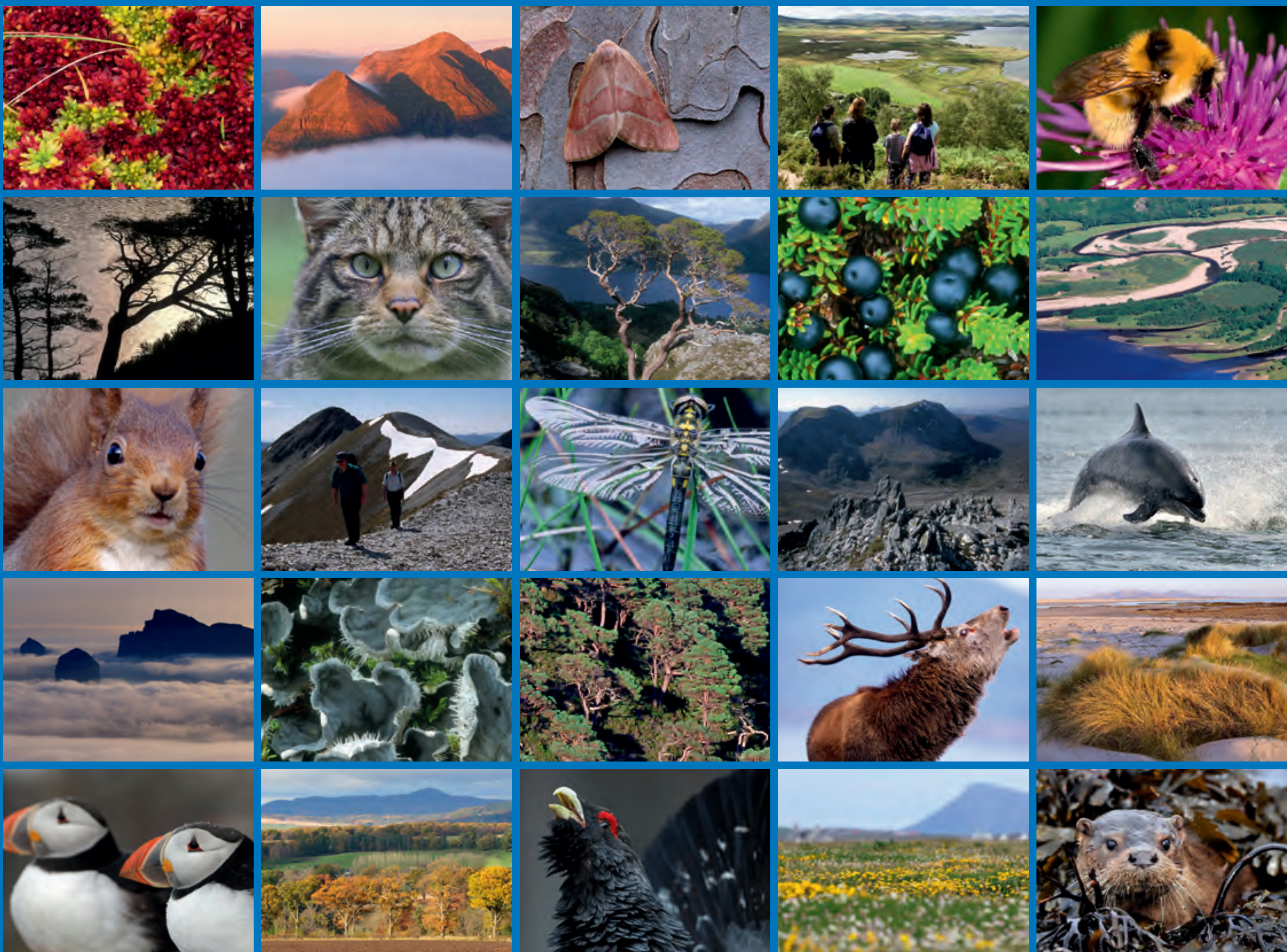
Scottish Natural Heritage
Commissioned Report No. 875

A geospatial analysis of potential Eurasian beaver (*Castor fiber*) colonisation following reintroduction to Scotland



COMMISSIONED REPORT

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Summary

A geospatial analysis of potential Eurasian beaver (*Castor fiber*) colonisation following reintroduction to Scotland

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Keywords

Castor fiber; geospatial analysis; reintroduction; woodland; damming; watercourse connectivity; seaward dispersal.

Background

The reintroduction of Eurasian beaver (*Castor fiber*) to Scotland has been proposed by many workers and over a considerable period of time (e.g. Macdonald *et al*., 1995; Rushton *et al.,* 2000*;* South *et al.,* 2000). Previous work considering the feasibility of a reintroduction has utilised a range of predictive factors from the literature to identify potential beaver habitat (Webb *et al*., 1997). This report updates earlier analyses, and uses new woodland datasets, notably the Native Woodland Survey of Scotland. New analyses are undertaken to identify areas in Scotland where beaver damming is predicted to be less likely, and offshore islands which beavers may colonise. Furthermore, the extent to which beavers may cross catchment boundaries is considered. Finally, a recent survey of beavers in Tayside and Clackmannanshire is used to test reliability of our approach. It is anticipated that the datasets will be useful tools in any future beaver management planning that may be necessary, and that they will be regularly reviewed and revised as data and ecological knowledge improves.

Main findings

- The 'potential beaver woodland' dataset used a variety of ecological factors and the presence of broadleaved woodland and shrub to identify 120,390 ha of woodland suitable for beaver use in mainland Scotland.
- The potential beaver woodland dataset included a number of small woodland patches that would be unlikely to be used by beaver for long-term territories. Hence we developed a 'potential core beaver woodland' dataset, which only included those habitat fragments that were more likely to be included in a long term territory. This dataset identifies 105,586 ha of potential core beaver woodland.
- Our results show that suitable woodland exists for beaver across many parts of Scotland, with the largest amount of potential core woodland in the River Spey catchment. In catchments where woodland is abundant, Loch Lomond has the densest distribution of core woodland patches.
- A population of about 32-33 beaver families was estimated from a 2012 survey in Tayside and Clackmannanshire. We used the survey of this population to estimate the accuracy of

our potential core beaver woodland dataset, and found that 82% of feeding signs (gnawed stumps, foraging trails, feeding stations, etc) and 84% of territory signs (lodges, burrows, scent mounds, etc) are within 1 km of core woodland patches. In particular, 91% of scent mounds, which are particularly associated with beaver territories, were predicted by the core beaver woodland dataset.

- A further analysis found 87% of watercourses in Scotland are predicted to be less likely to be dammed by beavers.
- Beaver movement between catchments is unlikely to be restricted by catchment boundaries within Scotland in the long term, as all catchments were judged to be highly permeable.
- A number of islands have the potential to be colonised by beaver in the long term, including Skye, Mull, and Arran. However, it is unlikely beavers will be able to naturally colonise the Outer Hebrides and Northern Isles.

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1. INTRODUCTION

When reintroducing a controversial keystone species that may have a wide range of ecological and social impacts, it is essential that we have an understanding of its potential distribution. The reintroduction of Eurasian beaver (*Castor fiber*) to Scotland has been proposed for many years (Macdonald *et al*., 1995; Rushton *et al.,* 2000*;* South *et al.,* 2000). Predicting future interactions of beaver with the natural and human environments is useful when evaluating the costs and benefits of a reintroduction. This includes identifying potential impacts on land use, but also natural heritage features. For example, the Scottish Beaver Trial identified Atlantic hazelwood communities as potentially vulnerable to beaver reintroduction without appropriate management (Genney, 2015).

Identifying the habitat requirements of beavers and using these to predict their future distribution has been attempted before (Allen, 1982; Maringer & Slotta-Bachmayr, 2006). Maringer & Slotta-Bachmayr (2006) utilised a GIS approach to estimate the predicted future distribution of beavers in the province of Salzburg, Austria. They utilised a variety of physical and ecological factors, such as stream gradient, land use, water depth, and woodland, to predict suitable beaver habitat. They concluded that 429 ha of optimal habitat existed in the province that could ultimately support between 23 and 51 beaver colonies.

Scottish Natural Heritage (SNH) has previously investigated the extent of beaver habitat in Scotland. Webb *et al*. (1997) produced two habitat maps. The first identified riparian broadleaf woodland, and the second aggregated woodland patches. The latter identified the densest woodland areas, and rejected smaller woodland patches. They predicted that there was enough suitable habitat in Scotland to support between 200 and 1000 beavers. These maps were updated by SNH in 2011 with more recent datasets, allowing a greater resolution (BSWG, 2015).

Here we attempt to predict the extent of woodland suitable for beaver territories in Scotland. This work updates previous attempts by performing a thorough review of new and old literature to update the basic parameters of the dataset. We also utilise a recent survey of beavers in Tayside and Clackmannanshire, in an attempt to assess the usefulness of our dataset when predicting the real world distribution of beavers. We also attempt a number of further analyses. These include identifying areas where beaver damming is unlikely, offshore islands that beavers may colonise, and the likelihood of beavers crossing catchment boundaries within Scotland. This work was used to inform the ‘Beavers in Scotland’ report to Scottish Government on beaver reintroduction (SNH 2015). If the decision is made to keep beavers in Scotland, then the datasets will be valuable tools in future planning for beaver reintroduction and management.

2. METHODS

The ecology of the two beaver species, *Castor fiber* and the North American beaver *Castor canadensis* is generally considered to be similar (Stringer *et al.* 2015; Collen & Gibson, 2001). Here we utilise literature on both species, but give preference to literature on Eurasian beaver where available.

SNH holds details of the full, technical GIS methodology.

2.1 Potential beaver woodland dataset parameters

2.1.1 Maximum feeding distance from watercourses

To assess the amount of habitat that is available to beavers, the distance a beaver will travel from the edge of a watercourse must be estimated. Beavers prefer to feed in close proximity to water. This may be due to an increased cost of foraging further from water and having to drag food and materials back to the watercourse, or it may be because being further from water makes beavers more vulnerable to predation (Baskin & Novoselova, 2008). Hence, the presence of predators may decrease foraging distance, as the landscape of fear will drive beavers closer to watercourses and safety. This is also reflected in the negative relationship between the distance from a watercourse and the number of beaver cut stems found there (Jenkins, 1980). Food resources close to watercourses are more valuable than food resources further from watercourses. Importantly, beaver do not increase their foraging time further away from a watercourse when resources become scarce (Fryxell, 1992, Iason *et al*., 2014). Therefore, foraging distance from watercourses will not be affected by the quality of the habitat that the beavers are occupying.

Evidence from the literature shows a variety of foraging distances from watercourses (Northcott, 1971, Jenkins, 1980, Allen, 1982, Belovsky, 1984, Maringer & Slotta-Bachmayr, 2006, Martell *et al*., 2006, Stoffyn-Egli & Willison, 2011). For instance, in Norway the mean maximum distance of feeding was 36 m from the river bank (Parker *et al*., 2001), while Pinto (2009) showed the abundance of deciduous trees within 40 m of the river bank was a key determinant of beaver presence/absence. In Germany, in an area where there were no predators, 99% of beaver cuts were within 45 m of the watercourse (Baskin & Novoselova, 2008). However, in Denmark 95% of foraging was within 5 m of water (Elmeros *et al*., 2003).

Using a smaller set distance risks excluding habitat that may be utilised, while using a larger set distance risks including habitat that is too far from a watercourse and hence very unlikely to be used. Based on the previously discussed evidence, and taking into account the fact that in Scotland there is likely to be low-levels of predation, we use a 50 m maximum foraging distance from watercourses.

To create the dataset, polygon and line water features were extracted from OS MasterMap® Topography Layer, although very small polygons less than 10 m^2 were excluded A 50 m wide area (or buffer) around the water features was then identified.

Beaver may forage at a greater distance than this, for instance there is an example of a North American beaver felling a tree 238 m from watercourse (Northcott, 1971). Also, beaver may extend the watercourse, through either water impoundment or canal building, and this would extend the foraging distance. The 50 m buffer, then, may not predict all potential beaver activity, but aims to predict the great majority. Hence, this threshold produces a relatively conservative estimate of suitable woodland for beavers.

2.1.2 Woodland

The main predictor determining the presence or absence of beaver is the availability of food. Pinto *et al.* (2009) studied a variety of river features, and showed that the most important factor determining beaver presence was the abundance of deciduous trees within 40m of the river bank. On lakes, Slough & Sadlier (1977) also showed food availability (aspen and shoreline brush abundance) explained 90% of beaver colony density. Hence, it is likely that a dataset created solely using food availability will give a reasonably representation of beaver habitat (Allen, 1982, Howard & Larson, 1985, Harrison & Stella, 2010).

To identify suitable woodland, two datasets were used - the National Forest Inventory (NFI) and Native Woodland Survey of Scotland (NWSS). The NFI types that were used were broadleaved, mixed–predominantly broadleaved, mixed–predominantly conifer (as this category includes 20-50% broadleaved woodland), coppice, coppice with standards, and shrub land. The NWSS types that were used were all native or nearly-native woodland with a canopy percentage >20%. This included native pinewoods due to the number of deciduous trees within this habitat (Patterson *et al*., 2014). Patches of woodland smaller than 0.5 ha were not included in our datasets because they are not mapped in the source data.

It is likely that in lochs beaver will also heavily utilise aquatic vegetation (Law, 2014). Unfortunately an estimate of aquatic vegetation could not be used in our model due to the lack of a suitable, nationwide dataset.

2.1.3 Stream gradient

Evidence frequently points to higher gradient streams being suboptimal habitat for beavers (Slough & Sadleir, 1977, Howard & Larson, 1985, Gurnell, 1998, Jakes *et al*., 2007, Cox & Nelson, 2009). However, higher stream gradients are often still utilized, only less frequently. Indeed, some studies show beaver adaptation to steeper gradients and montane conditions (Schulte, 1989, Zurowski, 1989, Czech, 1997, Collen & Gibson, 2001, Pinto *et al*., 2009).

To identify a cut-off gradient for the woodland dataset, above which beaver occupancy would be expected to be very rare, the literature was searched for references that compared beaver occupied streams with the number of available streams. Retzer *et al*. (1956) compared occupied and unoccupied streams and concluded that stream gradients >15% were usually unsuitable for beavers. Beier & Barrett (1987) use a similar analysis and their data support the 15% cut-off (Figure 1). Hence, only woodland on stream gradients <15% were included in our datasets. The previous habitat prediction for beavers in Austria also used this figure (Maringer & Slotta-Bachmayr, 2006).

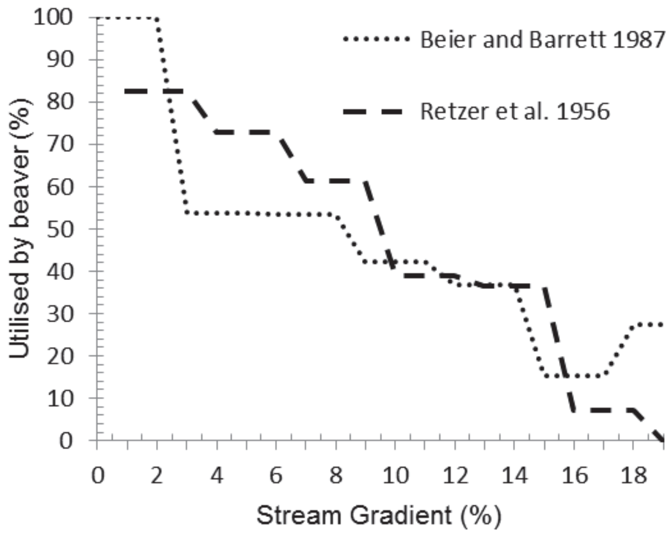

Figure 1. The percentage of stream reaches utilised by beaver with a variety of stream gradients from Beier & Barrett (1987) and Retzer et al. (1956).

As demonstrated in Figure 1, stream gradient has a gradual rather than absolute effect on beaver occupancy, and this is not reflected by using a single cut-off point. For instance, stream gradients between 10 and 15% are less likely to be occupied and colony longevity is likely to be shorter on these reaches (Howard & Larson, 1985). This is not currently reflected by our datasets.

2.1.4 Tidal

Beavers are only rarely observed in marine/salt water (Halley *et al*., 2013). However, Hood (2012) report that they do exist in some tidal zones, where the water is not more than 23% seawater (a salinity of < 8 ppt). Indeed, beaver may often utilise some tidal areas (B. Nolet pers. comm.). Data do not exist on salinity gradients in Scotland. Therefore, only non-tidal areas were included in our dataset, potentially slightly under-estimating beaver habitat in coastal areas.

2.1.5 Other variables that were not included

There is some data to suggest that bank slope (Pinto *et al*., 2009), valley width (Retzer *et al*., 1956), and bank substrate (McComb *et al*., 1990, Pinto *et al*., 2009) may be important factors in beaver occupation. However, as evidence is currently limited, and in some cases national datasets were lacking, they were not used in the current exercise. Also, stream depth and width may be important factors in determining when beavers dam, however they may not determine occupancy (Macdonald *et al*., 1995, Hartman & Tornlov, 2006, Baskin *et al*., 2011).

2.1.6 Discussion of the potential beaver woodland dataset

Webb *et al*. (1997) previously attempted to predict beaver habitat in Scotland. Their key criteria which differ from ours are the exclusion of the central urban/industrial belt, the exclusion of habitat above 400 m a.s.l., and only identifiying river sections which have a slope less than 2%. We did not use the same parameters for a variety of reasons. For example, beavers can be surprisingly adept at utilizing semi-urban areas (Pachinger & Hulik, 1999), and so areas with high human habitation were not excluded from our datasets. Also, there is evidence that beavers can adapt to montane conditions, so no altitude limit was placed on the datasets (Schandy, 1979, Maringer and Slotta-Bachmayr, 2006, Valachovič and Tomeček, 2006). However, this is unlikely to make a large difference as suitable woodland will be far less frequent at higher altitudes in Scotland. The 2% gradient cut-off may be reasonable if attempting to predict high quality beaver habitat (see 4.2 for further discussion), however we used the 15% figure to take account of the ability of beavers to utilize river sections up to this gradient (see Figure 1). A key improvement on the original dataset was the use of modern techniques and source datasets with much greater spatial accuracy. For example, this allowed us to buffer watercourses by 50 m, whereas Webb *et al*. (1997) had to use 500 m buffer zones to compensate for potential inaccuracies in watercourse positions.

We consulted with a number of beaver experts for their opinion on the criteria used for the potential beaver woodland dataset. They broadly concurred with our assessment. One of the key points highlighted was that while best predictions can be made, beavers have a degree of unpredictability like any species, and there will be likely exceptions to any boundary we put on a map (G. Hartman, pers. comm.).

2.2 Potential core beaver woodland dataset

2.2.1 Parameters

The potential beaver woodland dataset described above identifies all woodland that may be utilised by beavers. However, it identifies a number of very small woodland patches distant from any other woodland patches. These are of an insufficient size to maintain beaver territories. Therefore, this dataset potentially overestimates beaver distribution. To address this issue a ‘potential core beaver woodland’ dataset was created.

For many species of herbivore, territory size or home range decrease with habitat quality. This is intuitive as individuals would need more poor quality habitat to survive, and less high quality habitat. This also assumes that there is a larger cost to defending a larger territory size, hence individuals will revert to smaller territories in high quality habitat. For beavers this is not the case. Indeed, Campbell *et al*. (2005) shows a positive correlation between territory size and proportion of suitable habitat. Beavers, it seems, hold larger territories to extend the lifespan of a territory. This severely complicates our ability to estimate minimum habitat requirements for a single beaver colony, as a minimum viable territory size (assuming poor habitat quality) cannot be derived from the literature.

Beaver territory sizes are variable. There are a number of studies that report the lengths of watercourse bank used by beavers. Length of bank rather than stream reach is used as it allows estimates of home range on both lochs and rivers to be included. Macdonald *et al.* (1995) reviewed beaver territory size and reported a mean territory of 3 km (range 0.5-12.8 km), while Campbell (2005) reported a mean territory of 12.8 +/- 5.5 km in the Biesbosch, the Netherlands, and a mean territory of 4.0 +/- 2.1 km in Telemark, Norway. At the Scottish Beaver Trial in Knapdale, reported territory sizes were 3.7, 4.5, 3.0, and 1.8 km (mean 3.25 km). However, the amount of suitable woodland a territory contains is important. For example, territories in Telemark were on average 47 ± 13 % deciduous woodland, while in Biesbosch 36 ± 12 % of a territory was wooded. Norway was considered to most resemble Scottish habitat (B. Nolet, pers. comm.) and hence figures from Telemark were utilised (Campbell *et al*., 2005).

To map where beaver may establish territories, the minimum amount of woodland on which a beaver can survive needs to be identified. However this in itself is highly variable. A beaver may only need 500 m of high quality woodland, but many kilometres of very poor quality woodland. Therefore, if the lower figure is used, this will over-estimate beaver distribution, and small patches of poor quality woodland will be included.

There are therefore numerous difficulties when attempting to identify a minimum viable territory size with a minimum quantity of suitable woodland, to predict where beavers will, and will not, form territories. It was decided that the core beaver woodland dataset should attempt to identify only potentially longer-lasting beaver territories, and hence strict parameters of beaver territory and woodland size should be used. Therefore, we use the mean estimated woodland within the mean territory size within a high density beaver population in similar habitat to Scotland (Telemark, Norway). Any suitable woodland that cannot be part of 1.9 km of woodland within a 4 km territory is rejected. This dataset therefore under-estimates maximum beaver distribution to an extent, as woodland fragments smaller than the mean territory requirements in Telemark are not included. For example, small patches of high quality woodland not identified by this dataset may provide enough habitat for beaver to form a territory.

2.2.2 Methodology

Identifying where sufficient woodland for a beaver territory exists is difficult, and no previous or new methodology is without criticism. For example, Webb *et al.* (1997) buffered all woodland to 500 m. All buffered woodland >5 km in stream length (called woodland aggregates) were then identified as suitable habitat. The main criticism of these woodland aggregates is that each 5 km reach may contain vastly different amounts of habitat depending on how much woodland buffer they contain. In comparison, South *et al.* (2000) used fixed 5 km^2 squares, and identified any square that had a minimum of 2 km of suitable habitat as beaver habitat. However, this method also has its drawbacks (Rushton *et al*., 2002). Rushton *et al*. (2000) identified all continuous deciduous woodland blocks >3 km in length. However, this will not identify multiple fragmented woodland patches that may be utilised.

Identifying sections of river that contain enough suitable woodland is problematic from a GIS perspective. This requires the identification of 4 km stretches of watercourse bank that contain at least 1.9 km of woodland habitat (section 2.2.1). Our approach was to assume that the width of each woodland patch is normally distributed within the watercourse buffer and hence on average fills half the buffer width (25 m). If we also assume that a 1.9 km length of woodland is rectangular, we are looking for 4.75 ha of woodland within 4 km of bank. The NFI and NWSS datasets will omit small patches <0.5 ha of potentially high quality woodland (such as thin riparian strips). To help compensate for these the threshold was lowered by 0.5 ha to 4.25 ha. Hence, this means that areas equivalent to 1.7 km of woodland within 4 km of bank will also be included.

From each woodland patch a 2 km long (corresponding to 4km of bank) and 50 m wide buffer was created along the watercourse (1 km upstream and downstream). The edge rather than centre of each woodland patch was used as the starting point of the buffer. This is because the centre point would not take into account territories that could be formed using the ‘end’ of a long woodland patch and another patch within 1 km. This method means woodland patches could not be within the same territory if not on the same watercourse, with the exception of any two watercourses that are within 100m of each other as their buffers would be joined. Where any watercourse branches there will also be some methodological error, as the buffer would extend 1 km up both branches, hence the total amount of bank covered would exceed 4 km. We then calculated the area of woodland within this buffer to see if the total exceeded 4.25 ha. If it did we assumed a beaver territory could be formed and retained those patches of woodland (in their entirety, not clipped). The process was repeated for all woodland patches.

2.3 Ground truthing analysis

Our core beaver woodland dataset applied a beaver territory size of 2 km of watercourse length. Hence, from the centre of a territory a beaver may be expected to travel 1 km in either direction along a watercourse to forage. We assume that the centre of a territory is always within core woodland patches. Hence, any beaver activity >1 km along watercourses from core woodland patches is outside any territories predicted by the dataset.

To test the accuracy of our dataset, we overlaid the predicted beaver territories with a map of beaver field signs from the 2012 Tayside and Clackmannanshire survey (Campbell *et al*., 2012). This survey mapped all beaver feeding signs and territory signs in the Tayside area. Feeding signs recorded were; feeding on aquatic vegetation (n = 5), feeding on herbaceous vegetation (n = 8), feeding on agricultural crops (n = 9), foraging trails (n = 80), feeding stations (n = 128), cutting or gnawing of woody vegetation (n = 1132), and food caches (cut woody vegetation stored in front of the main lodge over winter, n = 2). Recorded territory signs were; dams (n = 9), scent mounds (n = 67), small areas of concentrated scent mound activity (n = 14), lodges (n = 38), and burrows (n = 75).

This overlap analysis showed us where beaver activity was within predicted territories and outwith predicted territories, and allowed us to assess the accuracy of our predictions by reporting the percentage of beaver signs that are predicted by our dataset. However, to see whether our datasets are better than may be expected by chance alone, we would also need to show where beaver have rejected predicted beaver habitat, and also rejected non-habitat areas (see section 4.3). This data will only become available if and once beavers reach their maximum population within the catchment.

2.4 Watercourses which are less likely to be dammed

Ideally it would be useful to predict where beavers may build dams in Scotland. However, key ecological measures which might help predict damming sites are not currently available in national geospatial datasets (e.g. stream depth). Therefore it was decided that this dataset could not be created at the present time. Instead, a dataset was created to predict where beavers are *less likely* to dam, and areas where there is an unknown potential for damming.

The building of dams is a high cost activity for beavers. The assumption was made that beavers would only justify the investment in building and maintaining a dam where resources exist to sustain a long-term beaver territory (Harrison & Stella, 2010). Hence, watercourses not adjacent to potential core beaver woodland were identified as being unlikely to be dammed.

Beavers do not tend to build dams in rivers over a certain width. Hartman and Tornlov (2006) studied dam building in Sweden, and found all beaver dams were on watercourses <6 m in width. Similarly, Suzuki & McComb (1998) studied the impact of river width on dam building in North America and found that >90 % of dams were on watercourses <6 m in width. Hence, all watercourses >6 m in width were identified as being unlikely to be dammed.

It is often noted that optimal areas for beaver damming are on low gradient streams (e.g. <6 %) (Suzuki & McComb, 1998, Jakes *et al*., 2007). However, this dataset predicts where beaver are unlikely to dam, and beaver have been found to dam on gradients up to 15% (Retzer *et al*., 1956). This figure was previously included in the potential core woodland dataset, and hence already incorporated into this analysis. A stricter stream gradient figure was not used. However, if a dataset is created in the future that attempts to predict where beaver will dam, it is recommended a stricter figure (such as <6% stream gradient) is used.

Numerous other factors may predict dam building behaviour, such as water depth, watershed size, and valley floor width (Retzer *et al*., 1956, Barnes and Mallik, 1997, Suzuki and McComb, 1998, Hartman and Tornlov, 2006, Jakes *et al*., 2007). However, these were not included because either available evidence for these factors is currently limited, or datasets were not available. For the future refinement of this dataset (i.e. predicting river sections likely to be dammed, rather than unlikely to be dammed), stream depth may be particularly useful. Finally, beavers may sometimes be recorded damming along rivers where there is no woodland, and so this needs to be taken into account when examining stretches identified in the dataset as being *less likely* to be dammed.

2.5 Watercourse connectivity

To predict how beavers may expand from their current and any future populations, a dataset of the connectivity between river catchments was produced. Beavers usually disperse along watercourses and only occasionally overland. Indeed, it is thought that the overland or seaward dispersal required to move between river catchments can severely slow the population range expansion of beavers (Hartman 1994, Halley 2002, Halley 2013). For instance, Hartman (1995) reported that a watershed divide dramatically slowed the expansion of a beaver population in Sweden, although this was not shown for all catchment boundaries.

An approximate threshold of 300 m was set on the maximum overland dispersal distance for beaver, based on the limited ecological information available. This distance was reduced in the dataset depending on the presence of urban areas, or of very steep slopes. There is little published literature about overland dispersal distances and factors that affect them, although a similar dispersal distance was proposed in a separate study (Campbell-Palmer *et al.* 2015). Therefore, a cost-distance of 150 m from each watercourse was run. The maximum dispersal distance was reduced depending on the presence of urban areas or particularly steep slopes. Slopes <35 degrees were viewed as not limiting to beaver movement, slopes between 35 and <80 degrees as somewhat limiting, and slopes ≥80 degrees as very limiting. Urban land cover, as identified in the EUNIS Land Cover Scotland dataset, was also viewed as very limiting. A caveat to this dataset is that steep slopes and urban areas within 50 m of watercourses containing suitable woodland will not have been taken into account, as this area had already been buffered previously as part of the woodland datasets.

A specific analysis was run for catchments where beaver are currently present (Knapdale and Tayside). The proportion of main catchment (using the SEPA dataset) potentially crossable by beavers was also determined at the national level. This analysis only incorporates inland catchment boundaries and not seaward boundaries. It also does not include the English border unless this was a catchment boundary.

2.6 Islands potentially reachable by beaver

The extent to which offshore islands could be colonised by beaver was estimated. Beaver do not permanently utilise salt water, although there is some evidence of beaver dispersing through coastal waters in Norway (Halley *et al*., 2013), Denmark (MJG, pers. obs.) and Scotland (Harrington *et al*., 2015). In Tierra del Fuego, *C. canadensis* have crossed a number of stretches of sea. The furthest islands that have been colonised are Lennox and Nueva (Menvielle *et al*., 2010). Seaward crossing distances to these islands are estimated to be a minimum of *c.* 6 km. Hence, a 6 km sea crossing was used as a maximum distance beavers could colonise offshore islands.

A further consideration is whether beaver will use islands as stepping stones. Assuming a beaver will initially swim 6 km to an island, if there is no suitable habitat on the island it is unknown whether they will continue their seaward dispersal. This is one of a number of unknowns associated with seaward dispersal. For example, we also do not know how local currents will affect the ability of beaver to cross stretches of sea.

The GIS method initially involved buffering a map of mainland Scotland by 6 km. All island polygons which intersected this buffer layer where then identified as islands within 6 km of the mainland. This process was repeated from these islands, to identify a second set of islands within 6 km of the first. This differs from previous datasets of beaver in Scotland for which only mainland Scotland was considered.

3. RESULTS

3.1 Potential beaver woodland and potential core beaver woodland

The potential beaver woodland dataset of mainland Scotland identifies 120,390 ha of woodland, while the core beaver woodland dataset identifies 105,586 ha of woodland (Figure 2). The potential core beaver woodland dataset rejects small woodland fragments as they will not form part of long-term beaver territories. In total, 12% of potential beaver woodland were rejected, from across a range of Scotland. A good example of how this might affect the predicted distribution of beavers is seen to the west and north of Aberdeen, where a large number of small woodland patches are not included in the core beaver woodland dataset (Figure 2 and Annex 1). Particularly large amounts of core beaver woodland at high density were found in the Spey catchment (Table 1).

Table 1.The top 10 river catchments with the most core beaver woodland area. The smallest catchment is the River Leven (79,566 ha) and the largest the River Tay (498,705 ha). The number in brackets shows the rank of the catchment if these 10 catchments were ranked by the density of woodland present. Catchments with less, but potentially denser, core woodland areas are not presented.

Catchment name	Potential core beaver woodland area (ha)
River Spey	7,086(3)
River Tay	6,996(9)
River Dee (Grampian)	4,421(5)
River Tweed	3,875(10)
River Ness	3,670(6)
River Clyde	3,364(7)
River Leven (Loch Lomond)	2,650(1)
River Forth	2,649(2)
River Lochy	2,184(8)
River Beauly	2,182(4)

3.2 Ground truthing statistics

The number and percentage of surveyed beaver field signs predicted by the potential core beaver woodland dataset are provided in Table 2 and illustrated in Figure 3. The potential core beaver woodland dataset predicted >78% of all common (n >15) beaver signs, and 82% of all feeding signs and 84% of all territory signs. The location of scent mounds was the best predicted common beaver sign, with 91% predicted. Figure 3 shows that beaver signs which were not well predicted were often clustered in specific areas.

Table 2. Statistics showing the number of beaver signs from Campbell et al. (2012) that lie within 1 km (along watercourses) of core beaver woodland (CBW) patches. Only common beaver signs with >15 data points are shown. Total percentages were calculated using all signs from the survey (see 2.3).

Activity type	Field sign	Within 1 km of CBW	Total in survey	Total predicted by CBW	
Feeding signs	Cutting or gnawing of woody veg.	940	1132	83%	Total 82%
	Feeding station	109	128	85%	
	Foraging trail	62	80	78%	
Territory signs	Burrow	59	75	79%	Total 84%
	Lodge	30	38	79%	
	Scent mounds	61	67	91%	

3.3 Watercourses which are less likely to be dammed

Our dataset predicts that 150,334 km of the 171,995 km of watercourses (87.4%) in mainland Scotland (excluding lochs) are less likely to be dammed by beavers. The River Tweed catchment (in Scotland) is given as a more specific example, with 90% of the length of watercourses within it identified as being less likely to be dammed by beavers (Figure 4). Note that the chance of beaver damming is unknown in any remaining sections not identified by the dataset (although some will be dammable).

3.4 Watercourse connectivity

The interconnectivity of the catchments currently containing beaver populations can be seen in Knapdale (Figure 5), and Tayside (Figure 6). These show that the interconnectivity between catchments is high, and it is likely that beaver should be able to find multiple routes into other catchments when dispersing. Figure 7 shows that across Scotland the great majority of catchments will have high levels of permeability.

3.5 Islands potentially reachable by beaver

It is not known which islands beaver may be able to colonise from the Scottish mainland. However, Figure 8 shows islands within 6 km of the mainland, where the likelihood of colonisation is higher. An additional 2,486 ha of potential core beaver woodland is found on these islands (Figure 9 and Figure 10). Islands that are within a further 6 km of the first set of islands are also identified, to show how beaver may utilise islands as stepping stones. A further 553 ha of potential core beaver woodland is found on the second set of islands.

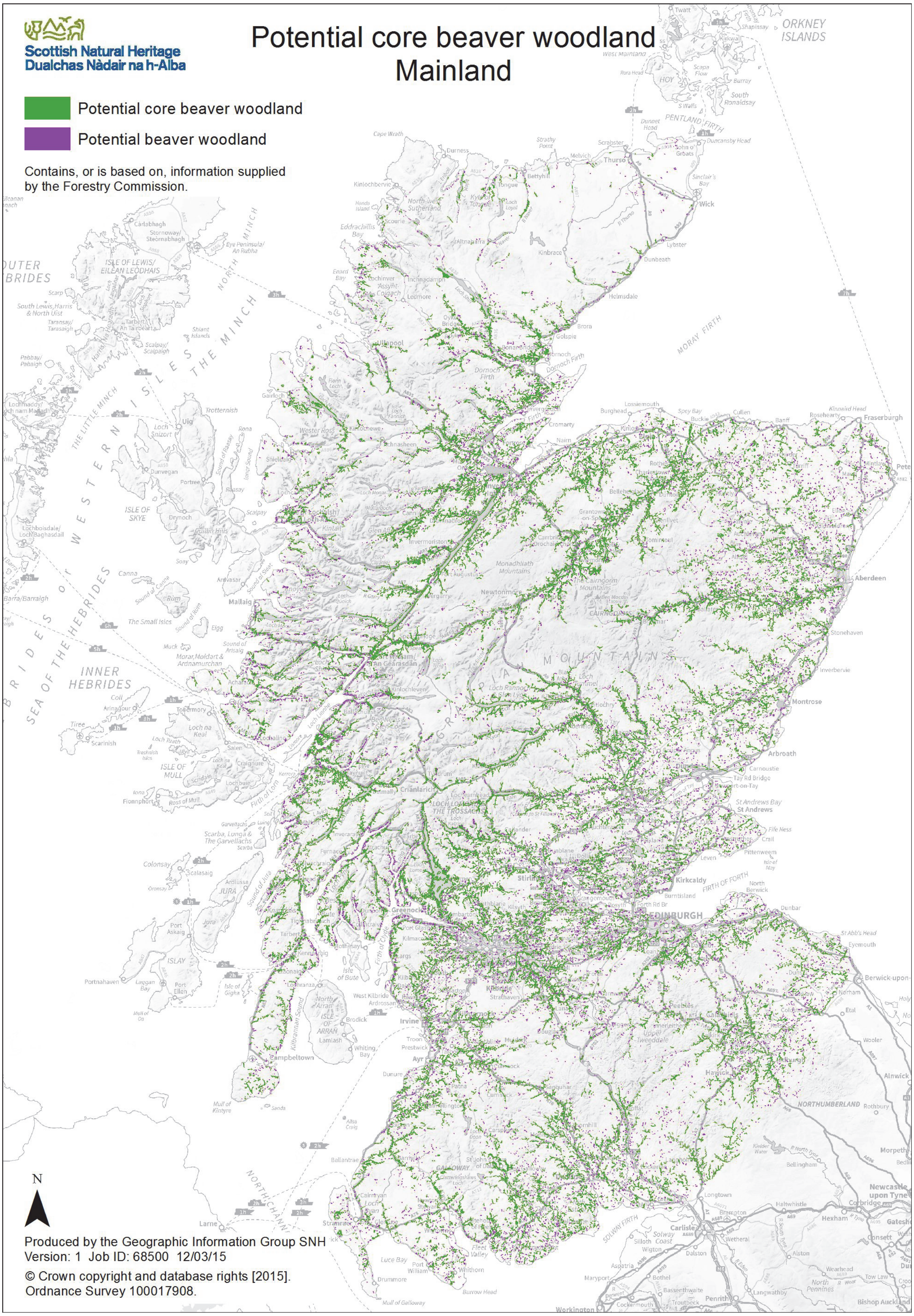

Figure 2. Potential beaver woodland on mainland Scotland. For a more detailed version please see Annex 1.

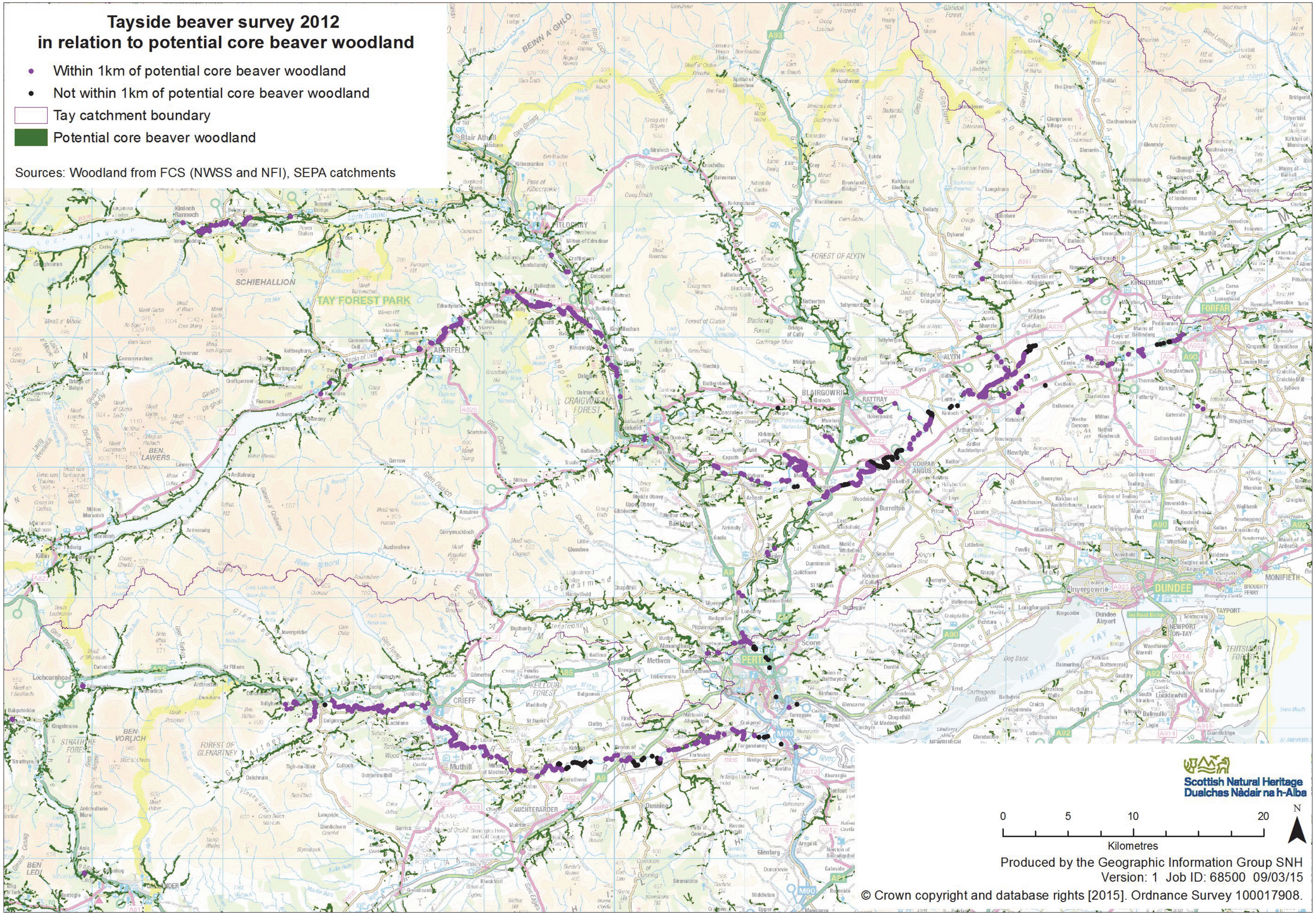

Figure 3. Tayside beaver survey 2012 in relation to potential core beaver woodland

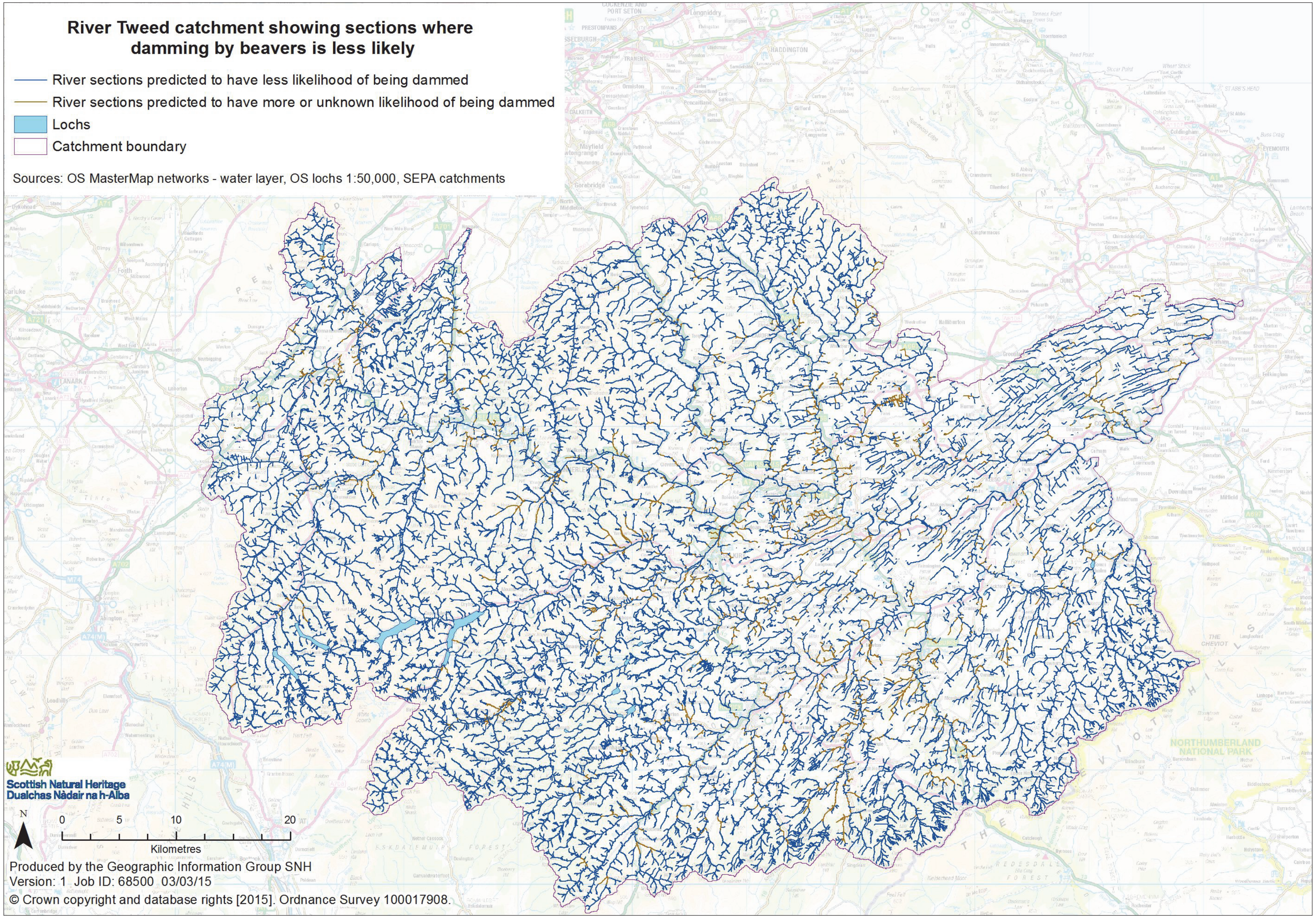

Figure 4. River Tweed catchment showing sections where damming by beavers is less likely.

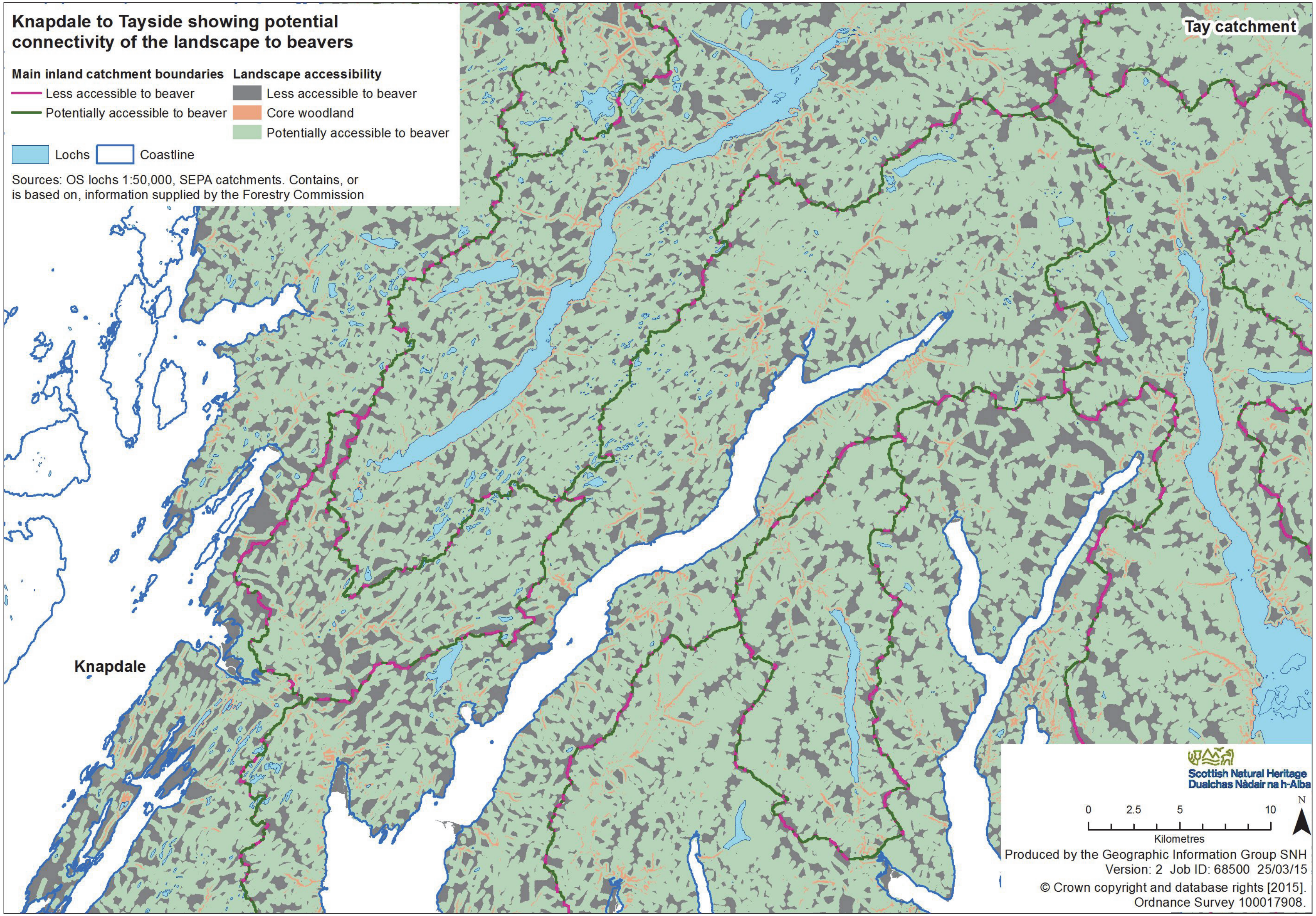

Figure 5. Knapdale to Tayside showing potential connectivity of the landscape to beavers

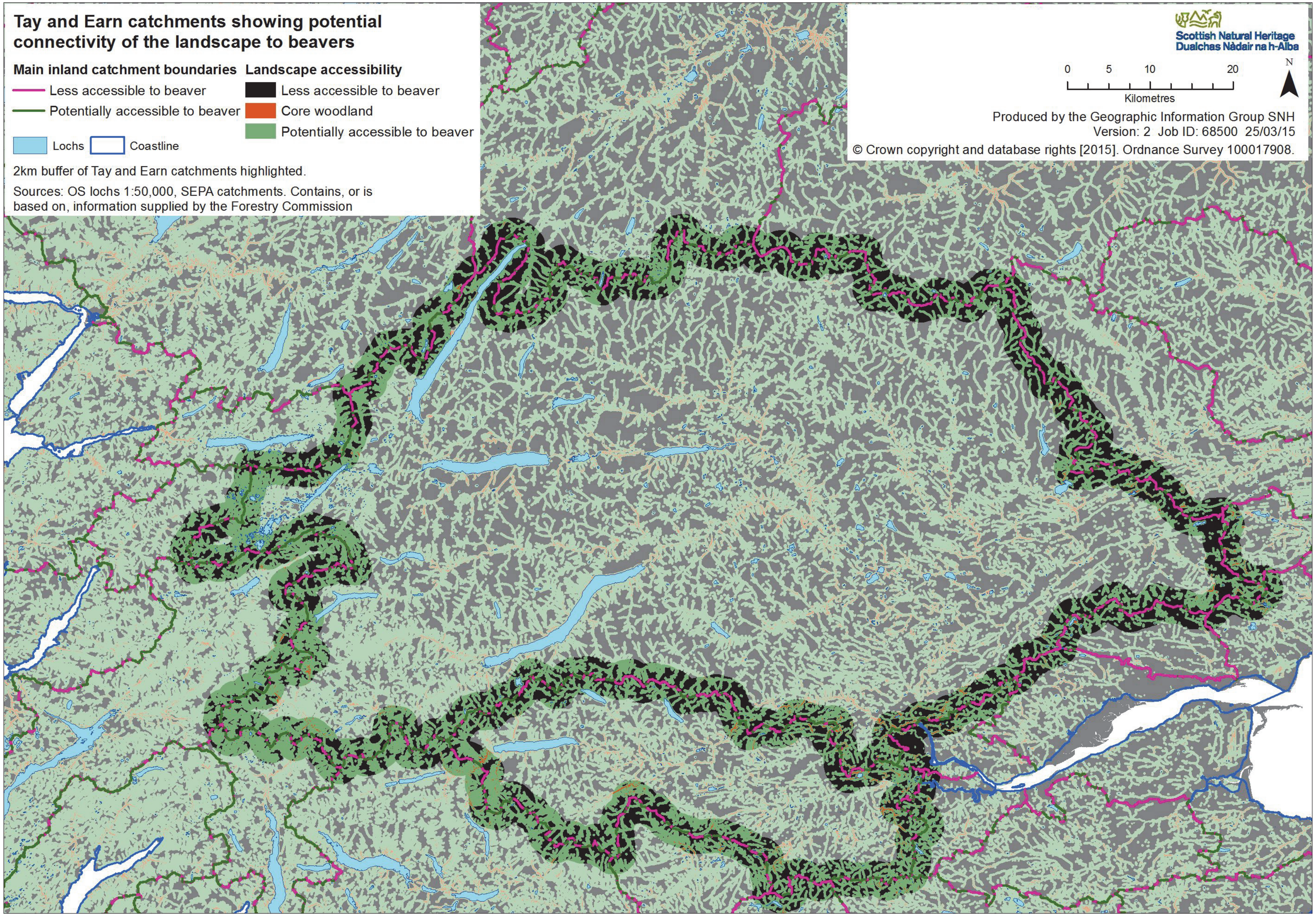

Figure 6. Tay and Earn catchments showing potential connectivity of the landscape to beavers.

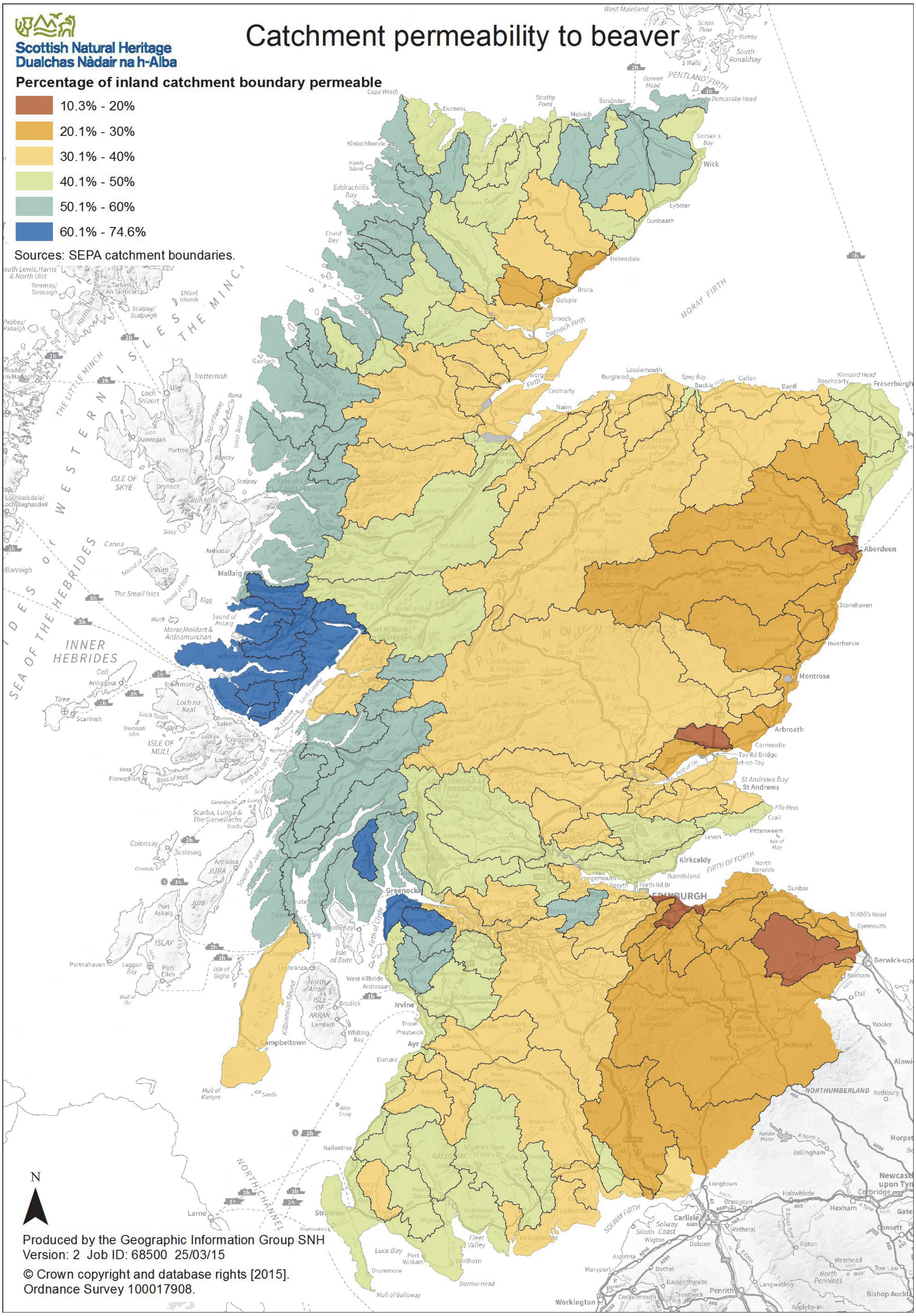

Figure 7. Map showing the percentage of inland catchment boundaries which are permeable to beavers.

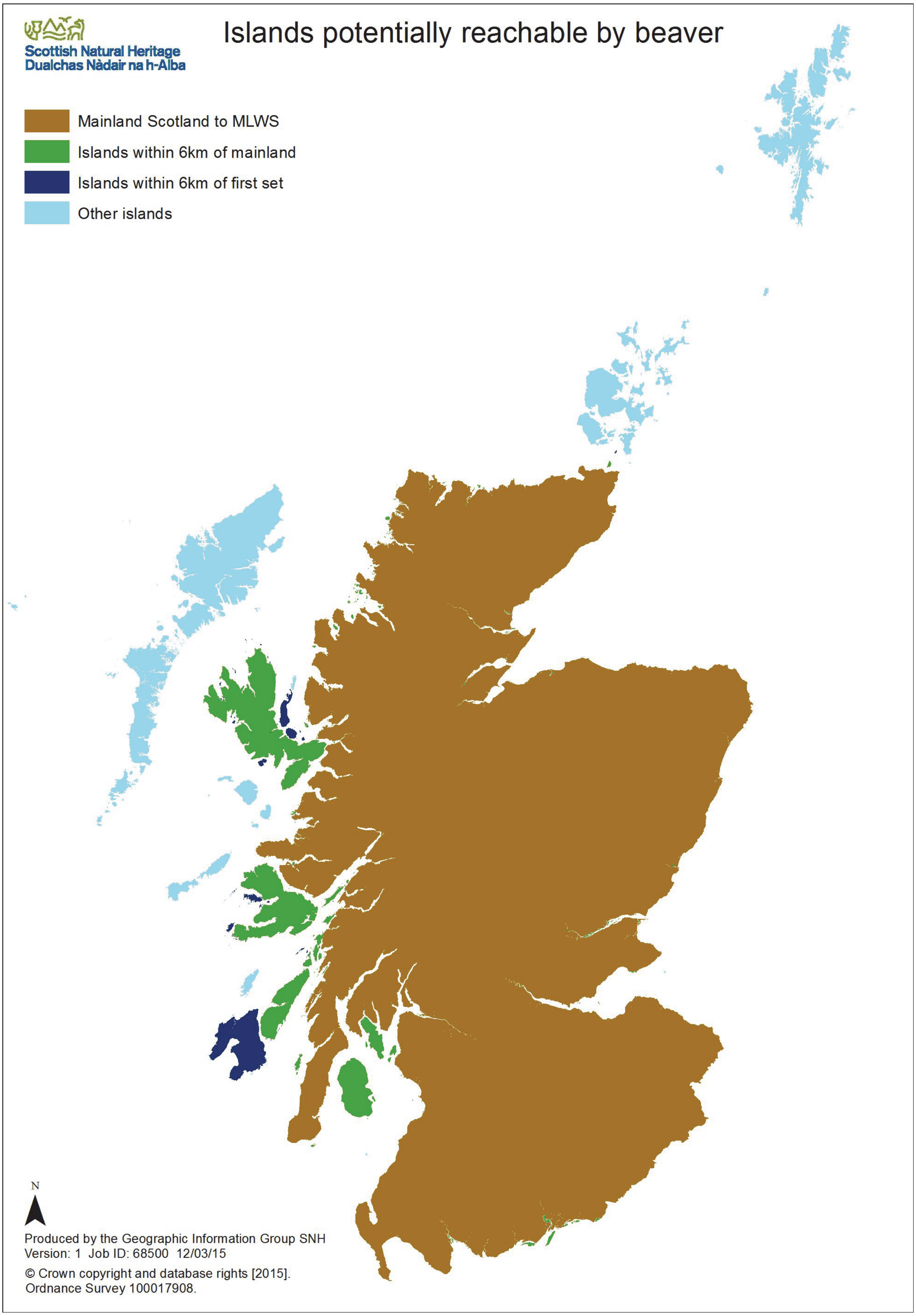

Figure 8. Islands within 6 km of mainland Scotland and within 6 km of these to illustrate the potential colonisation of offshore islands by beaver.

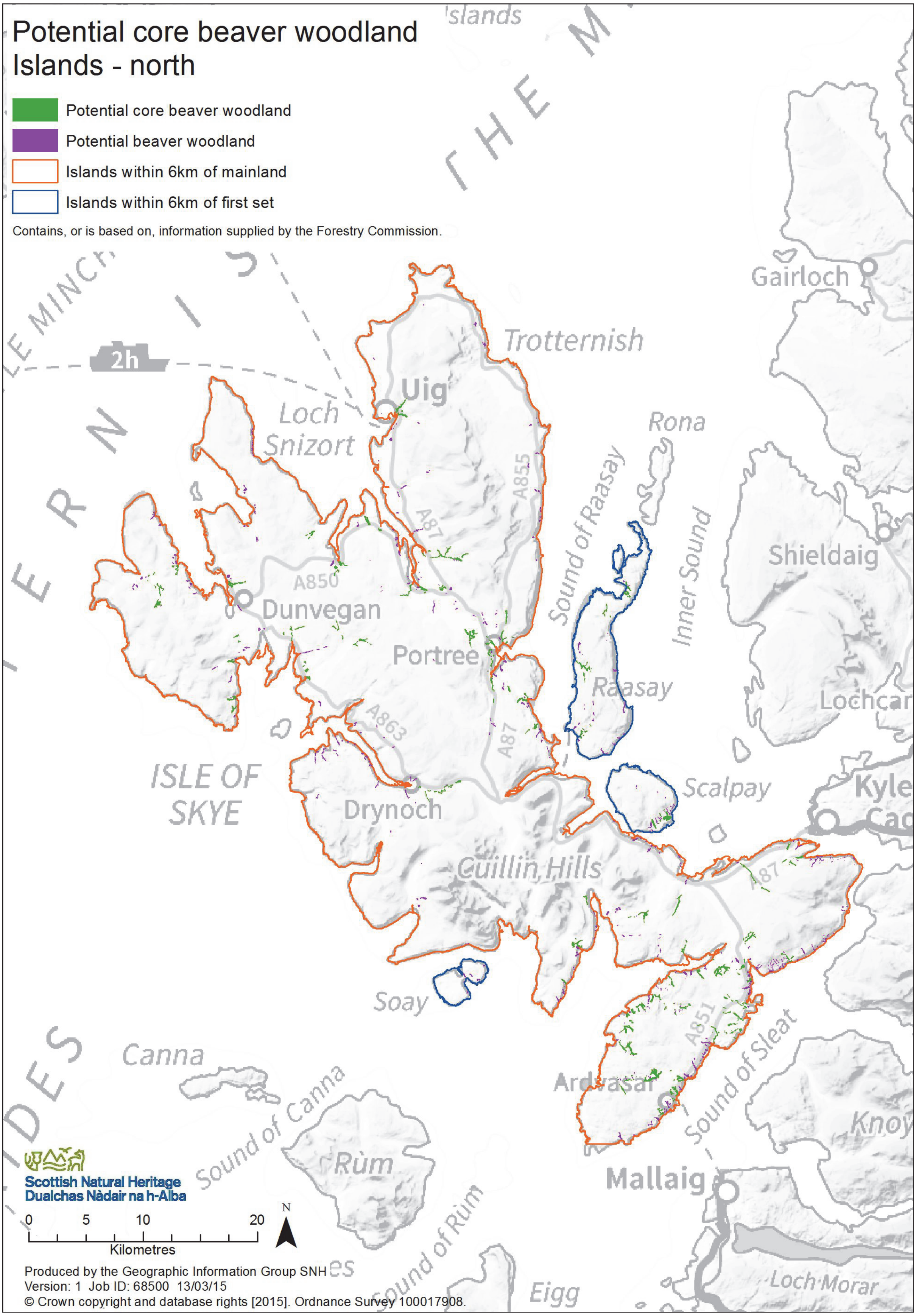

Figure 9. Potential core beaver woodland on Islands – the northern islands which may be colonised are shown.

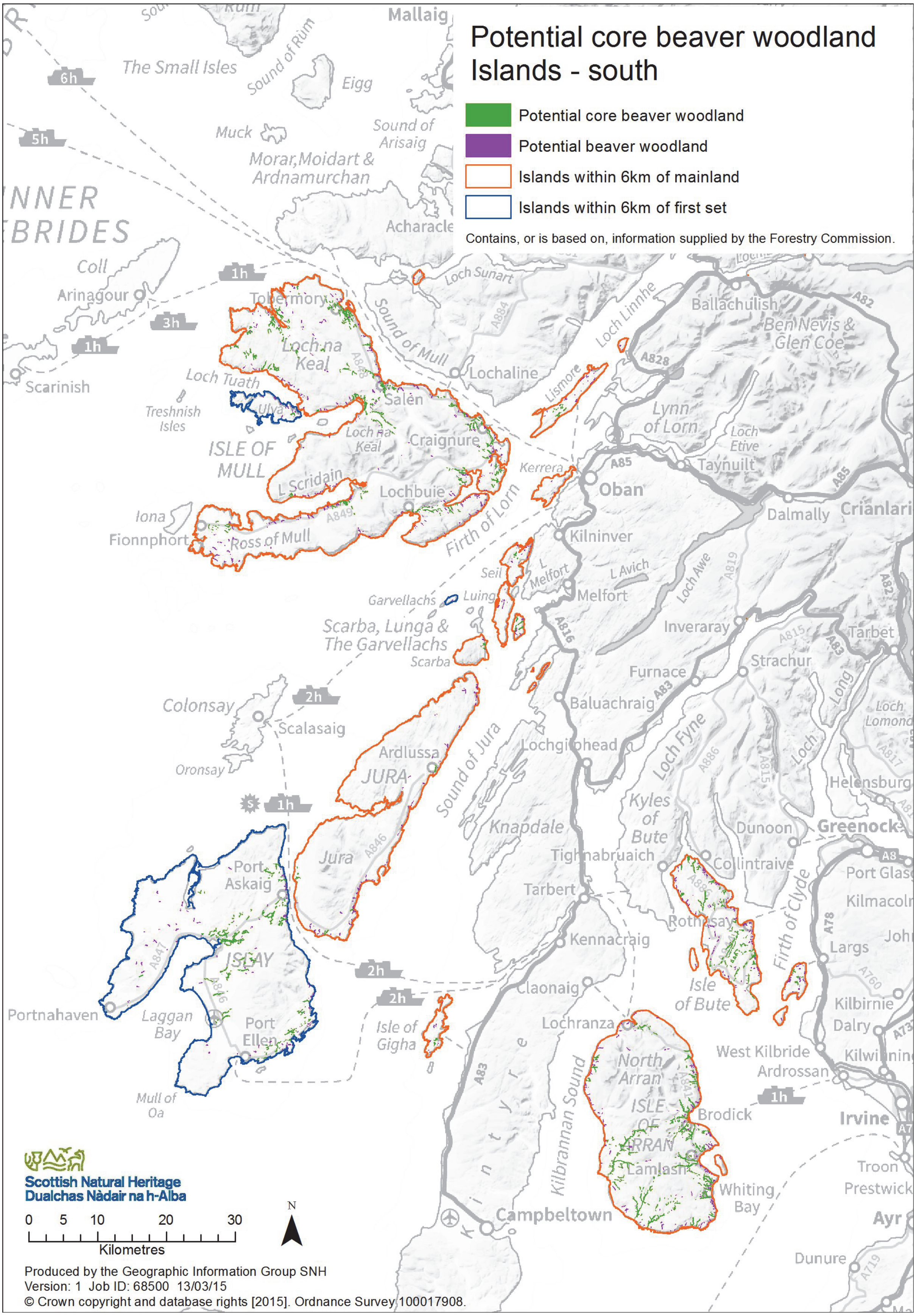

Figure 10. Potential core beaver woodland on Islands - the southern islands which may be colonised are shown.

4. DISCUSSION

4.1 How the datasets have changed from previous work

The dataset created by Webb *et al*. (1997) identified 771 km^2 of suitable woodland, while more recently SNH updated the beaver habitat dataset in 2011(used for BSWG, 2015) and identified 1720 km^2. In comparison, our new potential beaver woodland dataset identified 1204 km^2 of which only 437 km^2 overlapped with the 2011 dataset. However, there are a number of key differences between the woodland datasets that make comparisons difficult. Primarily, our exercise used different, more modern woodland datasets - the previous projects used the National Inventory of Woodland and Trees, and Scottish Semi Natural Woodland Inventory datasets, and ours used the NFI and NWSS datasets (section 2.1.2). Also, due to limitations with the resolution of datasets, Webb *et al*. (1997) used a 500 m buffer, while the SNH 2011 dataset used a 200m buffer. Our new datasets utilise a more biologically reasonable 50m buffer, which reduced the area of woodland identified in our datasets. However, we included more urban areas and areas above 400 m a.s.l, and rivers with gradients >2 %, which may all increase the woodland in our datasets in comparison. The earlier datasets also identified more small woodland segments, because of the datasets used.

4.2 The distribution, dispersal, and activity of beavers

A previous mapping exercise identified four catchments as key woodland areas for beavers in the Lomond, Tay, Spey, and Ness catchments (Webb *et al*., 1997). Our analysis showed that the catchments with the most potential core beaver woodland were the Tay and Spey catchments (Table 1). A number of catchments in close proximity also have a high abundance of core woodland, such as the Lochy, Ness, and Beauly catchments. Analysing which catchments have the most core beaver woodland is useful, but biased by the size of the catchment. For instance, the River Tweed has high total amounts of woodland, but it is sparsely distributed. The River Leven (Loch Lomond) catchment has the densest quantities of potential core beaver woodland patches.

There are a number of limitations to the current potential beaver woodland datasets. In particular, the abundance of aquatic vegetation is not included, even though it may be a key component of beaver diet. Also, a 50 m water buffer is used, but beaver may extend watercourses by building dams and canals, which may increase their maximum foraging distance. Future datasets could be refined by including a wider suite of variables as better evidence and datasets become available. For instance, the Black Rock Gorge near Inverness is currently classified as within core beaver woodland. However, the steep sides of the gorge will probably preclude beaver from utilising this watercourse to any great extent. Therefore, there may be a number of situations in Scotland where the beaver woodland datasets over- or under-estimate beaver woodland, and so the use of other and/or refined predictive variables should help to refine the datasets in the future.

The potential core beaver woodland dataset attempts to identify where beaver will establish long-term territories. However, we did not use a Habitat Suitability Index approach (Maringer and Slotta-Bachmayr, 2006), and so all of our core woodland patches are treated as the same. One advantage of a Habitat Suitability Index approach is that it can identify where the best beaver habitat is located. This may be a useful approach for the identification of optimal release sites if required and the detailed attribute data available within the Native Woodland Survey of Scotland could enable this refinement.

A dataset of watercourse sections where we predict beaver damming to be less likely is presented. Watercourse sections not identified by the dataset are a combination of those that cannot be dammed and those that can, but we do not have the datasets, or ecological information, to specify which. We anticipate that eventually it will be possible to produce a reasonable database of watercourse sections that beavers could possibly dam. In particular, water depth is thought to be a key determinant of beaver damming activities, and so a database which provides geospatial measurements would assist greatly (Hartman and Tornlov, 2006). It should also be noted that beavers may sometimes be recorded damming along rivers where there is no woodland, and so this needs to be taken into account when examining stretches identified in the dataset as being *less likely* to be dammed.

It is clear from our map of watercourse connectivity that there is a high likelihood of beavers moving between catchments (Figures 5, 6, & 7). For example, for all catchments in Scotland, >10% of the catchment boundary is predicted to be permeable to dispersing beavers. Therefore, it is likely that any catchment surrounded by beaver populations will eventually experience multiple colonisation events. This is in part a reflection of Scotland's climate and geology, with high densities of watercourses throughout the country.

It is difficult to predict which islands may eventually be colonised by beavers. Here we have argued that 6 km is a reasonable limit to offshore dispersal, but it is based on limited evidence. Our datasets identify islands within 6 km of the mainland (and then within 6 km of these islands to indicate that they may be used as stepping stones to other islands). This provides a broad indication of possible colonisation, and at least highlights the possibility that some of the closer islands to the mainland may be colonised one day.

However, the island dataset was not developed further due to the range of unknown factors which may affect seaward dispersal. These include how currents may affect the ability of beaver to cross the sea, and whether beaver will use islands without habitat as stepping stones. There are a number of obvious potential refinements to the dataset, for example how other islands may be colonised through more stepping stone islands.

4.3 Ground truthing the potential core beaver woodland dataset

In comparison to other signs of beaver activity, the potential core beaver woodland dataset predicted the location of scent mounds better than any other field sign. This is encouraging as the abundance of scent mounds is correlated with the quality of a territory and the length of beaver occupancy (Rosell and Nolet, 1997), which suggests that scent mounds are the most important sign of long-term beaver occupancy.

The result that the core beaver woodland dataset overlaps with 91% of scent mounds suggests that it is a useful broad-level, predictive tool. However, we cannot yet test whether the dataset is better than may be predicted by chance alone. We have evidence of beaver presence inside and outside predicted beaver habitat. However, for a suitable statistical analysis we would also need evidence of beaver rejecting areas inside and outside of predicted beaver habitat. This is not currently possible as beaver have not yet reached carrying capacity within the Tay catchment. This is an important consideration as the abundance of woodland in the Tay catchment is broadly high (see Table 1). A key test of the dataset will come if beaver move into areas where habitat is less abundant, and where the population may become more dispersed, and more difficult to predict.

The parameters of the potential core beaver woodland dataset were picked on the basis that they could predict the location of long-term beaver territories, not all beaver activity. The beaver signs and activity not predicted by the dataset may therefore reflect presence not associated with established territories, such as dispersing individuals and temporary residents, or it may be the result of errors associated with the assumptions the dataset is based on. For example, there were obvious, specific areas of beaver activity from the Tay beaver survey that were not predicted by the core woodland dataset (Figure 3). This may be due to the presence of small woodland patches on the ground, which are not identified by the woodland datasets used. One of the major groupings of beaver signs that were not predicted by the potential core beaver woodland dataset were on the River Isla near Coupar Angus. Some of these stretches have a thin strip of riparian woodland on river banks that is visible from aerial imagery of the areas, but these are not picked up in the national woodland inventories. This highlights that the dataset provides a good, broad-level predictive tool, but any detailed and localised assessment of beaver habitat suitability needs to also involve field survey and other methods.

4.4 Further use of the datasets

To date, the woodland datasets have been used to identify where species and habitats of conservation importance may overlap with potential beaver woodland. For example, the datasets were used to identify overlap with Atlantic hazelwood communities, and it was found that 27% of all potential beaver woodland, and 19% of potential core beaver woodland overlapped with Atlantic woodland communities that had ≥80% hazel (Genney, 2015). This has allowed potentially vulnerable areas of this habitat to be identified, which would therefore require appropriate management if a wider reintroduction of beavers occurs in the future.

There is also scope to plan appropriate management using the dataset that highlights watercourse sections that are less likely to be dammed (e.g. identifying sections where monitoring for dam presence may not be a priority for fishery managers).

Although our datasets predict where beaver will utilise woodland, they do not attempt to predict the size of beaver populations, or indeed whether there is enough suitable woodland within a catchment to sustain a beaver population. However, the datasets produced for this study have been used in a recent modelling exercise to predict the population performance of the beaver populations within Knapdale and Tayside if they are allowed to remain (Shirley *et al.*, 2015)

The datasets provide useful predictive tools which may be used in the planning of any future reintroduction and management. However, at the local, detailed level, there would also be a need to use additional assessment techniques, including field surveys.

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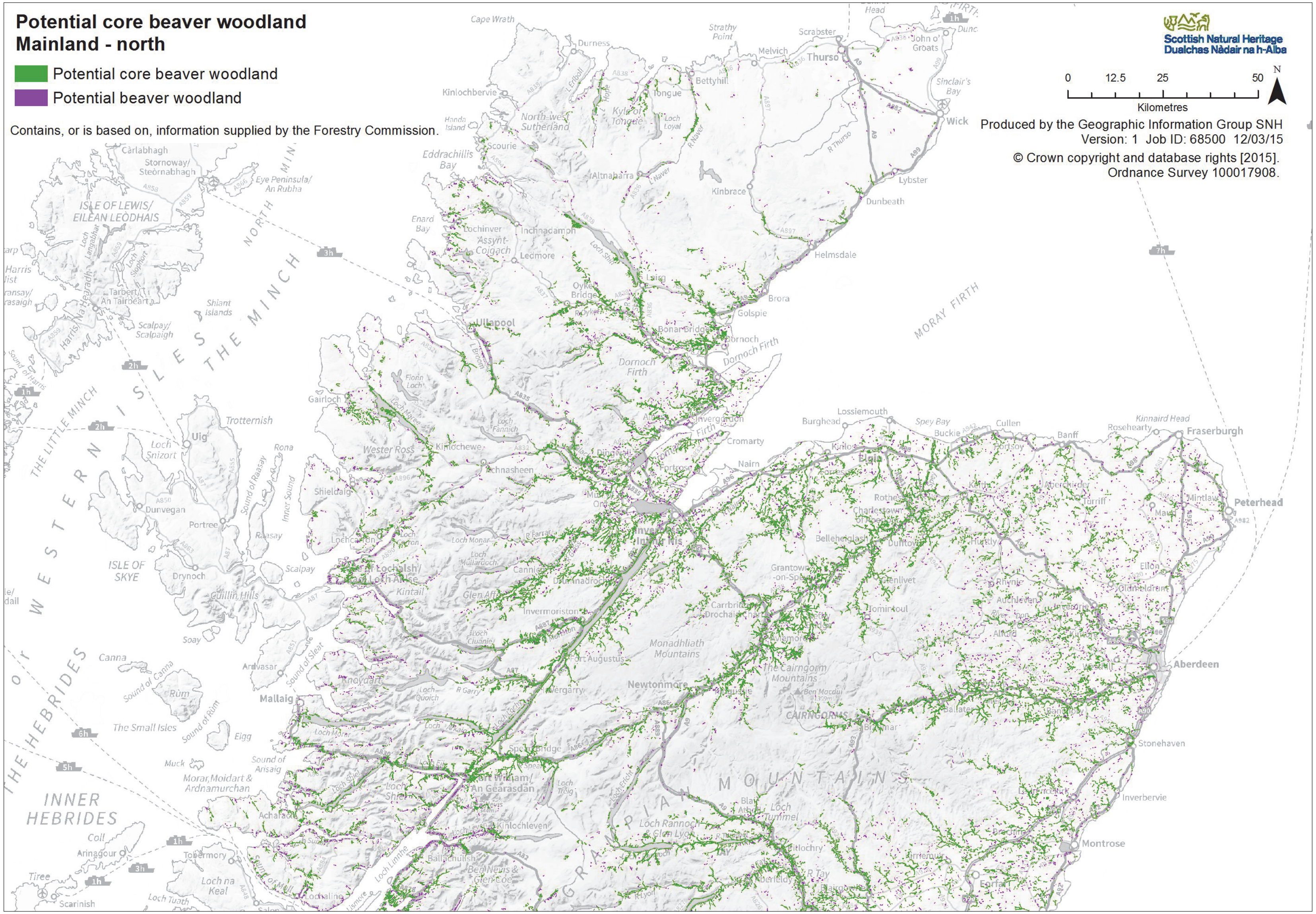
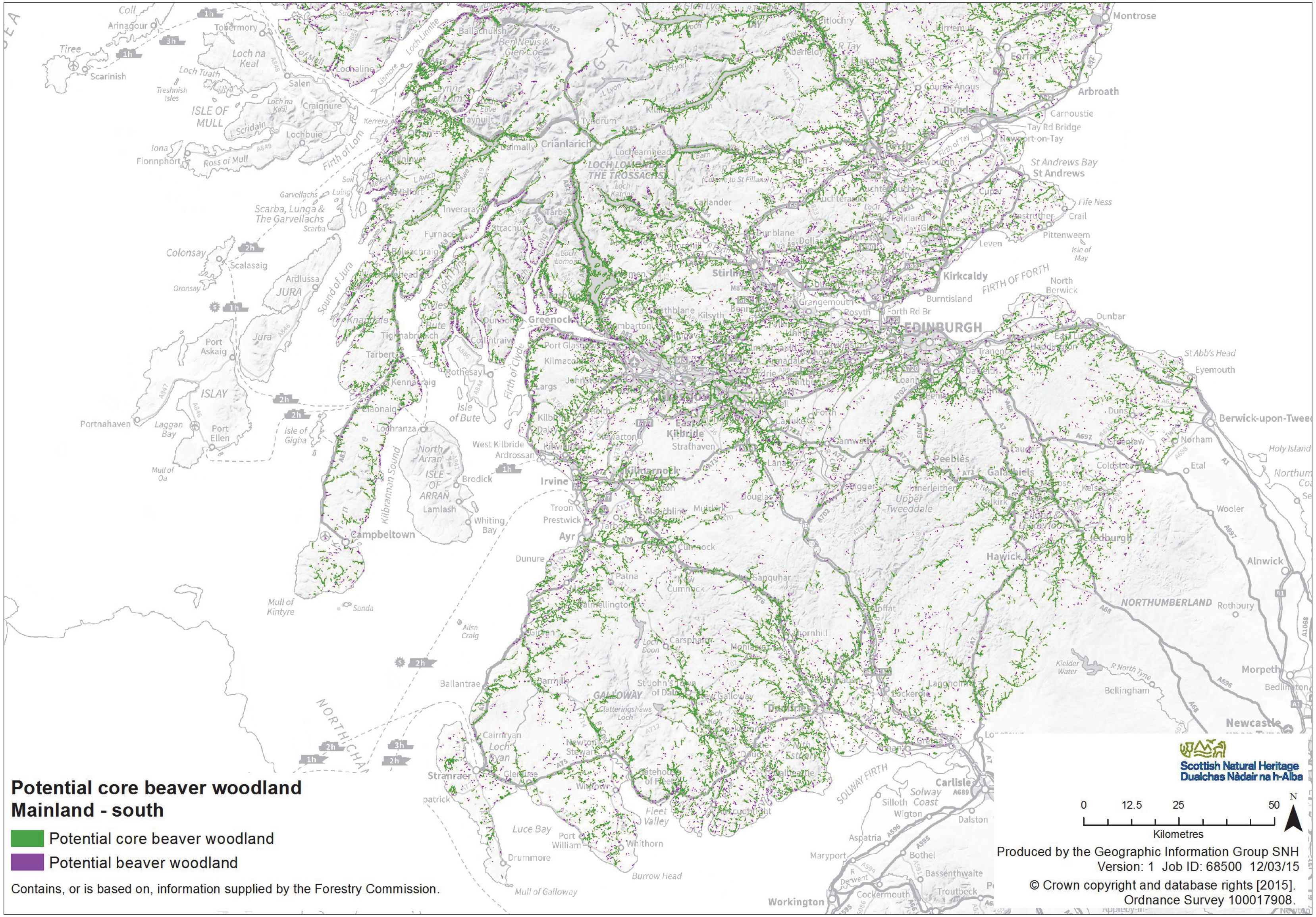
ANNEX 1: POTENTIAL WOODLAND MAPS FOR NORTH & SOUTH SCOTLAND

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