal elements (dark grey shaded) are retention frequencies; off-diagonal elements are transition frequencies. Upper off-diagonal transitions (light grey shading) represent successional processes, and lower off-diagonal transitions (non-shaded) represent disturbance events. 'Other' represents land cover classes including ice/ glacial cover, water and 'mountain' vegetation which represents areas which may not have been deglaciated during the last ice age (high altitude areas), NV = non-vegetated, C'wd = cottonwood

		1999 image						
(a)		NV	Alder	C'wd	Spruce	Mature	Open	Other
1987 image	NV	**52.7**	21.3	3.1	1.0	0.8	15.8	5.0
	Alder	3.6	**49.7**	16.1	0.5	-	28.5	1.6
	C'wd	2.2	17.3	**64.9**	14.0	0.3	1.3	0.1
	Spruce	2.9	1.1	23.8	**68.5**	3.7	-	-
	Mature	15.3	0.2	2.8	33.8	**45.8**	-	1.6
	Open	1.0	15.6	2.1	0.1	-	**71.4**	9.7
	Other	8.4	2.1	0.3	3.6	19.3	19.1	**47.2**

		2009 image						
(b)		NV	Alder	C'wd	Spruce	Mature	Open	Other
1999 image	NV	**56.5**	24.7	7.3	2.4	1.2	7.1	0.9
	Alder	1.6	**46.6**	34.4	0.3	-	16.2	0.7
	C'wd	0.5	11.2	**62.7**	24.4	0.3	1.0	-
	Spruce	0.6	0.3	14.4	**79.5**	-	5.3	-
	Mature	2.6	-	1.1	33.9	**62.0**	-	0.5
	Open	0.2	31.8	5.1	-	-	**51.7**	10.4
	Other	10.5	5.7	0.8	0.8	15.1	26.2	**40.8**

to 2009; 16.1% of alder pixels transitioned to cottonwood vegetation cover from 1987 to 1999, 34.4% from 1999 to 2009). In addition to confirmation of the successional transition of vegetation classes, the matrices also revealed an element of 'disturbance', where land cover transitioned in a manner not explained by succession (represented by the lower off-diagonal elements of Table IV(a), (b)). Alder and open land cover and spruce and mature forests appeared to have frequently transitioned from one to the other, and there was also a high incidence of non-vegetated land cover transitioning to mature forest from the 1987 to 1999 image.

Land cover change within GBNP over 22 years (1987 to 2009) 'temporal analysis'

Comparison of the classified Landsat images from 1987 to 2009 (Figure 4) indicate changes in land cover which occurred over the intervening 22 year period. Areas in the middle of the bay (representing landforms 130–170 years since deglaciation) revealed a progression from cottonwood to spruce and limited spruce–hemlock forest during this time period. The upper bay showed a change from non-vegetated glacial deposits and exposed sediment to alder and cottonwood communities. Land cover in the lower bay did not change as rapidly over the 22 year period, with limited expansion of spruce and mature (spruce–hemlock) vegetation. These changes may be more clearly identified when comparing the change in vegetation cover within the six study catchments over a temporal representation of 206 years, via the back-calculation of catchment development.

Using the back-calculation method to assess overall trajectory of landscape development within GBNP from 16 to 206 years following deglaciation, it is possible to model the rate of vegetation development (Figure 5). Loess analysis of the changes in vegetation cover over time shows that general trends in the rate and direction of percentage cover changes can be detected for all vegetation types. Non-vegetated/bare sediment is highest in the youngest catchments, decreasing rapidly up to ~50 years, before increasing slightly between 100 and 150 years, although it is important to note that this increase is driven by a single site; Ice Valley Stream which has a higher percentage of bare sediment than the other catchments. This result may reflect the occurrence of a braided river section at the headwater of the stream, where numerous small tributaries meet at a broad floodplain at the base of a large mountain range. The percentage cover of alder was shown to peak at approximately 50 years, just as sediment cover is at its lowest percentage. Alder remains in small percentages as catchment age increased. Open vegetation remained relatively stable over time since deglaciation. There was a large spread in the percentage cover of open vegetation within subcatchments, as well as catchments, with NFS having much higher open vegetation cover than any of the other study catchments. Percentage cottonwood cover varied within subcatchments, resulting in a broad spread from approximately 50 years onwards. In general, however, the percentage cover of this vegetation type was moderate, ranging from 20–60% of the total subcatchment once established. Spruce cover increased slowly up until approximately 125 years following deglaciation, after which time the rate of increase rose to a maximum of approximately 60% of total vegetation cover within the oldest catchments. Similarly, mature (spruce–hemlock) coverage was very slow to develop until approximately 150 years following deglaciation, after which time it increased. Berg Bay South has a high percentage of mature forest cover, likely causing the modelled peak in percentage cover at 175 years.

Detailed analysis of the changes in land cover over the 22 year period from the 1987 to 2009 satellite images (Figure 6) provides an indication of the rate and trajectory of broad-scale vegetation development resulting from successional processes. SFC was shown to undergo a rapid transition from non-vegetated (bare sediment) land cover to an increased alder dominated landscape, with limited cottonwood. WPC illustrated a transition from alder to cottonwood vegetation, while spruce began to replace cottonwood over the documented 22 year period. Spruce cover became increasingly dominant within the older catchments (BBS and RPC), as vegetation cover characteristic of earlier successional stages decreased (predominantly cottonwood).

Spatial analysis of soil and vegetation type characteristics within GBNP

There was a clear change in soil characteristics over time and vegetation succession. Exposed sediments and *Dryas* vegetation, characteristic of early successional stages display high bulk density as well as low soil organic matter. As site age increased and vegetation cover changed to mid (cottonwood) and late (spruce and mature) successional vegetation types, soil bulk density decreased and soil OM increased (Figure 7).

Discussion

Using the repeat-survey capabilities of the Landsat sensors in conjunction with the space-for-time chronosequence present

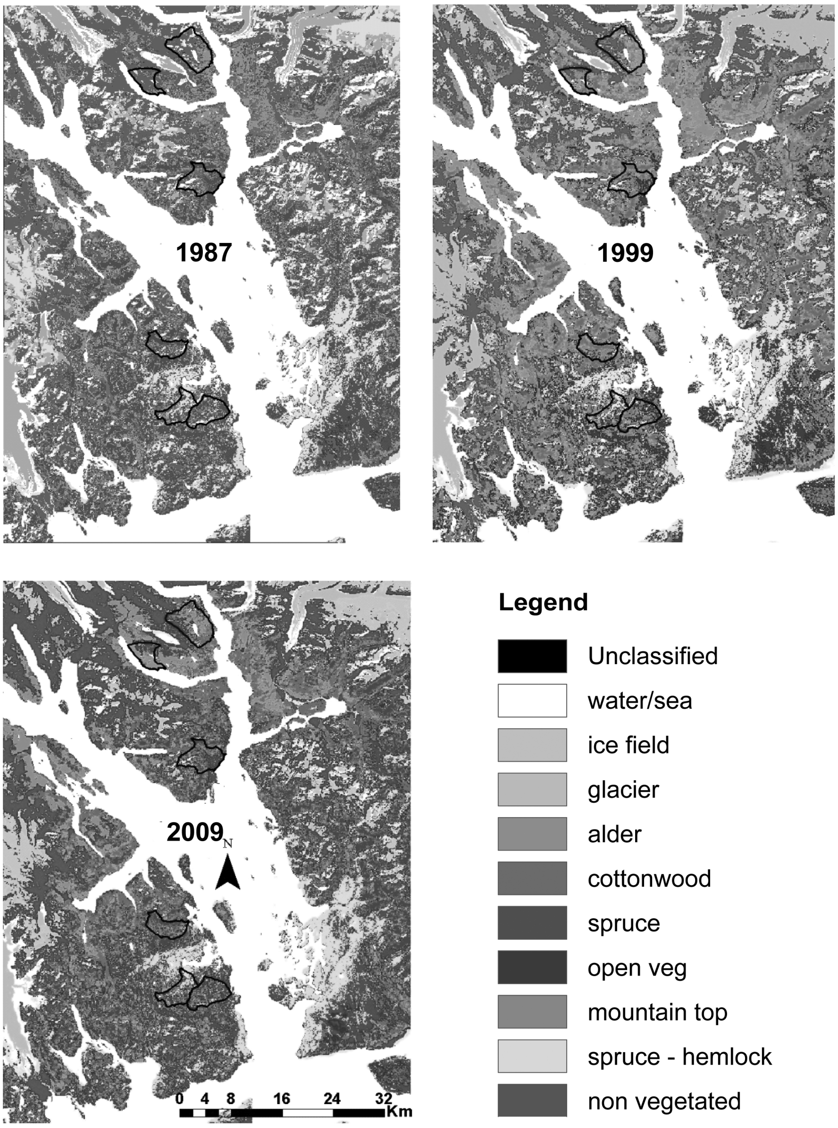

Figure 4. Classification of vegetation cover within GBNP using Landsat images from 1987, 1999 and 2009. Areas highlighted indicate the position and representative vegetation cover within the six catchments studied in closer detail. This figure is available in colour online at wileyonlinelibrary.com/journal/espl

within GBNP, we have monitored the rate and extent of vegetation succession within six catchments which represent 206 years of landscape development following glacial recession. By combining this large-scale analysis of vegetation succession with existing data on the influence of vegetation development on sediment availability, we can suggest how terrestrial vegetation succession contributes to sediment exhaustion during paraglacial sediment reworking, and hence, improve estimates of paraglacial adjustment timescales.

Use of Landsat imagery to determine broad-scale vegetation development within GBNP

The accuracy of the satellite images to classify broad-level changes in vegetation development within GBNP was verified and provided information on vegetation development over the entire ~11 000 km^2 area. However, analysis of pixel transition matrices suggests a high two-way transition rate between open and alder land cover classifications. This transition may be a real shift in vegetation cover as alder and open vegetation in young landscapes are known to be dynamic, due to frequent disturbance events (e.g. river channel migration) resulting in fluctuating patch size and density of species typical of ‘young’ successional stages (Beechie *et al.*, 2006).

Percentage change of mature (spruce–hemlock) cover from 1987 to 2009 revealed a decline in nearly all catchments, twinned with a relatively high pixel transition rate between these land cover classifications (Table IV), both in the ‘succession’ and ‘disturbance’ transitions. These changes may be a result of classification error or may reflect actual transition in vegetation types. For example, the slow growth rate of hemlock species in comparison with spruce in the mixed spruce–hemlock (mature) classification may have resulted in an increase in stand density and height of spruce in comparison with hemlock over the 22 year satellite image period, resulting in a change in vegetation reflectance received by the Landsat sensors. However, the high retention of pixels within each of these classes between satellite images and the increase in ‘mature’ vegetation cover from 1999 to 2009 (62%) in comparison with the 1987 to 1999 image (45.8%) suggests that the classification remains robust in tracking the successional transition from spruce to mature forest.

The Landsat images therefore confirm the large-scale patterns of primary succession previously documented for Glacier Bay through observation (Crocker and Major, 1955; Reiners *et al.*,

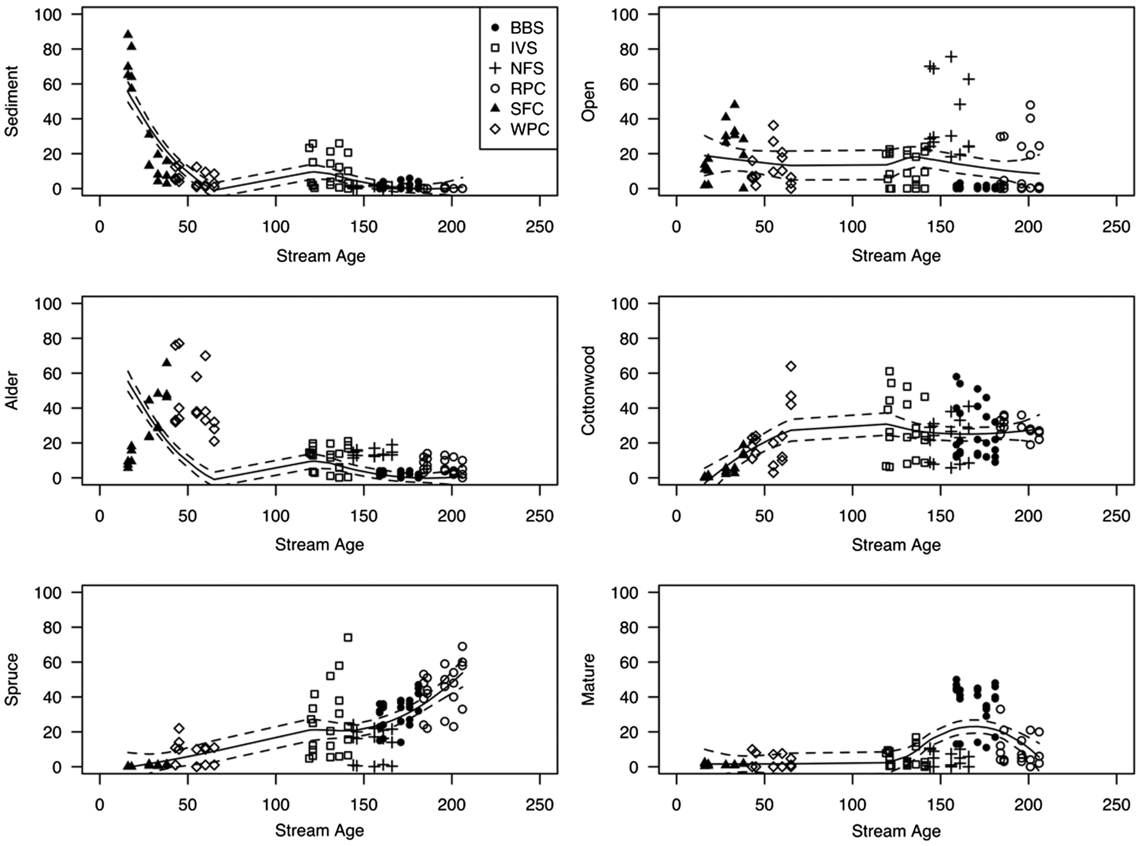

Figure 5. Loess analysis of changes in percentage cover of vegetation classes following deglaciation. Dashed lines indicate ± 1 SE.

1971; Chapin *et al.*, 1994). The spatial analysis (comparison of vegetation composition between study catchments of differing ages) illustrated a gradual transition in vegetation cover from bare, non-vegetated land immediately following deglaciation, to an alder and later cottonwood, spruce and mature spruce–hemlock mixed forest community which remains limited in coverage up to the maximum 206 year period studied here. Importantly, estimates of the rate of vegetation change over time provide quantitative information of biological community development which can then be treated as a dynamic feature within landscape evolution models.

Estimation of the trajectory of vegetation development using a back-calculation from satellite images (Figure 5) generally confirmed the estimated rates of successional turnover reported in other studies in GBNP (Reiners *et al.*, 1971). However, two catchments, namely North Fingers South Stream (NFS) and Berg Bay South Stream (BBS), do not follow the general line of trajectory. For example, NFS consistently contained a higher percentage of open vegetation (Figure 5), and a lower than expected percentage of spruce cover. Analysis of aerial photos from this site suggests that these deviations from the trajectory may be owing to local hydrogeological conditions which suggest some of the catchment is waterlogged, creating a muskeg-like plant community which may limit the growth and establishment of spruce and other coniferous species. The higher than expected percentage of mature vegetation cover in BBS may give weight to the multiple pathways theory of GBNP succession proposed by Fastie (1995), which suggests that local seed rain of mature and later successional species (e.g. from nearby Rush Point Creek (RPC) or areas of older refugial forest located in the lower bay) facilitates more rapid invasion by western hemlock, resulting in accelerated vegetation development than would otherwise be expected. Further investigation of the impact of this change in successional pathway on sediment dynamics and continued landscape evolution may help to decipher the physical-biotic linkages that drive biogeomorphic interactions.

The role of vegetation succession in paraglacial adjustment following deglaciation

The analysis of landscape development within GBNP using Landsat satellite images has allowed broad-scale successional processes to be quantified to a greater spatial extent than previous studies. Using the longer temporal resolution of vegetation succession (16–206 years) following deglaciation, insights into the role of vegetation development in determining sediment availability and hence paraglacial adjustment can be made.

Previous research has shown the importance of earlier colonising species (i.e. equivalent 'alder' and 'open' vegetation cover used within this study; cf. Orwin and Smart, 2004; Eichel *et al.*, 2013) during the paraglacial period for limiting sediment erosion by increasing sediment cohesion and rainfall interception, thereby increasing landform stability. However, the continued development of vegetation communities from shrub (alder) vegetation to cottonwood, spruce and later spruce–hemlock forests, as observed within GBNP will continue to influence sediment availability to fluvial and aeolian systems. In the initial post-glacial phase, evapotranspiration will consist entirely of evaporation from the bare surface resulting in a high runoff regime (Gorham *et al.*, 1979; Matthews, 1992). The dominance of unconsolidated sediments at this time have a high bulk density (Figure 7), associated with a high degree of compaction and decreased water infiltration, resulting in increased rates of erosion, as previously illustrated by Crocker and Major (1955). These soils are subject to physical and chemical weathering, leading to the leaching of organic matter and nutrients (Luizao *et al.*, 2004; Milner *et al.*, 2007) and low

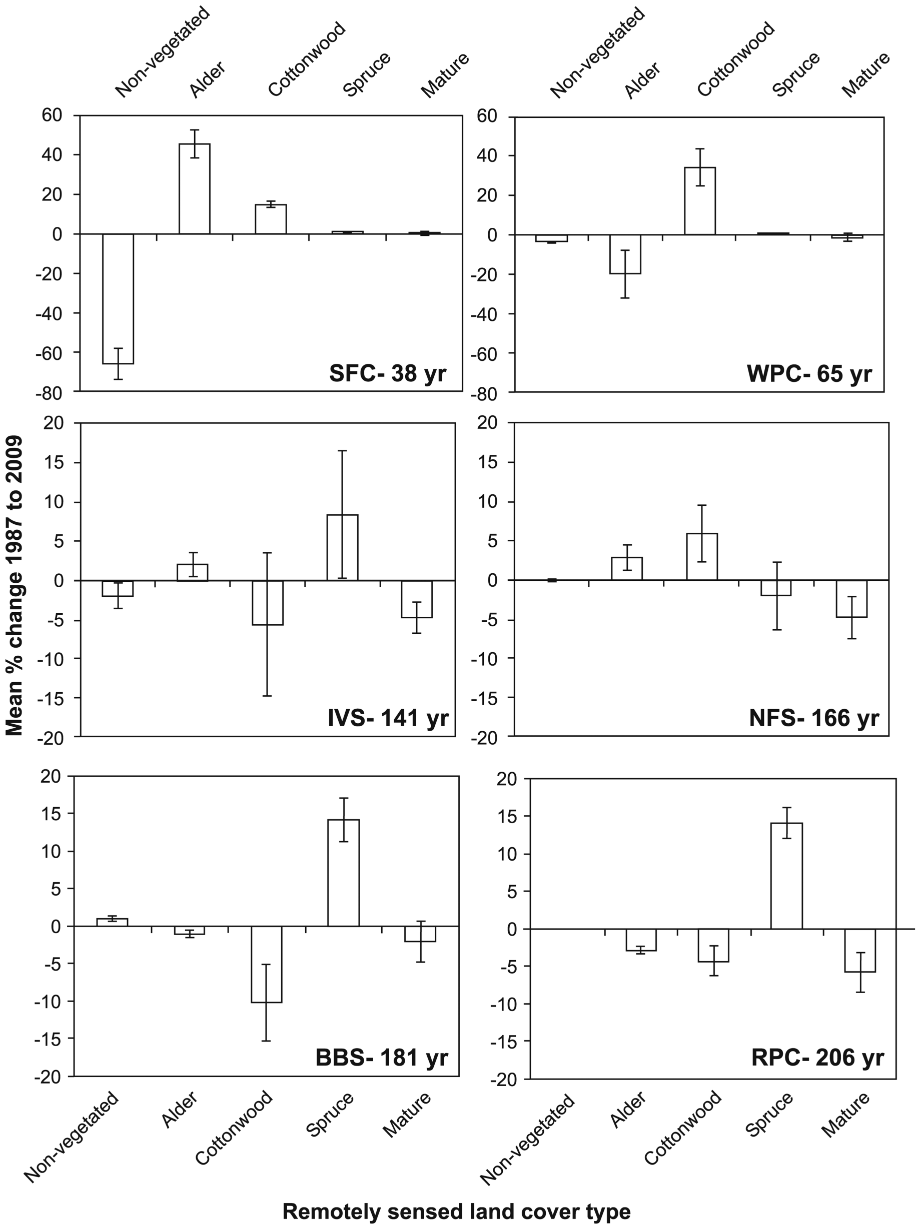

Figure 6. Mean percentage change (± 1 SE) in vegetation cover from 1987 to 2009 within the study catchments. Note the difference in y-axis values on the top row (SFC and WPC). Catchment age refers to the age in 2009.

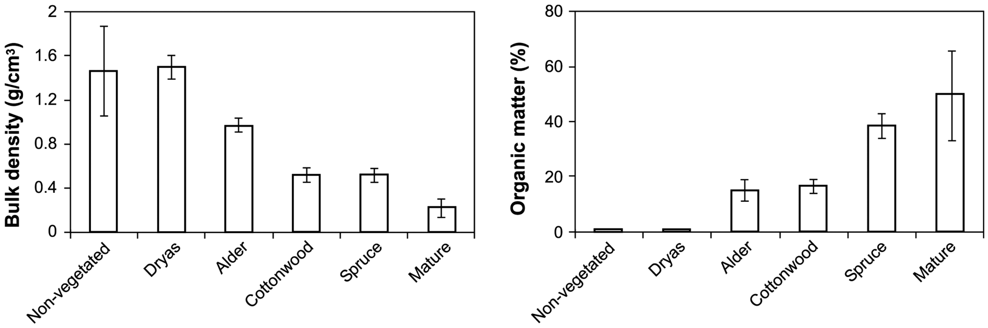

Figure 7. Soil characteristics within vegetation and land cover types in GBNP (± 1 SE).

organic matter and moisture content. The colonisation of bare sediment by open vegetation (i.e. *Dryas* domination) and later alder cover increased organic matter and decreased bulk density (Figure 7; Crocker and Major, 1955) as plant colonisation helped to stabilise the sediment structure.

Organic matter accumulation has been shown to be rapid within the early stages of landscape development within GBNP (Milner *et al.*, 2007), particularly under alder vegetation, where organic soils have been reported to accumulate up to 6–7 cm deep within 40–50 years following deglaciation resulting in increased water infiltration and decreased runoff at this time (Crocker and Major, 1955). As soils and vegetation develop, increased buffering of precipitation will occur, lowering surface runoff, while vegetation will provide a more effective route for evapotranspiration to occur (Leuschner and Rode, 1999). As succession progresses, the increasingly dense (and complex) stages of vegetation will increase evapotranspiration rates and rainfall interception, leading to a greater cycling of water back to the atmosphere, while allowing a greater residence time for water within the more developed soil structure, including the accumulation and decomposition of soil OM (Barrett and Burke, 2000; Milner *et al.*, 2007). Increasing levels of OM deposition and root development result in increased soil water retention, particularly as coniferous species began to dominate, developing a thick, well aerated soil layer (Ambus and Beier, 2006) as shown by the low soil bulk density underlying these later successional species (Figure 7). The continued formation of denser canopies, increased woody vegetation and understory and humus layer cover facilitated by continued terrestrial vegetation succession will further increase the rate of paraglacial adjustment processes (Gorham *et al.*, 1979; Leuschner and Rode, 1999) as the landscape transitions from glacial to non-glacial conditions (Slaymaker, 2009).

Previous research within GBNP and elsewhere has shown that terrestrial riparian vegetation development further stabilises post-glacial stream banks (Sidle and Milner, 1989; Gurnell *et al.*, 1999; Milner and Gloyne-Philips, 2005; Cowie *et al.*, 2014), resulting in a decrease in sediment supply from these banks and proximal channel areas with increasing catchment age (Sidle and Milner, 1989). The improved channel stability and associated reduction in channel width and increased stream power leads to greater efficiency of fluvial sediment transport processes and hence, entrainment of fine sediments and gradual fining of downstream sediments (Gurnell *et al.*, 1999), and subsequent movement and exhaustion of glacially influenced sediment loads.

Analysis of the rate and trajectory of vegetation development, and associated changes in soil development and sediment availability at an intermediate timescale (206 years) and larger spatial scale (>11 000 km^2) as undertaken as part of this study has highlighted the importance of biogeomorphic interactions in stabilising recently deglaciated landscapes during paraglaciation. A previous lack of investigation at this spatial and temporal scale has resulted in the dominance of physically based processes in paraglacial adjustment models which have underestimated, or even ignored, the role of biological processes (Benn and Evans, 2010). Information on the processes and timescales of paraglacial adjustment is fundamental in enhancing our understanding and reconstruction of past landscape evolution, as well as informing current research on landform stability. The term ‘paraglacial’ has been defined as a descriptor of landforms and landscapes in transition from glacial to non-glacial conditions for a period of time until glacially conditioned sediment has been removed or attained stability (Schumm and Rea, 1995), indicating that paraglacial adjustment is predominantly a feature of landscape stabilisation and geomorphic change. Cast in this light, the importance of the rate and trajectory of landform and landscape change become major indicators of paraglaciation (Slaymaker, 2009). Omission of vegetation–landform interactions in determining sediment transport rates and soil/landform stability within current landscape evolution models prevents accurate analysis and interpretation of landform features and ongoing landform evolution (Marston, 2010; Reinhardt *et al.*, 2010). Currently, these interactions are unlikely to have been fully incorporated into field-based investigations and subsequent modelling, due to the limited spatial and temporal scales such investigations have incorporated.

Continued stabilisation of terrestrial and aquatic environments resulting from paraglacial adjustment and terrestrial succession are important in the creation of landscape, species and habitat diversity (Odum, 1969; Connell and Slatyer, 1977; Milner *et al.*, 2007). This development from a highly disturbed, resource-limited environment, to a stable, functionally diverse landscape facilitate the establishment of diverse terrestrial and riverine communities (Reiners *et al.*, 1971; Benda *et al.*, 1992; Matthews, 1992; Beechie *et al.*, 2001; Milner *et al.*, 2007; Cowie *et al.*, 2014).

Conclusion

This study has illustrated the application of remote sensing techniques coupled with a space-for-time substitution to assess paraglacial adjustment over a longer time period (up to 200 years following deglaciation) and spatial scale (>11 000 km^2) than previously available. Assessment of broad-scale landscape development over this time using satellite imagery highlights the importance of both physical and biological interactions in the development of terrestrial and fluvial systems during paraglacial adjustment, further elucidating the role of biogeomorphic interactions in landscape development. Further use of remote sensing, space-for-time substitutions and other techniques to ascertain community and landscape development over intermediate timescales are urgently required for integrating long-term paleoecological and short-term ‘real-time’ investigations, into a cohesive time continuum (Rull, 2012). Currently, a lack of testing and validation of ecological theories and models which rely on assumptions of long-term processes, based on short-term observations, present a risk that some important ecological processes which operate at intermediate timescales are missing or misrepresented. The recent launch of the Landsat Continuity Mission in February 2013 will provide future continuity to the existing Landsat datasets (Wulder *et al.*, 2008), enabling studies such as this and others to continue the observation and monitoring of vegetation change over longer time periods following large-scale landscape change.

Acknowledgements—This research was funded by a NERC research grant (NE/G016917/1). We thank the US National Park Service in Glacier Bay, Alaska, in particular Bill Eichenlaub, Rusty Yerxa and Whitney Rapp for assistance in obtaining aerial photographs and GIS data of the area and Captains Justin Smith, Tom Howard, Hadley Owen and David Koschmann (Fritz) for logistical support. Thanks to Svein Harald Sønderland, Debra Finn, Ian Fielding, Alex Bence, Emma Mildon and Laura German for field work assistance, and Anne Ankcorn and Grace Garner for assistance with figures. We are grateful to Debra Finn, Nick Barrand and Dan Lawson and two anonymous reviewers and the special issue editors for insightful comments on earlier drafts of this paper.

References

Ambus P, Beier C. 2006. Factors controlling regional differences in forest soil emission of nitrogen oxides (NO and N$_2$O). *Forest Research* **1**: 651–661.

Ballantyne CK. 2002a. A general model of paraglacial landscape response. *The Holocene* **12**(3): 371–376.

Ballantyne CK. 2002b. Paraglacial geomorphology. *Quaternary Science Reviews* **21**: 1935–2017.

Barrett JE, Burke IC. 2000. Potential nitrogen immobilization in grassland soils across a soil organic matter gradient. *Soil Biology and Biochemistry* **32**(11–12): 1707–1716.

Beechie TJ, Collins BD, Pess GR. 2001. *Geomorphic Processes and Riverine Habitat. Water Science and Application*,**4**: 37–54, American Geophysical Union.

Beechie TJ, Liermann M, Pollock MM, Baker S, Davies J. 2006. Channel pattern and river-floodplain dynamics in forested mountain river systems. *Geomorphology* **78**: 124–141.

Begon M, Harper JL, Townsend CR. 1996. *Ecology. Individuals, Populations and Communities,* 3rd edn. Blackwell Science: Oxford.

Benda L, Beechie TJ, Wissmar RC, Johnson A. 1992. Morphology and evolution of salmonid habitats in a recently deglaciated river basin, Washington State, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 1246–1256.

Benn DI, Evans DJA. 2010. *Glaciers and Glaciation,* 2nd edn. Hodder Education: Abingdon, Oxfordshire.

Chambers JQ, Asner GP, Morton DC, Anderson LO, Saatchi SS, Espírito-Santo FDB, Palace M, Souza Jr C. 2007. Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. *Trends in Ecology and Evolution* **22**(8): 414–423.

Chandler G, Markham BL,Helder DL. 2009. Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Remote Sensing of Environment* **113**: 893–903.

Chapin FS, Walker LR. 1988. *The Importance of Glacier Bay to Tests of Current Theories of Plant Succession*, Milner AM, Wood JDJ (eds). National Park Service, US Department of the Interior: Glacier Bay Lodge, Alaska; 136–139.

Chapin FS, Walker LR, Fastie CL, Sharman LC. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* **64**(2): 149–175.

Church M, Ryder JM. 1972. Paraglacial sedimentation: a consideration of fluvial processes conditioned by glaciation. *Geological Society of America Bulletin* **83**: 3059–3071.

Collins JB, Woodcock CE. 1996. An assessment of several linear change detection techniques for mapping forest mortality using multitemporal Landsat TM data. *Remote Sensing of Environment* **56**: 66–77.

Congalton RG. 1991. A review of assessing the accuracy of classifications of remotely sensed data. *Remote Sensing of Environment* **37**: 35–46.

Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**: 1119–1144.

Cooper WS. 1923. The recent ecological history of Glacier Bay, Alaska: the interglacial forests of Glacier Bay. *Ecology* **4**(2): 93–128.

Cooper WS. 1937. The problem of Glacier Bay, Alaska: a study of glacier variations. *Geographical Review* **27**(1): 37–62.

Corenblit D, Gurnell AM, Steiger J, Tabacchi E. 2008. Reciprocal adjustments between landforms and living organisms: extended geomorphic evolutionary insights. *Catena* **73**: 261–273.

Corenblit D, Steiger J, Gurnell AM, Naiman RJ. 2009. Plants intertwine fluvial landform dynamics with ecological succession and natural succession: a niche construction perspective for riparian ecosystems. *Global Ecology and Biogeography* **18**: 507–520.

Cowie N, Moore RD, Hassan MA. 2014. Effects of glacial retreat on proglacial streams and riparian zones in the Coast and North Cascade mountains. *Earth Surface Processes and Landforms* **39**(3): 351–365.

Crocker RL, Major J. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology* **43**(2): 427–448.

Dymond JR, Shepherd JD. 1999. Correction of the topographic effect in remote sensing. *IEEE Transactions on Geoscience and Remote Sensing* **37**(5): 2618–2620.

Eichel J, Krautblatter M, Schmidtlein S, Dikau R. 2013. Biogeomorphic interactions in the Turtmann glacier forefield, Switzerland. *Geomorphology* **201**: 98–110.

ERDAS 2009 *ERDAS Field Guide. November 2009*, ERDAS Inc: Norcross, GA, USA.

ERDAS (2010) *ERDAS Imagine 2010*, ERDAS Inc: Norcross, GA, USA.

ESRI (2009) *ArcMap 9.3*. Environmental Systems Resource Institute: Redlands, California.

Fastie CL. 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology* **76**(6): 1899–1916.

Fitzsimons SJ. 1996. Paraglacial redistribution of glacial sediments in the Vestfold Hills, East Antarctica. *Geomorphology* **15**: 93–108.

Geiselman J, Dunpal J, Hooge P, Albert D (eds). 1997. *Glacier Bay Ecosystem GIS CD-ROM Set.* Anchorage and Juneau: AK.

Gorham E, Vitousek PM, Reiners WA. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. *Annual Review of Ecology and Systematics* **10**: 53–84.

Gurnell AM, Edwards PJ, Petts GE, Ward JV. 1999. A conceptual model for alpine proglacial river channel evolution under changing climatic conditions. *Catena* **38**(3): 223–242.

Gyssels G, Poesen J, Bochet E, Li Y. 2005. Impact of plant roots on the resistance of soils to erosion by water: a review. *Progress in Physical Geography* **29**: 189–217.

Hall FG, Botkin DB, Strebel DE, Woods KD, Goetz SJ. 1991. Large-scale patterns of forest succession as determined by remote sensing. *Ecology* **72**(2): 628–640.

Hobley DEJ, Sinclair HD, Cowie PA. 2010. Processes, rates, and time scales of fluvial response in an ancient postglacial landscape of the northwest Indian Himalaya. *Geological Society of America Bulletin* **122**(9–10): 1569–1584.

Irvine-Fynn TDL, Barrand NE, Porter PR, Hodson AJ, Murray T. 2011. Recent high-arctic glacial sediment redistribution: a process perspective using airborne lidar. *Geomorphology* **125**: 27–39.

Leuschner C, Rode MW. 1999. The role of plant resources in forest succession: changes in radiation, water and nutrient fluxes, and plant productivity over a 300-yr-long chronosequence in NW-Germany. *Perspectives in Plant Ecology, Evolution and Systematics* **2**(1): 103–147.

Luizao RCC, Luizao FJ, Paiva RQ, Monteiro TF, Sousa LS, Kruijit B. 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. *Global Change Biology* **10**(5): 592–600.

Marston RA. 2010. Geomorphology and vegetation on hillslopes: interactions, dependencies and feedback loops. *Geomorphology* **116**(3): 206–217.

Matthews JA. 1992. *The Ecology of Recently-Deglaciated Terrain. A Geoecological Approach to Glacier Forelands and Primary Succession.* University Press: Cambridge.

McColl ST. 2012. Paraglacial rock-slope stability. *Geomorphology* **153–154**: 1–16.

Milner AM, Gloyne-Philips IT. 2005. The role of riparian vegetation and woody debris in the development of macroinvertebrate assemblages in streams. *River Research and Applications* **21**: 403–420.

Milner AM, Knudsen EE, Soiseth C, Robertson AL, Schell D, Phillips IT, Magnusson K. 2000. Colonisation and development of stream communities across a 200-year gradient in Glacier Bay National Park, Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 2319–2335.

Milner AM, Fastie CL, Chapin FS, Engstrom DR, Sharman LC. 2007. Interactions and linkages among ecosystems during landscape evolution. *BioScience* **57**(3): 237–247.

Moreau M, Laffly D, Joly D, Brossard T. 2005. Analysis of plant colonisation on an arctic moraine since the end of the Little Ice Age using remotely sensed data and a Bayesian approach. *Remote Sensing of Environment* **99**: 244–253.

Moreau M, Mercier D, Laffly D, Roussel E. 2008. Impacts of recent paraglacial dynamics on plant colonisation: a case study on Midtre Lovenbreen foreland, Spitsbergen (79 N). *Geomorphology* **95**: 48–60.

Odum EP. 1969. The strategy of ecosystem development. *Science* **164**: 262–270.

Orwin JF, Smart CC. 2004. The evidence for paraglaical sedimentation and its temporal scale in the deglacierizing basin of Small River Glacier, Canada. *Geomorphology* **58**: 175–202.

Osterkamp WR, Hupp CR, Stoffel M. 2012. The interactions between vegetation and erosion: new directions for research at the interface of ecology and geomorphology. *Earth Surface Processes and Landforms* **37**: 23–36.

Passmore DG, Waddington C. 2009. Paraglacial adjustment of the fluvial system to Late Pleistocene deglaciation: the Milfield Basin, northern England. *Geological Society, London Special Publication* **320**: 145–164.

Quinton JN, Edwards GM, Morgan RPC. 1997. The influence of vegetation species and plant properties on runoff and soil erosion: results from a rainfall simulation study in south east Spain. *Soil Use and Management* **13**: 143–148.

R Core Team 2013 *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing: Vienna, Austria. URL http://www.R-project.org/.

Reiners WA, Worley IA, Lawrence DB. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. *Ecology* **52**(1): 55–69.

Reinhardt L, Jerolmack D, Cardinale BJ, Vanacker V, Wright JF. 2010. Dynamic interactions of life and its landscape: feedbacks at the interface of geomorphology and ecology. *Earth Surface Processes and Landforms* **35**: 78–101.

Rice S, Stoffel M, Turowski JM, Wolf A. 2012. Disturbance regimes at the interface of geomorphology and ecology. *Earth Surface Processes and Landforms* **37**: 1678–1682.

Rossi G, Ferrarini A, Dowgiallo G, Carton A, Gentili R, Tomaselli M. 2014. Detecting complex relations among vegetation, soil and geomorphology. An in-depth method applied to a case study in the Apennines (Italy). *Ecological Complexity* **17**: 87–98.

Rull V. 2012. Community ecology: diversity and dynamics over time. *Community Ecology* **13**(1): 102–116.

Sader SA, Ahl D, Liou W-S. 1995. Accuracy of Landsat-TM and GIS rule-based methods for forest wetland classification in Maine. *Remote Sensing of Environment* **53**: 133–144.

Schumm SA, Rea DK. 1995. Sediment yield from disturbed earth systems. *Geology* **23**(5): 391–394.

Sidle RC, Milner AM. 1989. Stream development in Glacier Bay National Park, Alaska, USA. *Arctic and Alpine Research* **21**(4): 350–363.

Slaymaker O. 2009. *Periglacial and Paraglacial Processes and Environments,* Knight J, Harrison SSC (eds). Special Publication 320, The Geological Society: London; 71–84.

Streveler G, Paige B. 1971. *The Natural History of Glacier Bay National Monument, Alaska. A Survey of Past Research and Suggestions for the Future*. US Department of the Interior: Anchorage.

Thorne CR. 1990. *Vegetation and Erosion*, Thornes JB (ed). Wiley: Chichester; **125–144**.

Tunnicliffe J, Church M, Clague JJ, Feathers JK. 2012. Postglacial sediment budget of Chilliwack Valley, British Columbia. *Earth Surface Processes and Landforms* **37**: 1243–1262.

Viles HA, Naylor LA, Carter NA, Chaput D. 2008. Biogeomorphological disturbance regimes: progress in linking ecological and geomorphological systems. *Earth Surface Processes and Landforms* **33**: 1419–1435.

Wulder MA, White JC, Goward SN, Masek JG, Irons JR, Herold M, Cohen WB, Loveland TR, Woodcock CE. 2008. Landsat continuity: Issues and opportunities for land cover monitoring. *Remote Sensing of Environment* **112**: 955–969.