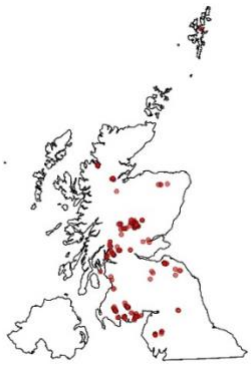
The Ecology and Genetics of Scotland's Native Wild Apple: Malus sylvestris



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Supported by Scottish Forestry Trust, Sustainable Forestry SCIO, Patsy Wood Trust, Forest Enterprise Scotland

2018

Summary

This project provides the first account of the ecology and genetics of wild apple (*Malus sylvestris*), which is probably Scotland's least understood and most under-appreciated native tree. Commonly known as crab apple, it is familiar to people as a small tree planted in hedgerows; and on this basis foresters and ecologist appear to have dismissed it as unimportant. In fact it is a characterful and ecologically important native tree, occurring in semi-natural woodland and wood pasture across most of Scotland.

Wild apple is a progenitor of the domestic (eating) apple – this being a hybrid between a sweet apple from eastern Asia and both European and Asian wild (crab) apples, estimated to have arisen 1500-4500 years ago. Different apple species hybridise easily, and in recent centuries widespread planting of domestic apples in Europe has led to these hybridizing with wild apples; and recent DNA studies show that between 7-36% of apparent wild apples in various European countries are in fact hybrids. This project investigated the situation in Scotland and northern England by comparing DNA markers in 342 wild-grown apples; and showed that 27% of apparent wild apples are in fact hybrids between wild and domestic apple. However, in several parts of Scotland there are substantial populations of more or less pure wild apple; these occurring where there is a high incidence of semi-natural woodland, for example in Loch Lomond and the Trossachs, Galloway, Highland Perthshire and the Lake District. In contrast in the Central Belt and lowland Angus, Aberdeenshire and Moray about 50% of apparent wild apples turned out to be hybrids. There were some interesting local differences; for example, in the Lake District, trees from Borrowdale were almost all wild apples, whereas samples from Patterdale included many hybrids. There appear to be quite high levels of genetic variation in all populations of wild apple, with no genetic structure to individual populations and low genetic differentiation between populations. The study also revealed several Asian crab apples have been planted in Scotland and that these are also hybridizing with wild apple.

In native woodland and wood pasture the vast majority of apple trees appear to be self-set rather than planted. In agricultural areas in the lowlands trees were generally of planted origin. This project provides the first unambiguous account of the distribution of wild apple in northern Britain. It has strongholds in Loch Lomond, Trossachs, Highland Perthshire, Dumfries and Galloway, Ayrshire, Lake District, Eastern Borders and around Contin and as far northwest as Dundonell. It is apparently largely absent in many parts of Deeside and Strathspey and appears oddly scarce in much of the Western Highlands, but is not wholly absent here. The incidence of wild apple reduces markedly on acid lithology, but does occasionally occur on favourable sites. Trees located at Dundonnell, near Ullapool, are the most north-westerly in Europe and one tree was located on a seacliff of an uninhabited island in Shetland. The highest elevation trees were located at about 300 m in both Scotland and northern England, but it is apparent they can grow at higher elevations than this. They show a very wide climatic tolerance and some of the finest woods for wild apple were near Seatoller, Lake District, the UK's wettest location (annual rainfall 3550mm).

Wild apple is well represented in woodland (45% of occurrences), and wood pasture (37%); with only 16% of occurring in hedges and pastures. In woodland, 87% of occurrences of wild apple were in native woodland and 76% were in ancient woodland. Hybrid apples also occur in woodland, including ancient woodland, but a higher proportion were found in hedges and pastures (33%). It is in ancient wood pasture that wild apples reach their highest densities, with up to 10 mature trees per hectare. In spring, these trees constitute a very unexpected and attractive feature. There is reason to believe that the pasturage of cattle in these woods, which continues to this day in some, helps the recruitment of apple regeneration. A significant proportion of wild apple were found in uplands gulley and riparian woodlands. There is an interesting, large population at high water mark on the islands and shoreline of Loch Lomond and we assume these have spread via floating apples.

Wild apples are most common in oak-birch woodland, but also occur in ash woods and alder wet woodland. The most common associated plant species were bracken, bluebell, wood sorrel, broom and woodsage (indicators of oak-birch woodland); wood avens and dogs mercury (indicators of ash woodland); and creeping buttercup and rushes (indicators of alder wet woodland). Epiphytic lichen and moss communities on apple bark appear to be acidic in nature and not particularly diverse. Old horizontal branches host luxurious moss carpets, sometimes including common polypody ferns.

Wild apples are more substantial trees than suggested in the literature; the trees in this study had an average stem diameter of 52 cm (at ground level), and a maximum of 120 cm. Eleven of the 127 mature trees measured had stem diameters over 90 cm. Mean height was 8 m, with a maximum of 14 m. We need to revise our mental picture of mature wild apple trees from small trees, to something more the size of wild cherry trees.

Most foresters and ecologists are not looking out for wild apples, and are not good a recognizing them when they see them. Apples trees are fairly distinctive, both close up and when viewed at distance. Key characteristics are: they have very dense complex crowns (rather like large hawthorns or blackthorns and far denser than garden apples); the upper crown often has a somewhat irregular appearance, with sparse straggly individual twigs emerging; the crown in winter has a distinctive dark slate-grey colour. When in flower (mid-late May) they can be spotted at distance by the pink (turning to white) flowers, which come out a week or so before hawthorn. This paper provides guidance on distinguishing wild apple from feral domestic apples; but it is impossible to reliably distinguish hybrids apples from wild apples by morphology alone.

Wild and hybrid apple trees flower and fruit regularly and profusely; 84% of wild apples and 92% of hybrid / feral domestic apples were recorded as flowering or fruiting during the 2 years of this project. Seedlots from 36 parent trees were planted; and 40% germinated in the first spring, and 53% germinated the following spring. Far more seedlings germinated the second spring (75%), as opposed to the first spring (25%). Naturally regenerated saplings are rare; and the best examples are in areas of wood pasture where there is a history of pasturage of cattle.

Both wild and hybrid trees appear to be about 60-120 years old, so originating in the late 19th to mid 20th centuries. They appear to be incredibly resilient. They blow over and resprout freely as 'phoenix trees'; about 20% of mature trees were phoenix trees, making wild apple one of the most adept species at this growth form. Only 2 of the sampled trees were affected by disease.

Foresters and ecologists need to revise our view of the tree, and set about sorting some of the issues that have accompanied our collective neglect of the species. We suggest that the name “wild apple” is adopted (as in other European countries) to differentiate the native *Malus sylvestris* from the miscellany of other trees that go by the name “crab apple”. Wild apple is regarded as threatened in several European countries because of hybridisation and lack of regeneration; though IUCN’s overall assessment for Europe is that the species is “data deficient”. It is good conservation practice to ensure that we maintain our best pure populations of wild apple. In upland areas with fewer domestic/hybrid apples (Galloway, Loch Lomond/Trossachs, Highland Perthshire) hybridization is likely to be proceeding only slowly and these populations could be used as seed sources. There is a need for forest nurseries and seed suppliers to ensure they are selling *M. sylvestris* and not a mix of wild apple and hybrids. Nurseries should DNA test samples of their existing stock and in the light of the results, reconsider their seed sources.

Wild apple needs to be rehabilitated as a more prominent and valued member of Scotland’s native trees and woods. The priorities are as follows:

1. Professional and popular forestry and ecology literature should feature wild apple with the same prominence as other tree species and provide an accurate account of the species.
2. The main populations of pure wild apple in native woodland and wood pasture should be catalogued, and owners, managers and agencies made aware of their existence and value.
3. In areas with frequent wild apple, owners should be encouraged to establish a new generation of trees. Planting of other apple species in the wild should only take place with good reason. Elsewhere across Scotland, small admixtures of wild apple should be planted as part of new native broadleaved woodland.
4. Seed collections from known pure populations should be encouraged and seed orchards set up using known wild apple parents from across Scotland. Nurseries wishing to sell hybrid apples should label and market them accordingly and make customers aware of the differing conservation value of wild and hybrid apples.
5. The potential of wild apples to help support our threatened pollinator species needs to be explored.
6. Research needs to be undertaken to clarify the invertebrate, plant and fungal associates of wild apple, its regeneration biology and its adaptive genetic variation.

Contents

Acknowledgements: This project was funded by Patsy Wood Trust, Scottish Forestry Trust, Sustainable Forestry SCIO and Forest Enterprise Scotland. The report is dedicated to the memory of Patsy Wood and special thanks go to Robin Buxton, Sarah Buxton, Colin Hughes, Bob Stubbs and Andrew Fairbairn. We are grateful to the many people who located trees for us or sent in leaves for sampling; especially Mary-Ann Smythe, Richard Cunningham, Crystal Maw “Queen of Cowpats”, Neil Mackenzie, Joyce Gilbert, Alistair Godfrey, Iain Brodie, Simon Pepper, Graham Gill, Rob Soutar, Rob Coope, Steve Brown and John Parrot. Donald Rice and Will Soos located the important wild apple trees at Dundonnell, the most north-westerly known in Europe. Paul Harvey took a cold swim to collect a leaf sample from a sea cliff in Shetland; the most northerly tree in the UK. Elizabeth Leighton ably steered our canoe around the Loch Lomond Islands finding 25 remarkable wild apple trees. Our work was also supported by Falkland Stewardship Trust who handled the finances and Forestry Commission Scotland who sent us data from the Native Woodland Survey of Scotland. The genetic analysis at Royal Botanic Garden Edinburgh was supported by the Scottish Government’s Rural and Environment Science and Analytical Services Division.

1. Introduction and Aims

This project came about as a result of having encountered impressive wild apples in ancient woodlands, in unexpected places (figure 1). Firstly, it turned out to be surprisingly difficult to verify whether these were the native apple (*Malus sylvestris)*, and then we got puzzled by the fact that nothing useful appears to be known about the species, either in Scotland or the UK. There are no papers published in the UK on *Malus sylvestris* at all; and those few forestry books that include a section on apples seem to make a hash of the topic. So we know virtually nothing about where wild apples grow, nor their site requirements; and their distribution in Scotland has never been properly described. Of course, most people are familiar with the name 'crab apple' and think of small, scruffy trees planted in hedgerows ("scroggies"); and on that basis it seems that both foresters and ecologist have dismissed the tree as unimportant. Overturning that perception is one of the aims of this paper.

Malus sylvestris is the 'forest apple' according to its latin name, and is generally called the "wild apple" in other European countries, where it has been rather better studied. It is a characterful, rare and ecologically significant tree that grows widely across central and western Europe, as far north as 67° N in coastal Norway – see figure 4 (Stephan et al 2003). Interestingly, recent genetic studies have shown that the lowly crab apple is a major contributor to the genetic make-up of domestic (eating) apples, via historical hybridisation with sweet apples from Asia (Cornille et al. 2012, 2014). Hybridisation came about by the sweet apple (*Malus sieversii*), which grows in spectacular apple-dominated forests in mountain foothills in China and Kazakhstan, making its way towards Europe over the millennia, with the help of trade along the Silk Road. On arrival in the middle east and Europe it crossed with European crab apples, forming our domestic apple *(Malus domestica)*; these crosses being estimated to have taken place between 4500 and 1500 years ago (Cornille et al 2012). Domestic apples are now grown the world over and are one of mankind's most economically and culturally important tree crops, with annual sales in the UK alone worth 846 million in 2014 - for comparison the GVA[1] of forestry in 2014 was £540 million and sawmilling £356 million (Forestry Commission 2017). So by providing a critical part of genome of eating apples, the wild crab apple made a very significant contribution to human wellbeing. Wild apple is thought to have contributed several valuable traits, such as later flowering, climate adaptation, resistance to pests and diseases, and capacity for longer storage of fruits (Cornille et al. 2012)

1.1 Genetic issues

However, the rampant success of the domestic apple - which has been grown in many parts of the world for centuries - now appears to be starting to threaten the long term survival of the wild apple as a species. This is because the two species (*M*. *sylvestris* and *M*. *domestica*) interbreed, raising the possibility of *Malus sylvestris* being threatened by hybridization – in a similar way to the fate of the Scottish wildcat (e.g. Larsen et al 2006, Reim et al 2012, Cornille et al. 2014, Ruhsam et al. 2018). Hybrid apples (*M. domestica × sylvestris*) have recently been shown to make up a significant proportion (7-36%) of populations of wild crab apples across a range of European countries (Cornille et al 2014). This has contributed to the species being listed on IUCN red data lists in several European countries (IUCN 2011). This raises the question of what is happening in Scotland. Are the apple trees we see in Scottish woods really *Malus sylvestris*, or actually hybrids that have developed over the centuries?

DNA markers have been developed in recent years which allow us to differentiate between *M. sylvestris, M. domestica* and their hybrids (Cornille et al. 2013) - this being necessary because they cannot be distinguished reliably by morphological characteristics. We also set out to discover which other apple species are present in

[1] GVA is Gross Value Added

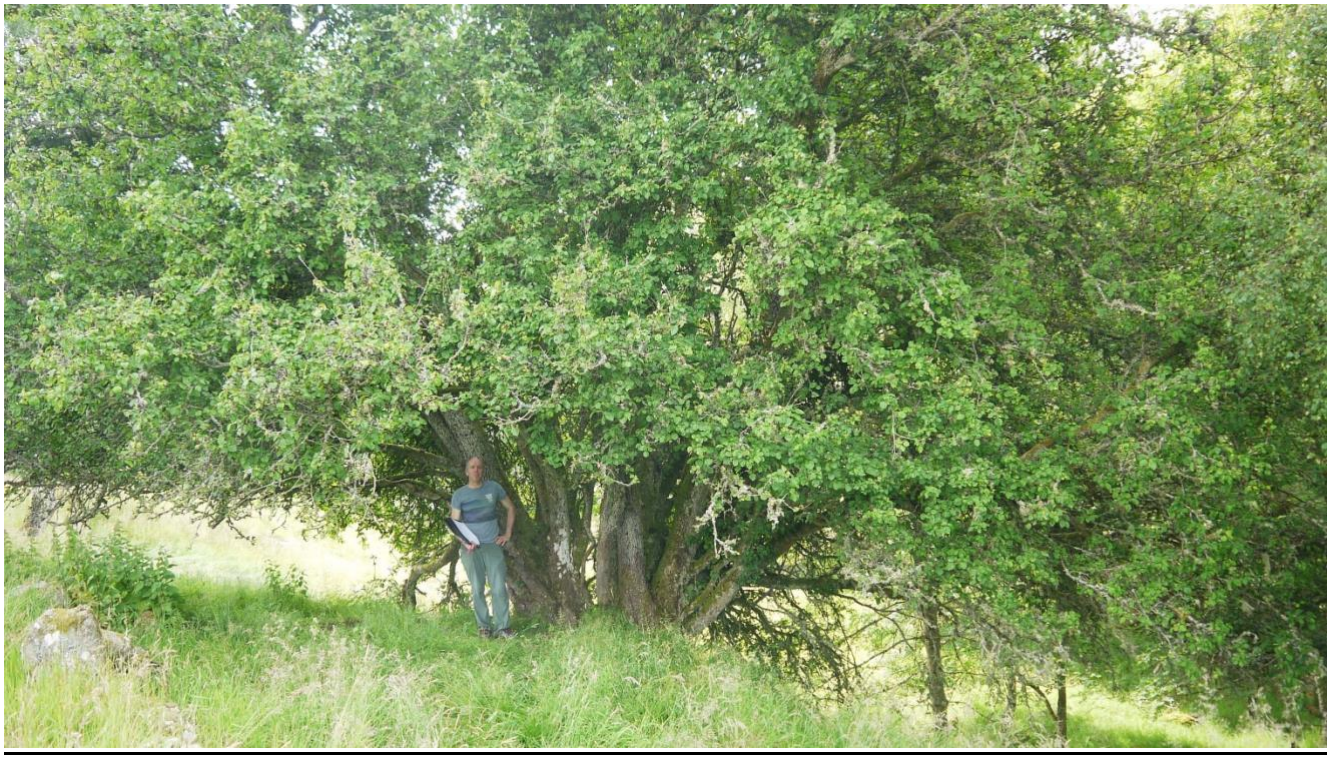

Figure 1a A large coppice wild apple (*Malus sylvestris)* at the edge of a wooded gulley, Grandtully, Perthshire.

Fig 1b Small wild apple in ancient oak woodland in spring Grandtully, Perthshire

Figure 1c Wild apple with a 17 m crown span coming into flower in ancient wood pasture, Cree Valley, Dumfries and Galloway.

Figure 1d Large wild apple on a Forestry Commission Plantation on Ancient Woodland Site (PAWS) Frenich, Tay District, Perthshire.

woods in Scotland, either due to planting, or due to the spread of feral apples. There are roughly 30-40 species of crab apples worldwide, and some of these have been planted quite widely in Scotland, especially Siberian and Chinese ones (*M. baccata and M. hupehensis* respectively); and those also potentially hybridise with wild apple (Corban 1986).

1.2 Using the term "wild apple"

The term 'crab apple' is problematic. Firstly it does not necessarily refer solely to the European apple *M. sylvestris,* but is generally used for any apple species producing small fruits, to distinguish these from cultivated apples. Some garden trees sold as crab apples appear to be domestic apples specially bred to produce small apples, adding to the confusion over what a "crab apple" is. In addition, hybrid apples (*M. sylvestris × domestica*) are also referred to as crab apples, as are the myriad horticultural species and cultivars sold in garden centres and nurseries. These cultivars include many complex crosses amongst apples species from all over the world, and often the parentage is obscure. To clarify this situation, in this paper we adopt the term "wild apple" to describe genuine native *M. sylvestris*, and we would encourage forestry and ecology interests to adopt this term. This is the same way that the distinction is made in other British native species with domestic counterparts e.g. wild cherry, wild raspberry, wild strawberry. Wild apple is the form used in most other European countries e.g. "villeple" in Scandinavian countries and "pommier sauvage" in France. This simply makes it clear that we have one species of apple that is native and grows in the wild like any other native tree. This avoids clumsy alternative terms like "true crab apples" or "wild-type crab apples" to distinguish native *M. sylvestris* from the various other crab apple species, hybrids and cultivars.

1.3 Aims

The main research questions addressed were:

- What is the distribution of the wild apple (*M. sylvestris)* in Scotland and what are its basic ecological characteristics?
- Is hybridization with *M. domestica* occurring in Scotland, and if so, what effects might this have?
- Are there other apple species growing in the countryside in Scotland (planted or feral) and what species of apple are being sold as *M. sylvestris* by forestry nurseries?
- Can we develop management and conservation guidance for wild apple?

By talking to nurseries and seed suppliers we also concluded that there are highly likely to be problems of seed supply, because of hybrid or even feral domestic apples being used as seed sources. So another objective of this project was to encourage seed collection from genuine *M. sylvestris* and then plan the development of grafted seed orchards, which brings together genuine wild apple parents. We also consider if there might be locations where genetic conservation of wild populations would be feasible and useful.

Our fieldwork revealed signs of past management and use of wild apples and their hybrids, and so this paper briefly reviews the evidence about the common history of people and wild apples in Scotland. We end by proposing how wild apples might be used in the future: as a component of native woodlands, as a spectacular landscape tree, as a prolific producer of a "non-wood forest product", as an important species for threatened pollinator insects; and in the longer term even as a producer of decorative timber.

2. Methods

2.1 Locating apple trees

A total of 342 apple trees were located in Scotland, focusing primarily on wild apples (*M. sylvestris*) and probable hybrids (*M. sylvatica × domestica*), but also including a few feral domestic apple trees. Additional species were recorded when encountered; mainly Chinese crab apple (*M. hupehensis*) and Siberian crab apple (*M. baccata*). Trees were located by the authors and some were volunteered by land owners. Several datasets proved helpful i.e. the Native Woodland Survey of Scotland (NWSS), which identified woods with apples present; the National Biodiversity Network (NBN), and Ancient Tree Hunt Inventory. Some trees were recorded in Northern England to add geographic context.

The trees were allocated to one of the following eight geographical regions (**Error! Reference source not found.**2): Lake District (LD, n=24), Dumfries (DF, n=89), Central Belt (CB, n=66), Loch Lomond (LL, n=50), West Coast (WC, n=9), Perthshire (PS, n=72), Aberdeenshire (AB, n=9) and Northern Highlands (NH, n=23), including one sample from Shetland.

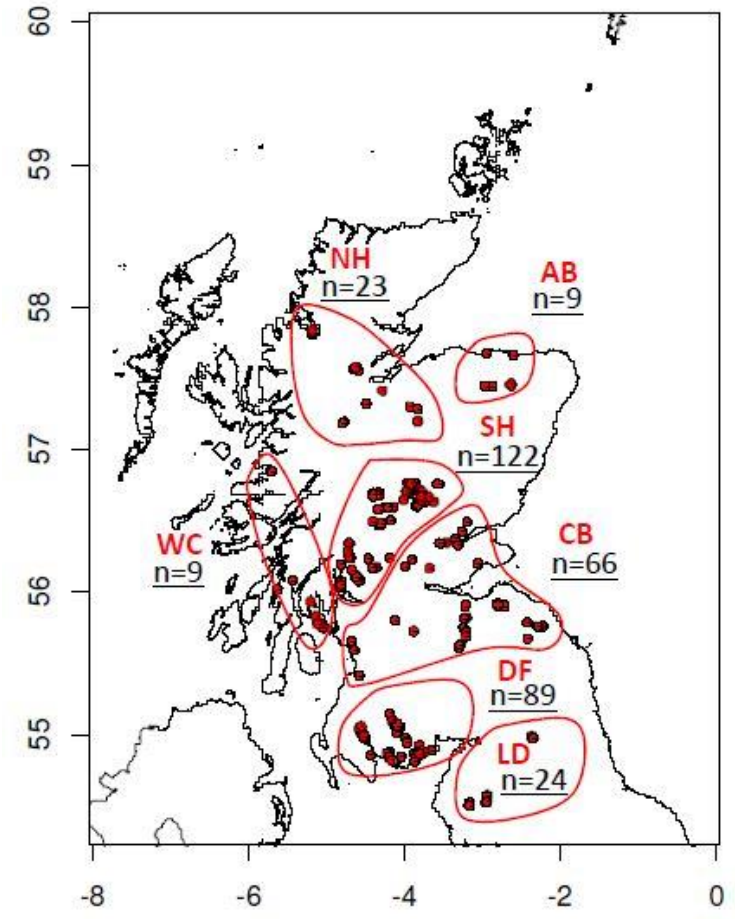

Figure 2. The locations of the 342 trees divided into broad geographical regions (see Ruhsam et al. 2018).

2.2 Data collection

The following information and samples were recorded:

Location: National Grid reference and other information describing location of all trees.

Tree size and structure: Height, crown diameter and stem diameter at ground level and number of stems (183 trees). Trees thought to have been pollarded were noted (11 trees).

Leaf characteristics: The hairiness of the lower leaf surface as viewed through a hand lens, was scored on a scale 0-4. This is a key characteristic differentiating *M. sylvestris* and *M. domestica* (see table 1).

Fruit size: Where trees with fruit were sampled in the autumn, the diameter (horizontal) of a small sample of fruits were measured to give values for maximum, minimum and mean fruit size (86 trees).

Site characteristics: Elevation, topographic position, habitat (ancient woodland, native woodland, other woodland, wood pasture, hedgerow, field); NVC woodland community, ground flora species (205 trees).

Identification to species

Trees surveyed by the authors were identified in the field based on morphology, with emphasis on leaf hairiness, crown structure and, if available, fruit size (Stace 2010, Tollefsrud et al 2014). Trees were assigned to the following classes: wild apple, possibly wild apple, hybrid, possibly hybrid, domestic apple, other crab apples (Asiatic).

Table 1 Apple Leaf Hairiness Scoring and provisional assignment to species.

APPLE LEAF HAIRYNESS SCORING		
Scores by inspecting the underside of leaves with a hand lens		**Species**
0	Both petiole and lower leaf surface without hairs, or only a few sparse hairs on petiole and leaf margin at very base. Hairs stiff and spaced out.	**Probable Wild Apple Malus sylvestris**
1	Some hairs, generally sparse, on petiole, lowest parts of midrib (typically lower 20% of blade length) and lower lateral veins near leaf base. None on leaf blade surface. Hairs generally stiff and spaced out	
2	Petiole and lower midrib and lower veins obviously hairy to about 30% of leaf length. On most trees there will also be some hairs on lower leaf surface, mainly in vein axils.	**Probable hybrid apple Malus sylvestris × domestica**
3	Petiole and veins hairy to about 50% of leaf length. Lower leaf surfaces also hairy. Only upper leaf free of hairs. Hairs thin, downy, and frequent.	
4	Petiole, veins and leaf surface largely covered with felted hairs. Hairs thin, downy, and frequent.	**Probable Domestic apple (Malus domestica)**

Genetic sampling and DNA analysis method

A detailed account of the genetics work in this project has been published as a peer reviewed paper in Forestry (Ruhsam et al 2018) and the methods and results from that paper are summarized below in this report. A single leaf was collected from each tree and dried in silica gel. DNA was extracted using the DNeasy Plant kit (Qiagen, Hilden, Germany). All samples were assayed for 15 microsatellite loci using the four multiplex reactions MP1, MP2, MP3 and MP4 from Cornille et al. (2012). STRUCTURE v.2.3.3 (Pritchard et al. 2000) and NEWHYBRIDS v1.1 were used to investigate the population structure and levels of admixture of *M. sylvestris* and *M. domestica* in the 342 trees and 34 reference Malus samples. For details see Ruhsam et al 2018.

Germination studies

Apple seeds were collect from 31 trees, which were later identified to species by DNA analysis as 25 wild apple, 3 hybrids (*sylvestris × dometica*) and 3 domestic apples. The seeds were planted in the autumn in potting compost and the seedlings were also DNA tested to determine their species.

3. Results

3.1 Contacting professionals

Contacting professionals for help locating apple trees in the wild revealed some intriguing insights. Some people thought that *Malus sylvestris* was not native; but were feral apples having started life as randomly flung apple cores. Others thought that all “crab” apple trees had been planted. The otherwise excellent Native Woodland Survey of Scotland adds to this confusion by listing “crab apple” as non-native in the web browser tool, but as native in its main publication (Forestry Commission Scotland undated). Whilst a very few professionals were able to provide good information on local wild apple populations; most people contacted were largely unaware of the presence of the species.

3.2 Apple species in the wild in Scotland

The survey recorded a total of 342 apple trees and revealed that in woods, wood pasture, hedges and fields there are the following species:

- **wild apple trees** (*M. sylvestris*), most of which appear to be self-set, though with some obviously planted trees in the lowlands.
- a few trees which look like **horticultural cultivars of *M. sylvestris***, which have been planted in lowland hedges or are possibly garden escapes.
- **hybrids between wild apple and domestic apples** especially in lowland areas.
- **feral domestic apples** (*M. domestica*),
- **planted Asian crab apples**: Chinese crab apples (*M. hupehensis and Malus orientalis)*, and Siberian crab apples (*M. baccata*); and these have started to regenerate in the wild.

DNA analysis revealed that 70% of the trees recorded were wild apple and 27% were hybrids (mainly *sylvestris × domestica*) (see figure 3 from Ruhsam et al 2018). High proportions of wild apple trees were found in Loch Lomond and the Trossach and in Highland Perthshire, where 90% and 84% of trees (respectively) were wild apple. In the Dumfries and Galloway, the Lake District about 75% of trees were wild apple. Trees from the Northern Highlands, mainly around Contin and Dundonnell were 80% wild apple. In contrast, fewer than 50% of trees were wild apples in 3 regions: Central Belt, Aberdeenshire, and West Coast (mainly southern Argyll).

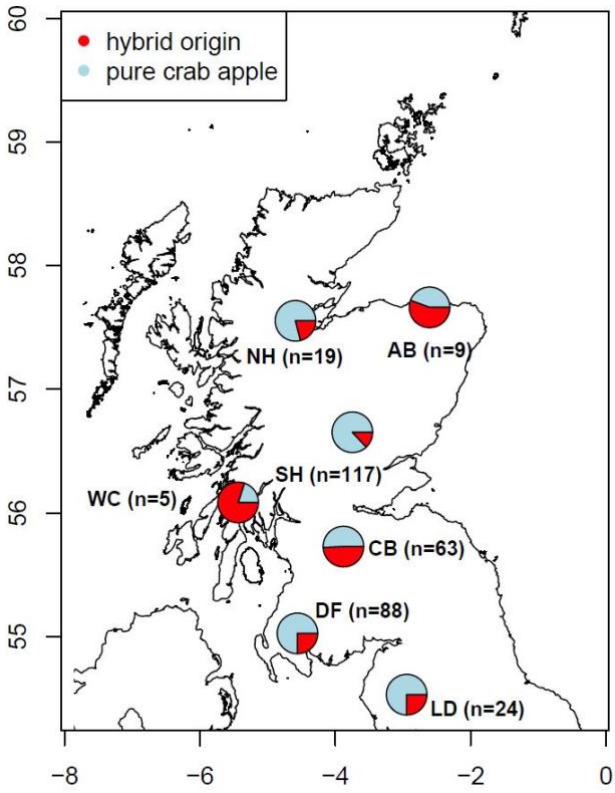

Figure 1. Proportion of field collected samples which were either pure *M. sylvestris* (blue) or of hybrid origin (red) (from Ruhsam et al 2018) in the 7 regions.

In general, areas with higher proportions of wild apples were in semi-natural woodland and wood pasture and mainly in upland areas. Trees from regions with intensive agriculture, higher human populations and relatively few native woodlands, like the Central Belt and northern Aberdeenshire, had many more hybrids. These will have arisen from past hybridisation events; in the wild or accidentally in by horticultural interests), and then multiplied by planting. Hedges in the lowlands sometime had a mix of tree species, all assumed to be planted i.e. wild apples, hybrids and occasional domestic apples. This pattern of increasing proportions of wild apples in upland semi-natural woodland appears to reflect decreasing hybridisation opportunities as the numbers of domestic apples in the landscape diminish.

There were some interesting local differences that were not apparent in the field. For example, in the Lake District, trees from Borrowdale were almost all wild apples, whereas samples from Patterdale included

hybrids; which was surprising because these trees were in ancient wood pasture at high elevation (up to 300 m) and appeared to be naturally regenerated.

There appear to be quite high levels of genetic variation in all populations of wild apple, with no genetic structure to individual populations and low genetic differentiation between populations (Ruhsam et al 2018). This indicates good movement of genes by pollination or seed dispersal (including movement by people). It is not possible to tell from DNA analysis if there are differences within the Scottish population in adaptive characteristics such as growth rate or survival – this would require provenance trials.

Interestingly, three trees from the West Coast and two from the Trossachs had genetic contributions of more than 90% from Asian crab apples. Chinese crab apple (*M. hupehensis*) and Siberian crab apple (*M. baccata*), have been quite widely planted, mainly by Forestry Commission, but also local authorities, mainly in the 1960-80s as landscaping elements on plantation edges, and around picnic sites and buildings. In Argyll, these have overcome staggering geographical shifts and started to regenerate freely (P. Quelch *pers. comm*.). These species appear to be hybridising with native wild apple.

3.3 Origins - self-set or planted ?

In native woodland and wood pasture the vast majority of apple trees appear to be self-set rather than planted, though this cannot be wholly verified. The opposite is true in agricultural areas in the lowlands where trees appear generally to be of planted origin. In wood pastures with frequent wild apples, the high densities of this otherwise rare tree raises the question of whether this is the result of particularly favourable regeneration conditions, or deliberate encouragement, or possibly even historic planting. In the lowland farming areas wild apples and hybrids occur mainly in hedges and small recently established woods, and most would appear to be of planted origin. We found planted trees of all sizes, suggesting planting had happened continuously over the last hundred years or more, and was ongoing. There is also a scattering of trees beside roads, tracks and railways which are clearly the result of accidental human dispersal; and these are mainly hybrids and domestic apples.

3.4 Species distribution

Figure 4 shows a European distribution map for *Malus sylvestris,* showing its wide distribution across Europe and its reduced frequency at its northern limits, including Scotland.

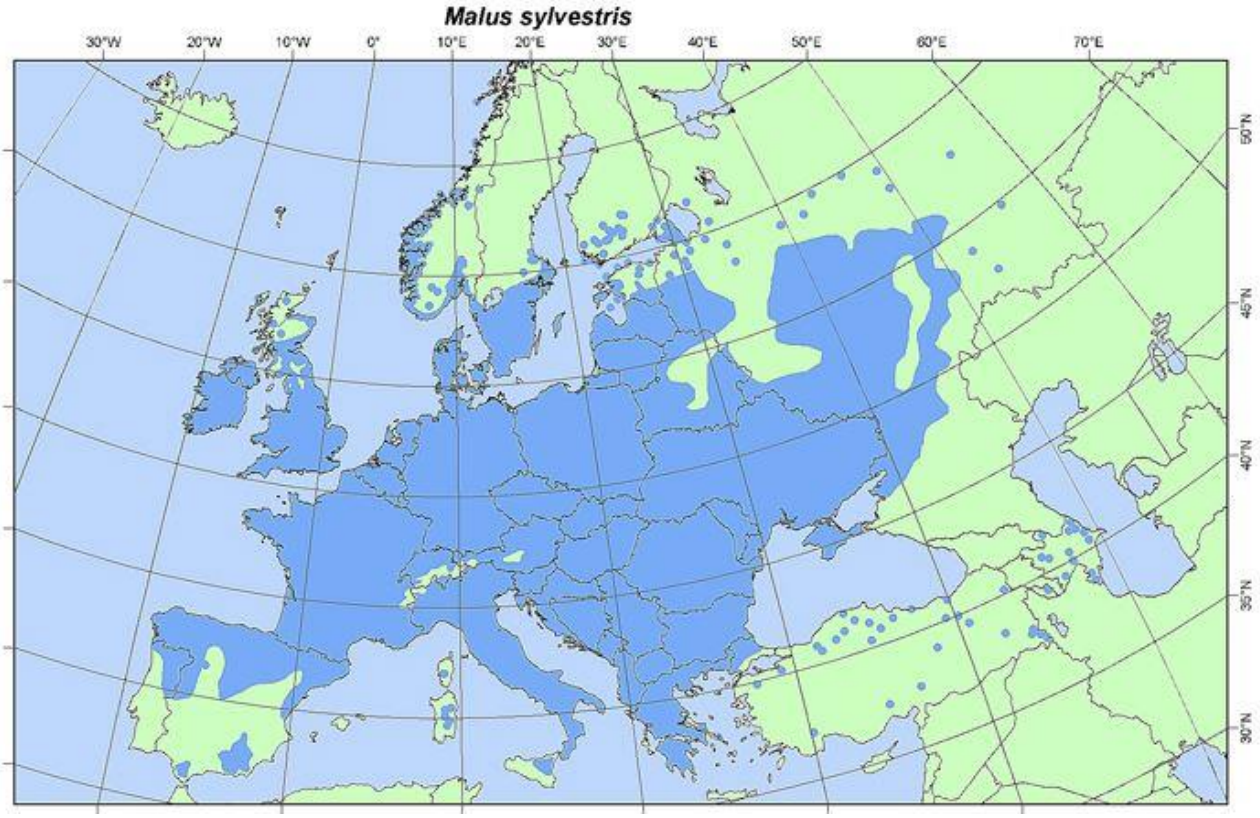

Figure 4. Distribution of wild apple in Europe (Stephan et al 2003).

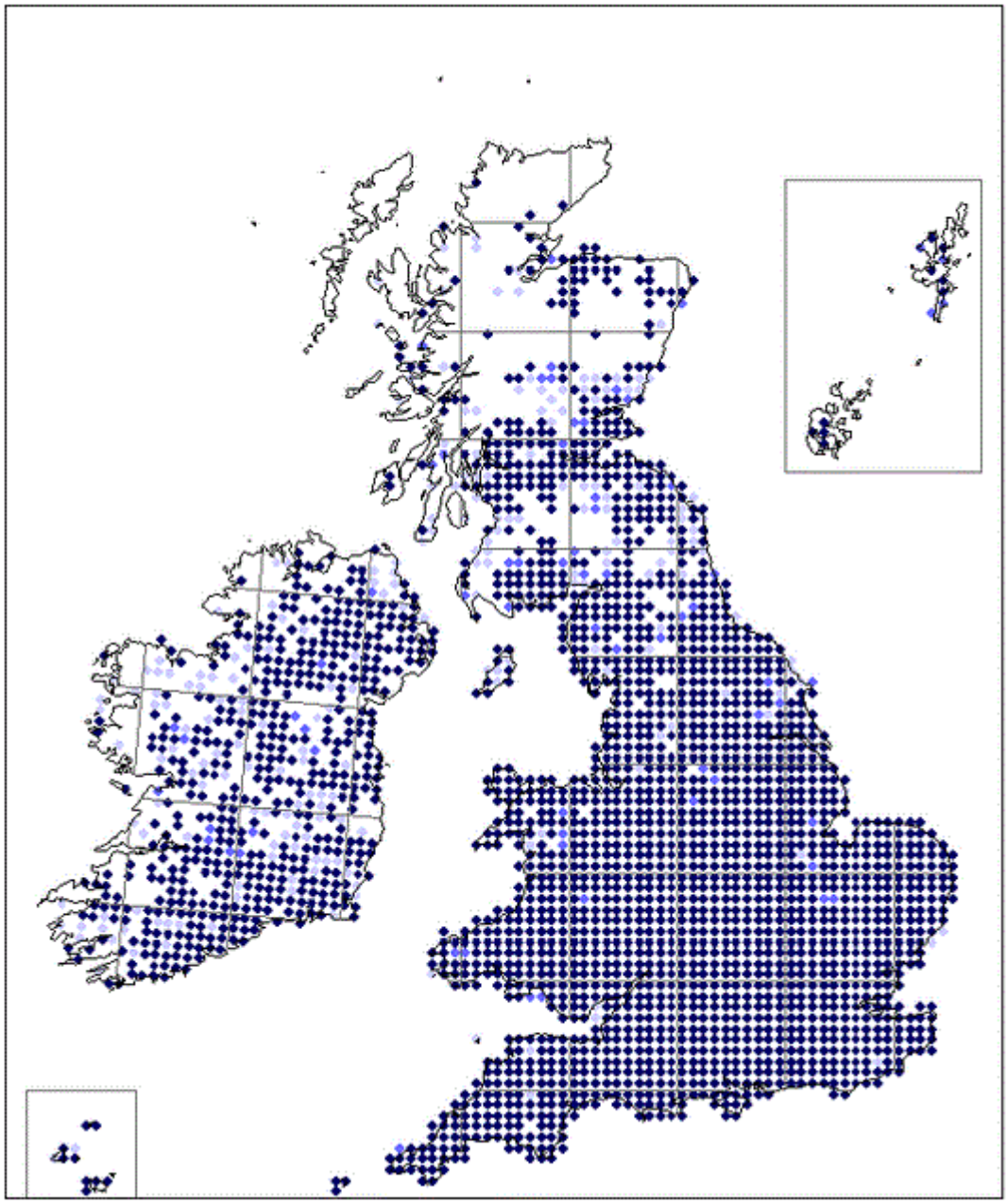

Figure 5 Distribution of *Malus sylvestris* in Britain according to the BSBI New Atlas (www.brc.ac.uk/plantatlas/plant/malus-sylvestris-sl)

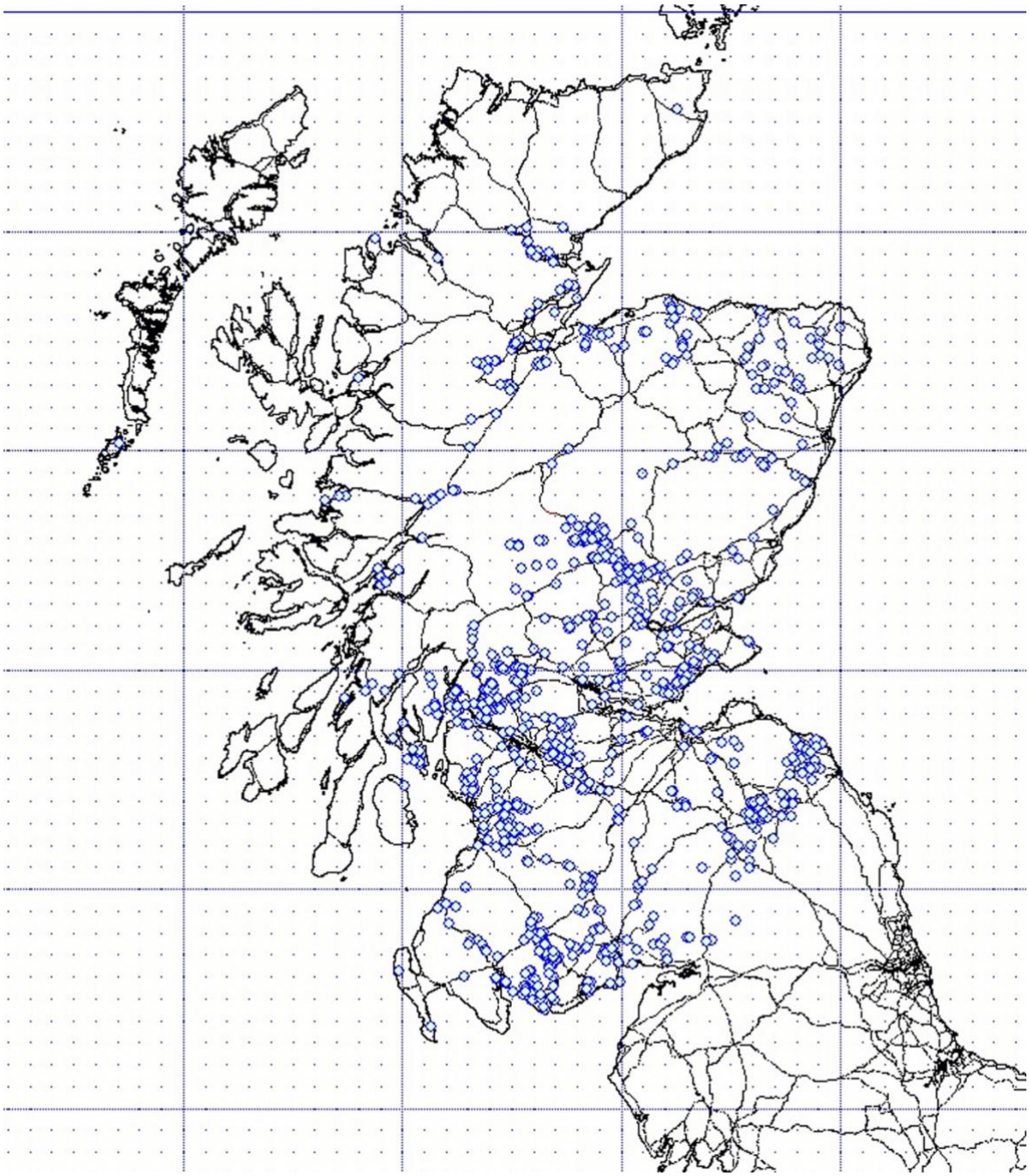

Figure 6 Occurrence of polygons contain records of “crab apple” from the Native Woodland Survey of Scotland (data courtesy of Forestry Commission Scotland). In practice the data include several species of apple and some records are not apple trees at all (e.g. in western Argyll and Strathghlas, Inverness-shire).

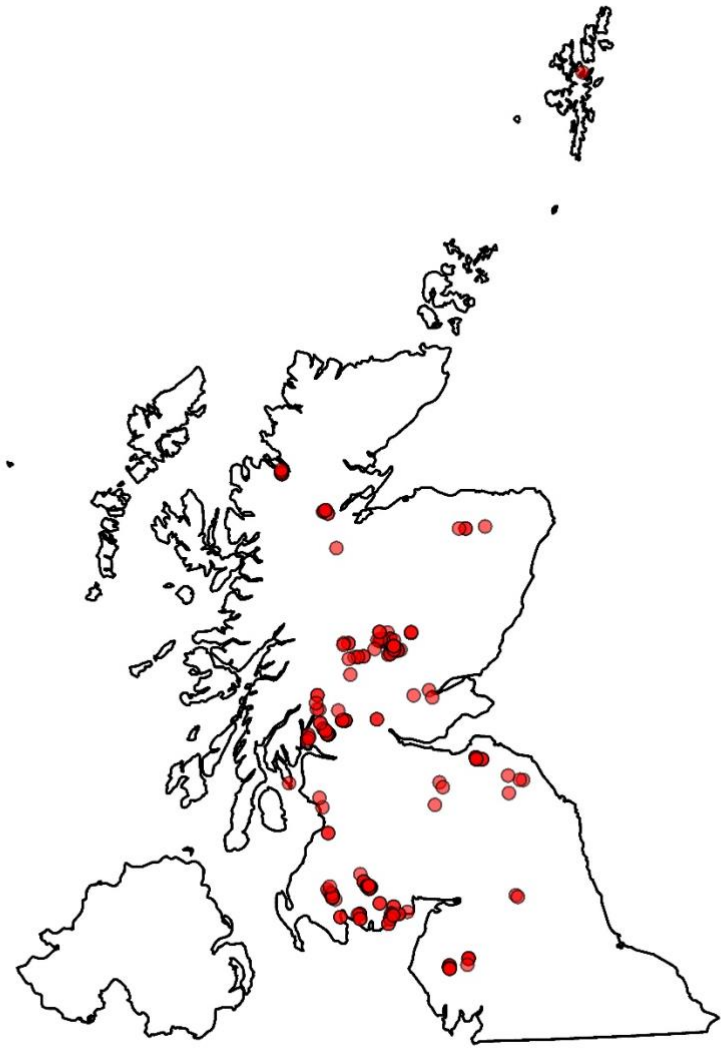

Figure 7 Distribution of wild apple trees verified by DNA analysis in this survey. This partly reflects natural factors and partly surveying effort. Note the lack of records in Central Lowlands; and the records in NW Scotland and Shetland. Darker dots represent multiple trees.

Figures 5 shows a distribution map for “Malus sylvestris” produced by Botanical Society of the British Isles prior to this project. The BSBI map comes with an important caveat, i.e. "*This map covers both the native M. sylvestris and the alien M. domestica and the two species hybridise and seem to be connected by a range of intermediates, which are included on the map and all records are mapped as if they are native*." (www.brc.ac.uk/plantatlas/plant/malus-sylvestris-sl). Figure 6 shows a distribution map of “crab apples” produced by the authors using data from the Native Woodland Survey of Scotland (NWSS). The same confusion regarding species turns out to apply to the NWSS map, which also records apples irrespective of species; and we have since discovered that a few of the NWSS records, including most in the western Highlands are false positives, i.e. they are not apple at all. Figure 7 show the distribution of known “wild apple” verified by DNA analysis using data from this project; and is the first map that overcomes difficulties of identification, showing only genuine wild apple (mainly natural origin, some planted).

The three maps have several common features i.e. that wild apple:

- has strongholds in Loch Lomond, Trossachs and Perthshire, Dumfries and Galloway, Ayrshire, and parts of the Eastern Borders.

- is apparently largely absent in many parts of Deeside and Strathspey.
- appears oddly scarce, in much of Western Highlands, but not wholly absent here.

Figure 7 suggests that wild apple is less common in the Central Belt and in lowland agricultural areas in Angus, Aberdeenshire and Moray than previous distribution maps.

The incidence of wild apple reduces markedly on acid lithology such as Moine and granites, in the same way as for elm and ash. However occasionally wild apple trees are recorded on acid geology on favourable sites e.g. several large trees at the western end of Loch Rannoch. Only low numbers of trees were located in the western Highlands. Possibly the most interesting location at which wild apple was found in the west was on the valley slopes above Dundonnell, near Ullapool, where 7 apparently self-set trees occur in ancient woodland and wood pasture. These were only recorded because the estate owner and gardener had a special interest in the trees, and these would otherwise not have been picked up in this survey. There had been botanical surveys on the estate that had recorded these trees as early as 1923 (Rice D. *pers. comm*.). If wild apple occurs naturally as far west and north as Dundonnell, it is almost certainly present elsewhere in the Western Highlands; so the apparent lack of it here is probably due to insufficient surveying. There is also a cluster of wild apple located around Contin and Torrachility, which are currently the most northern records on the mainland.

Elevation

The highest elevations trees located were at about 300 m in both Scotland and northern England. The highest tree in the Lake District is at 305 m in Patterdale, on an exposed ridge (see figure 9); and this hybrid tree had grown to 10 m tall and over 70 cm stem diameter, had its top 8 m blown out, but was regrowing vigorously – suggesting that apple is capable of growing at higher elevations than this.

3.5 Climatic conditions

Wild apples and their hybrids occur in a very wide range of climatic conditions (see figure 8) i.e. in areas with:

- annual rainfall ranging between 600mm (Lothians) to over 3000 mm (Lake District);
- annual temperature ranging from over 1500 day degrees (lowland Dumfries and Galloway coast) to 1100 day degrees (Shetland) and down to 700-800 day-degrees on some upland sites.

Some of the finest woods for wild apple, with the highest densities of apple trees, were at Thorneythwaite, near Seatoller, Lake District, the UK's wettest location (annual rainfall 3550mm). This climatic envelope encompasses conditions found over virtually over all of Scotland below about 2-300 m and it can be concluded that climatic conditions are unlikely to limit the occurrence of wild apples anywhere in Scotland below this elevation. This suggests that the scarcity of apples on fertile sites in northern and western Scotland is more likely to be the result of land use history rather than site limitations. It should also be noted that a tree from a sea cliff on an uninhabited island in Shetland turned out to be a wild apple, illustrating particularly impressive climatic tolerance.

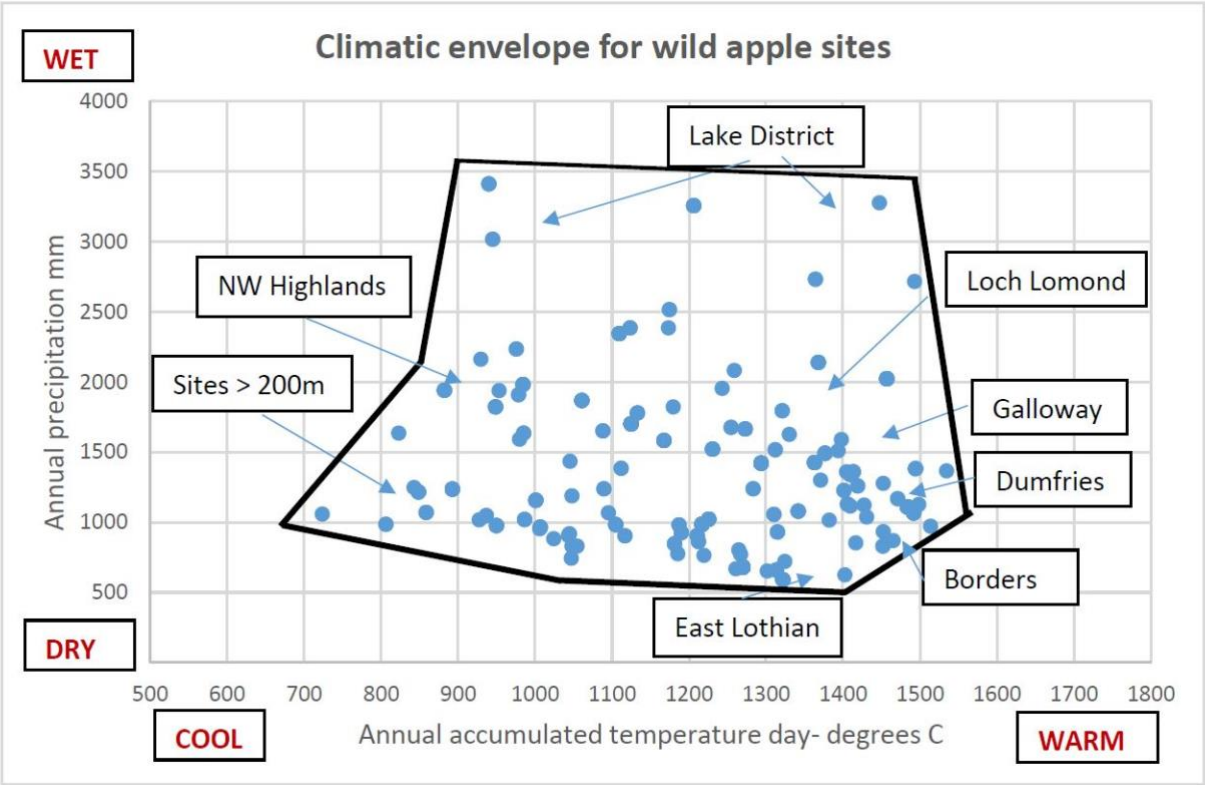

Figure 8 The climatic envelope of wild apple in Northern Britain in terms of annual temperature and precipitation.

3.6 Habitat and site characteristics

Table 2 shows the breakdown of broad habitats types in which wild and hybrid /feral domestic apples were recorded. Over the whole study area:

- wild apple is well represented in woodland (45% of occurrences), and wood pasture (37%);
- only 16% of wild apples occurred in hedges and pastures;
- in woodland, 87% of occurrences of wild apple were in native woodland and 76% were in ancient woodland.

The proportion of wild apples in ancient woodland was highest in Highland Scotland (44%), and lowest in Lowland Scotland (8%). So in Lowland Scotland where ancient woodland is scarce, most wild apples appear in hedges and pasture (58% of occurrences) and in recent woodland. Most of the wild apples in the Lake District were located in ancient wood pasture (75%) and are thought to be self-set. The occurrence of wild apples in ancient wood pasture was also high in the Southern Uplands (65%). This evidence confirms the view that there are two fairly distinct populations of wild apples i.e.

- A relatively large number of natural origin trees that are part of the natural composition of native woods (ancient and secondary) and wood pastures.
- A smaller number of planted trees in hedges and recent woodland.

The picture is rather different for hybrid and feral domestic apples (table 2). While most of these were still found in woodland (53% of occurrences), they were more commonly found in hedges, pasture and moorlands than wild apples (33% as opposed to 17%). It is interesting that we still found a few hybrid apples in ancient woodland (though only 11 trees in total). These have all the appearances of having arrived by natural means and as a result of natural hybridization (rather than being planted stock); but we will never know their origins for certain.

Table 2 The frequency of wild apples and hybrid/domestic apples in different broad habitats and regions. Note that for hybrid / feral domestic apples, sample numbers for individual regions are too low to draw conclusions.

	PERCENTAGE OF TREES IN DIFFERENT HABITATS					
	Wild apple					
HABITAT	**Highland Scotland**	**Southern uplands**	**Lowland Scotland**	**Lake District**	**Total**	**Total no. of samples**
Ancient Woodland	44	31	8	0	**34**	*56*
Other native woodland	5	4	8	0	**5**	*9*
Non-native (mixed) woodland	6	4	25	0	**6**	*10*
ALL WOODLAND	55	39	41	0	**45**	*70*
Wood pasture	29	65	0	75	**37**	*61*
Hedges, pasture, moorland	14	8	58	25	**16**	*28*
Other	3	0	0	0	**2**	*3*
TOTAL	**100**	**100**	**100**	**100**	**100**	***158***
	PERCENTAGE OF TREES IN DIFFERENT HABITATS					
	Hybrid and feral domestic apples					
HABITAT	**Highland Scotland**	**Southern uplands**	**Lowland Scotland**	**Lake District**	**Total**	**Total no. of samples**
Ancient Woodland	49	20	0	20	**26**	*11*
Other native woodland	6	0	21	0	**10**	*4*
Non-native woodland	12	0	36	0	**17**	*7*
ALL WOODLAND	67	20	57	20	**53**	*20*
Wood pasture	0	60	0	60	**14**	*6*
Hedges, pasture, moorland	33	20	43	20	**33**	*14*
Other						
TOTAL	**100**	**100**	**100**	**100**	**100**	***40***

Again there appear to be 2 populations of hybrid/feral apples:

- Planted trees in lowland hedges, pastures and recent woodland, which are the result of either seed having been collected in the wild from hybrid populations; or of breeding by horticultural nurseries (deliberate or accidental).
- A small number of natural origin hybrid trees in native woodland which have presumably arrived as the result of introgression of domestic genes into wild populations.

Figure 9 The highest wild apple located at 300m in Patterdale, Lake District. It has had its top 8 m blown out, but is regrowing vigorously.

Figure 10 The most north-western wild apple tree recorded in Scotland, at 200m elevation near Dundonnell, south of Ullapool.

A significant proportion of wild apples were found in upland gulleys and riparian woodlands, which may simply reflect that this is where remnant native woodland is most common, or may indicate an ecological preference. There is an interesting and quite large population at high water mark on the islands and shoreline of Loch Lomond and we assume these have spread via floating apples. These lochshore trees seem to be able to thrive in a surprisingly wide variety of soils including wet sand and gravel, rock crevices, bog myrtle mires and deep alluvial gleys and brown earths. We have also observed apples floating down watercourses, so water may be one dispersal method.

Wild apples are reported in the European literature as growing only in open conditions such as woodland edges and hedges; and this is interpreted as the species being intolerant of shade (e.g. Stephan 2003). In this survey we found several trees in far more shaded conditions including a few growing, and fruiting, in partial understory under oak. The species in Scotland is probably more shade tolerant than the literature suggests.

Wild apple in wood pasture

Wild apple is also strongly represented in wood pasture (37% of records); this being particularly obvious in southern Scotland and the Lake District; but also occurring elsewhere, as far north as Dundonnell, Inverness-shire. It is in ancient wood pasture that wild apples reach their highest densities, with up to 10 mature trees per hectare. In spring, these trees constitute a very unexpected and attractive feature (see figures 12). There is reason to believe that the pasturage of cattle in these woods, which continues to this day in some, is beneficial to recruitment of apple regeneration. This probably explains the striking frequency of wild apple in places like Galloway which have a particularly strong history of upland cattle farming.

Woodland communities and associated tree and plant species

Wild apples occurred in oakwoods, birch woods, ash woods and wet alder woodland, showing quite high ecological tolerances (see table 3). They are however most common in oak-birch woodland.

Table 3 Occurrence of wild apple in different woodland types

NVC Woodland type	**NVC type**	**Proportion of records**
Oak-birch woodland	Mainly W11, some W10	59%
Ash woodland	W9	23%
Alder wet woodland	W7	18%
		100%

The tree and shrub species growing in the immediate proximity of wild apple trees reflect the main woodland types i.e. oak, birch ash and alder (table 4). The high incidence of hawthorn is eye-catching; the species being one of the most common associates in wood pasture, and raises the question as to whether regeneration conditions that favour wild apple also favour hawthorn.

Table 4 Occurrence of native trees and shrubs growing in vicinity of wild apple

Tree species	**Proportion of locations with species (%)**	**Shrub species**	**Proportion of locations with species (%)**
Oak	17	Hawthorn	18
Birch	16	Hazel	9
Ash	12	Willow	3
Alder	9	Blackthorn	2
Rowan	5	Dog Rose	2
Holly	5	Juniper	1

Table 2 The frequency of wild apples and hybrid/domestic apples in different broad habitats and regions. Note that for hybrid / feral domestic apples, sample numbers for individual regions are too low to draw conclusions.

	PERCENTAGE OF TREES IN DIFFERENT HABITATS					
	Wild apple					
HABITAT	**Highland Scotland**	**Southern uplands**	**Lowland Scotland**	**Lake District**	**Total**	**Total no. of samples**
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Non-native (mixed) woodland	6	4	25	0	**6**	*10*
ALL WOODLAND	55	39	41	0	**45**	*70*
Wood pasture	29	65	0	75	**37**	*61*
Hedges, pasture, moorland	14	8	58	25	**16**	*28*
Other	3	0	0	0	**2**	*3*
TOTAL	**100**	**100**	**100**	**100**	**100**	***158***
	PERCENTAGE OF TREES IN DIFFERENT HABITATS					
	Hybrid and feral domestic apples					
HABITAT	**Highland Scotland**	**Southern uplands**	**Lowland Scotland**	**Lake District**	**Total**	**Total no. of samples**
Ancient Woodland	49	20	0	20	**26**	*11*
Other native woodland	6	0	21	0	**10**	*4*
Non-native woodland	12	0	36	0	**17**	*7*
ALL WOODLAND	67	20	57	20	**53**	*20*
Wood pasture	0	60	0	60	**14**	*6*
Hedges, pasture, moorland	33	20	43	20	**33**	*14*
Other						
TOTAL	**100**	**100**	**100**	**100**	**100**	***40***

Figure 11 Examples of wild apple trees at the shoreline on the Loch Lomond islands, growing in shingle, rock, and sand.

About 40 ground flora species were recorded growing with wild apples trees. The most common associated species were bracken, bluebell, wood sorrel, broom and woodsage (all indicators of oak-birch woodland); wood avens and dogs mercury (indicators of ash woodland); and creeping buttercup and rushes (indicators of alder wet woodland). Ancient woodland indicator species were well represented. Epiphytic lichen and moss communities on apple bark appear to be acidic in nature and not particularly diverse. Old horizontal branches sometimes host luxurious moss carpets, sometimes including common polypody ferns.

3.7 Tree dimensions and structure

Wild apples are rather more substantial trees than suggested in the literature, with an *average* stem diameter of 52 cm (at ground level), and a maximum diameter of 120 cm (see table 5). Eleven of the 127 wild apple trees sampled had stem diameters over 90 cm. This is very different to some published accounts; for example Stephan et al (2003) suggest a *maximum* stem diameter of 45 cm. Mean height was 8 m, with a maximum of 14 m; well in excess of the value of 10m which is generally quoted. Average crown diameter was 8 m, with a maximum of 17 m (which is the tree in figure 1c). So we need to revise our mental picture of mature wild apple trees from small trees, to something more the size of wild cherry trees.

Figure 12 Wild apple and oak in ancient wood pasture near St. Johns Town of Dalry, Galloway.

The hybrid apples in this survey were rather smaller than the wild apple trees, but we suspect this is not a biological reality but is an outcome of sampling. A higher proportion of hybrid trees were younger, smaller planted trees, whereas wild apples were larger older self-set trees. Apples coppice and pollard very easily. Our sample include 14 apparent pollard trees (see figure 13), and in the Lake District we found signs of relatively recent pollard cutting.

Table 5 Size of wild and hybrid apple trees

		Stem diameter at ground level (cm)[1]	Tree height (m)	Crown diameter (m)	Number in sample
Wild apple M. sylvestris	**Min**	**6**	**2**	**2**	**134**
	Max	**120**	**14**	**17**	
	Mean	**52**	**8**	**8**	
Hybrid apple M. sylvestris× domestica	**Min**	**10**	**2**	**2**	**31**
	Max	**101**	**11**	**13**	
	Mean	**44**	**6**	**6**	

[1] Diameter was measured at ground level because of the complex branching structure of many stems. The diameter estimates for multi-stemmed trees was done by summing the individual stems, and converting to an equivalent diameter.

Figure 13 Pollard wild apple tree at Loch Katrine

3.8 Identifying wild apples trees

One problem that has become apparent is that most foresters and ecologists are not looking out for wild apples, and are not good a recognizing them when they see them. The first challenge is distinguishing apples from other tree species. Apples trees are actually fairly distinctive, both close up and when viewed at distance. Key characteristics that help in recognizing them are: they have very dense complex crowns (rather like large hawthorns or blackthorns and far more dense than garden apples); the upper crown often has a somewhat irregular appearance, with sparse straggly individual twigs often emerging; the crown in winter has a distinctive dark slate-grey colour. When in flower (mid-late May) they can be spotted at distance by the pink (turning pale pink to white) flowers, which come out a week or so before hawthorn (but once both are in flower they are hard to distinguish at distance).

Figure 14 An open grown wild apple showing the dense complex crown similar to the nearby hawthorns, but larger and coming out into flower earlier

Figure 15 The typical dark slate-grey winter colour of a wild apple, with its dense crown, in contrast to nearby birches and ash.

The second challenge is differentiating wild apple from domestic and hybrid apples. Most studies have concluded that it is not possible to distinguish wild apple from hybrid apples without error using morphology alone; and this project came to the same conclusion. In this study 70% of trees were correctly identified in the field using morphological characteristics. It should be noted that the authors were attempting this with little prior knowledge or experience and we became more skilled as time progressed. Our results provide some guidance on how recognition of wild apple can be improved.

Wild apples are far more likely to have hairless lower leaf surfaces than hybrid or domestic apples, and this feature is used a diagnostic in many floras (e.g. Stace 2010). Wild apple leaves look superficially like the leaves of domestic apples, but are smaller, shinier and stiffer; and lack the dense downy hairs on the leaf underside (see fig 13). Leaf size was measured in a small in a subset of trees (the largest leaf in a typical whorl): for wild apples the average length (petiole plus blade) was 84mm (min 56, max 116), whereas for domestic apples the mean length was 125 mm (min 113, max 140) (see figure 16). Leaves are held in whorls (except on current year long shoots), with leaf size and shape varying hugely within individual whorls. The underside of leaves appear to be rather hairier in current years shoots compared with older growth; and this should be taken into account in assessing hairiness (best to use older growth from lower down the tree).

The association between leaf hairiness and species is far from perfect. Table 6 shows the leaf hairiness score (viewed carefully using a hand lens) recorded in the field, and the corresponding identification to species using the DNA markers. For trees with a leaf hairiness score of 0 (no hairs – see table 1), 84% turned out to be wild apple, meaning that this gives the correct identification 84% of the time (approximately 5 out of 6). For trees with a leaf hairiness score of 1 this drops to 75% (3 out of 4 trees). Trees with leaf hairiness scores of 2 and 3 (partly hairy), which one might assume were mainly hybrids, were in fact more often wild apples; and the diagnosis of hybrid apple was only correct 42% and 28% of the time. Things get better again with trees with a leaf hairiness score of 4, which were correctly assigned to hybrids 80% of the time; but even amongst the 5 “hairy” trees surveyed, one turned out to be a wild apple (Craig Farm, Galloway). Overall if one had used only leaf hairiness for distinguishing wild apples from hybrids (i.e. leaf hairiness 0 and 1 = wild apple, leaf hairiness 2,3 and 4 = hybrid), the diagnosis would be right 70% of the time.

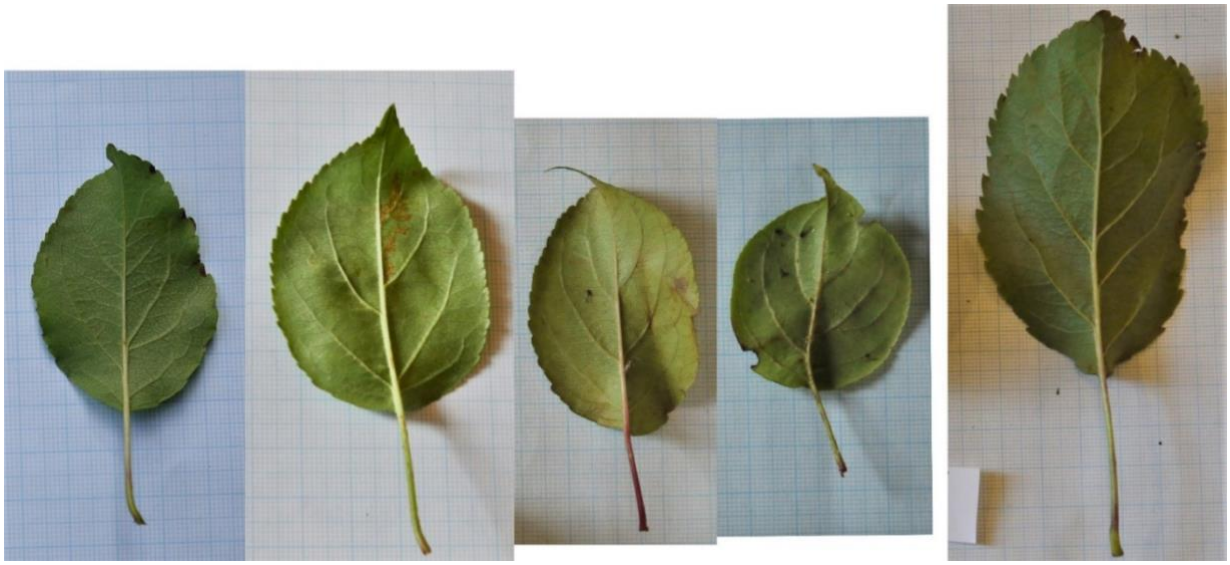

Figure 16 Leaves of wild apple (4 left hand pictures), with leaves chosen as the largest in a typical whorl on older short shoots; and a leaf from a feral domestic apple (right hand picture)

In reality leaf hairiness can help distinguish wild apples and feral domestic apples, but does not help with the identification of hybrids because of the overlap in characteristics between wild and hybrid apples. It should be born in mind that the assessment of leaf hairiness was done across all times of year, and only on a sample of 1-3 leaves; and if done more carefully might have yielded better results.

Table 6 Identification to species by leaf hairiness. Trees with score of 0 and 1 were assigned to wild apples, scores of 2, 3 and 4 to hybrids apples.

Leaf hairiness score (as per table 1)	**Species ID via DNA markers (numbers of trees)**		**Sample size**	**% correctly identified**
	Wild apple	**Hybrid apple**	**Total**	
0	81	16	97	84
1	50	16	66	76
2	20	15	35	43
3	13	5	18	28
4	1	4	5	80

Fortunately it is possible to make good informed field judgements to identify the more obvious wild apples and domestic apples. This requires multiple characteristics to be used; the most useful appearing to be hairiness of lower leaf, leaf size and stiffness, and crown density/complexity (see table 7). Using all these features together should be a fairly reliable way of identifying wild apples with “typical” characteristics, which is the majority. Other potentially useful specialist characteristics mentioned in the literature but not evaluated here are: wild apples have smaller diameter shoots; pointed smooth and largely hairless buds in winter; and the flower buds only have hairs on the edges of their scales (Mitchell 1992).

Table 7 Field characteristics for differentiating wild apple from feral domestic apple

CHARACTERISTIC	WILD APPLE	FERAL DOMESTIC APPLE
HAIRINESS OF LOWER LEAF WHEN VIEWED BY HAND LENS	Score = 0 Both petiole and lower leaf surface without hairs, or only a few sparse hairs on petiole and leaf margin at very base. Hairs stiff and spaced out. Score = 1 Some hairs, generally sparse, on petiole, lowest parts of midrib (typically lower 20% of blade length) and lower lateral veins near leaf base. None on leaf blade surface. Hairs generally stiff and spaced out	Score = 4 Petiole, veins and leaf surface largely covered with felted hairs. Hairs thin, downy, and frequent.
LEAF CHARACTERISTICS	Leaves are typically smaller than domestic apples i.e. petiole plus blade of largest leaves in typical whorl in July-October less than 100 mm. Leaves stiff, somewhat shiny on both surfaces.	Leaves larger, i.e. petiole plus blade of largest leaves in typical whorl in July-October <more 100 mm. Leaves softer and often matt.
CROWN	Densely branched, tangled, especially when mature.	Crown is more "see through", less complex and with some straighter branches.
APPLES	Small, less than 35 mm in diameter when mature horizontally when mature and often less than 30 mm; usually green, green-yellow, occasionally with red tinges (latter may be horticultural cultivars)	Large (typically >40 mm when mature); variable colours but often with some red colouration.

3.9 Flowering and fruiting

Both wild and hybrid apple trees flower and fruit regularly and profusely. In the two fieldwork seasons of this project, 84% of wild apples and 92% of hybrid / feral domestic apples were recorded as flowering or fruiting; though it is not possible to say how typical these years were. In this respect apples are like other regularly flowering trees in the *Rosaceae*, such as cherries and rowan; and different from many wind pollinated trees where flowering is more variable. Fruit is produced in significant quantities on most trees and represents a considerable annual investment of resources. The fall of apples is variable, with most trees dropping large quantities of fruit during the autumn (see figure 17), but others retaining apples in the crown during winter, and some very occasionally persisting into the following spring (see figure 18).

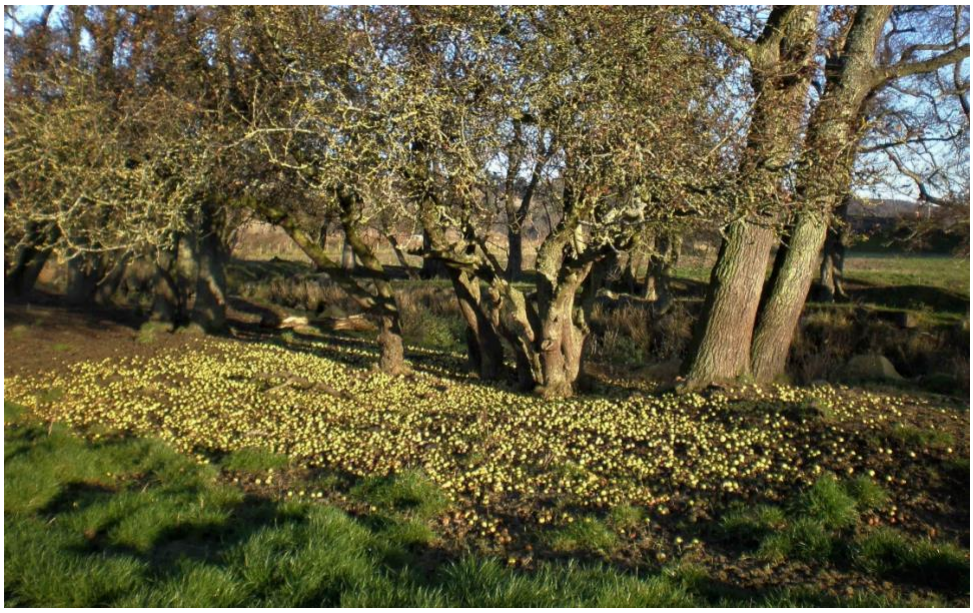

Figure 17 A heavy crop of fallen apples from a hybrid tree, Bridge of Earn (photo Andy Fairbairn)

Apples are insect pollinated, and much insect activity takes place around trees on still, sunny days during flowering in mid- late May, with bees being prominent, but also hoverflies, flies and occasionally beetles also present.

Figure 18 Previous years apples retained until next flowering season, Patterdale, Lake District

Apple size

Apples from wild apple trees are smaller than those of hybrid apples; on average wild apples are 28 mm in diameter, as opposed to 32 mm for hybrid apples (see table 8).

Table 8 Fruit size

SPECIES		**Mean fruit size (mm)**	**Total range in size**	**Number in sample**
Wild apple ***M. sylvestris***	Min	25	19	**59**
	Mean	**28**		
	Max	31	45	
Hybrid apple ***M. sylvestris× domestica***	Min	27	21	**25**
	Mean	**32**		
	Max	33	50	

There is considerable overlap between the fruit sizes of true and hybrid wild apple, which makes it difficult to use apple size as a means of telling the two species apart. However it is still possible to use apple size as a factor alongside others to help distinguish wild apples – if apple size is consistently below about 30 mm, this is useful supplementary evidence to support a identification of wild apple, and the smaller the apples the more likely it is to be wild apple; and if it is consistently above about 32 mm this is evidence for a hybrid tree.

3.10 Germination and regeneration

Seeds germinate readily. Seedlots from 36 parent trees were planted in compost in a seed tray and left outdoors over winter; and 40% of the seedlots germinated in the first spring, and the other 53% germinated

the following spring. Only 2 seedlots (7%) failed to germinate. Several seedlots produced seedlings both years. Far more seedlings germinated the second spring (75%), as opposed to the first spring (25%). Seedlings grew with recognisable leaves for the first season, but from 2 years onwards leaf size reduced until the plants looked more like blackthorn, including spines.

Naturally regenerated saplings are occasionally found; and the best examples are in areas of wood pasture where there is a history of pasturage of cattle. Older wild apple seedlings look rather like blackthorn (figure 19); and this adds to the challenge of finding it.

Figure 19 Left: A large seedling of wild apple showing blackthorn-like appearance; Right: A sapling, showing blackthorn-like lower crown and apple-like upper crown.

3.11 Tree age

Most trees, both wild and hybrid, were typically fairly old. By doing ring counts cutting sections of lower branches of a small sample of trees we estimate that most wild and hybrid trees were about 60-120 years old. This would date their establishment to the late 19th to mid 20th centuries, when many native woods expanded as a result of agricultural abandonment during economic depressions, or deliberate protection as forestry practice developed. A large proportion of older trees had many "veteran" characteristics. There appeared to be few very old trees and some large trees turned out to be younger than they first appeared.

3.12 A hardy tree

The vast majority of the trees surveyed were in very good health. They appear to be incredibly resilient. They blow over and resprout freely as 'phoenix trees'; about 20% of mature trees were phoenix trees, making wild apple one of the most adept species at this growth form. A sizeable proportion of the oldest trees grow hollow then collapse, but then get a second wind and start growing again as phoenix trees. Broken limbs will live on and recover provided they are connected to the main stem by the thinnest strip of bark. We have only found two tree apparently affected by disease.

Figure 20 Old trees often split as a result of a hollow stem and/or a codominant fork, but the fallen parts of trees usually completely recover and grow on as phoenix trees.

Figure 21 A tree recovering from having become hollow and collapsed. Like all phoenix trees they are susceptible to being killed by browsing after collapse and this probably happened to the right-hand part of this tree.

4. Discussion

This report highlights four main issues:

- Wild apple is one of our most characterful native trees, and one which is poorly understood and under-appreciated. Wild apple has potential as a spectacular landscape tree, as a prolific producer of a "non-wood forest product" and as an important species for threatened pollinator insects.
- Widespread hybridization between wild apples and domestic apples has been taking place, especially in lowland areas where domestic apples are common.
- We need to better understand ecological place and value of wild apple in our ancient woods and wood pastures.
- The current generation of wild apples is quite old, natural regeneration is apparently scarce and so we need to establish a new generation in our woods and wood pastures.

We have made good progress in the last few decades increasing our understanding of Scotland's rather limited palette of native trees and shrubs. This has involved a seemingly haphazard process whereby selected species received particular attention: first Scots pine and oak, then birch staring in the 1980s, followed by aspen, juniper and latterly our montane willows. Some species have missed the spotlight altogether, and none more so than wild apple. We suggest that foresters and ecologists need to revise our view of the tree, and set about sorting some of the issues that have accompanied our collective neglect.

Firstly we suggest that we adopt the name "wild apple" to differentiate the native *Malus sylvestris* from the miscellany of other trees that go by the name "crab apple"; so as we all know what we are talking about. The term "crab apple" is designed to confuse, because it sweeps up all sorts of apples with small fruits and confusing parentage, many of which have nothing to do with *M. sylvestris*. For example, the hugely popular garden crab apple Malus "Evereste" turns out to be cross between *Malus domestica* 'Rome Beauty' x *Malus floribunda* clone 821 (Decourtye 1977). The least we can do is to use a name that establishes clear water between our native tree and everything else.

4.1 Hybridisation

The next big issue is to publicise the ongoing hybridization (more correctly introgression) between wild apple and domestic apples. Imagine the furore there would be if we had discovered that Scots pine had been unobtrusively hybridizing, and now over a quarter of Scots pine in Scotland were in fact hybrids. That is more or less the situation with wild apple. This introgression comes about because there are no reproductive barriers between apples species, whilst at the same time they have strongly self-incompatible reproductive systems that favour outcrossing; and because of the widespread cultivation of apples (Cornille et al., 2015). It is good conservation practice to ensure that we hold on to our best pure populations of wild apple. We therefore need to be careful what we plant in the future where the intention is to plant wild apple. There is a need for forest nurseries and seed suppliers who claim to sell *M. sylvestris*, to ensure that they have grown the right thing, and not a mix of wild apple and hybrids, which we suspect to be the case currently. The route to this is straightforward. Nurseries should DNA test samples of their existing stock and in the light of the results, reconsider their seed sources. This is potentially important because a recent study in France showed that all commercially available seed there (and including a small sample from the UK) showed high levels of hybridization (Fuertey et al 2017). In the short term, seed collections could easily be arranged from wild apple populations shown to be more or less pure *M. sylvestris* by this project. Then seed orchards need to be established using genuine wild apples parents from across Scotland and located reasonably far away from cultivated apples. This could be is a cheap process and would start to yield seed fairly quickly. For owners who are less concerned about the species they are growing, say for hedging, hybrid apples might be acceptable; but again nurseries and their clients need to be informed about exactly what they are trading. Hybrid apples are interesting and characterful trees too, and there are no obvious signs of them being poorly adapted (Fuertey et al 2017), nor being poorer hosts to wildlife. So we can be relaxed about their presence in

certain circumstances i.e. where they are already common and in regions isolated from populations of wild apple.

Hybridisation requires insects to carry pollen to and fro between wild apples trees and domestic ones. Most of the hybrid trees are the result of a multistage process ("backcrosses to wild apple"). Firstly an F1 hybrid is formed when a wild and domestic apple tree cross; then this tree crosses with another wild apple to produce the backcross. Obviously many variants of this process can develop over multiple generations; and the long history of domestic apples in Scotland has created ample opportunities for this happen. One important aspect of this process hinges on the proximity of apples trees to each other, and how far a bee or other insect might be inclined to fly during pollination. A few studies have investigated this, and show that the *maximum* distance can vary considerably from as short as 300 m (Larsen & Kjær 2009) to as far as 4 km (Feurtey et al. 2017) and occasionally (presumably a windy day or a confused bee!) even 11 km (Reim et al. 2015). However where apple trees grow close together most pollination events are short distance, for example Feurtey et al. (2017) reported that 75% occurred at distances of less than 100 m and 25% below 15 m; and only about 5% of the pollination events occurred between trees more than 1 km apart. The number of hybridization events increased as the distance between wild apple trees increased, because pollinators then need to fly larger distances, which presumably increases the chance of encountering domesticated apple trees. What this tells us is that in upland areas with fewer domestic/hybrid apples and a reasonable number of wild apples (Galloway, Loch Lomond/Trossachs, Highland Perthshire) hybridization is likely to be proceeding only slowly because the pollinating insects will rarely encounter domestic or hybrid apples on their journeys. These populations should therefore be of priority for conservation action in order to safeguard *M. sylvestris* as a species; and these would also make good seed sources. However in lowland areas with more hybrids and domestic apples, hybridization will be proceeding faster and these should not be used as seed sources.

4.2 A new generation of wild apple trees

The current generation of wild apple in native woodland appear to be mainly 60-120 years old, and regeneration appears scarce. So more basic fieldwork needs to be done to evaluate the occurrence of regeneration; starting in wood pasture with frequent wild apple trees. We suggest searching for regenerating apples and protecting these if you are lucky enough to find any; otherwise planting a few to perpetuate the species.

4.3 Seed dispersal and an association between apples and animals

Association between cattle and wild apple regeneration has been reported from Denmark, with cattle and horses both eating and dispersing the seeds and providing germination sites in dung (Buttenschøn and Buttenschøn 1998). Seeds pass unscathed through the animals and the poaching of ground can create good regeneration conditions. In a study in Denmark, over 90% of wild apple seedlings we found to have grown in cow pats (Buttenschøn and Buttenschøn 1998), suggesting an almost obligate relationship. Wild boar and bears are reported as eating and dispersing wild apples; as have birds like blackbirds and thrushes. This points to important ecological associations between wild apple and some of our now extinct large mammals, especially auroch, which might partly explain the contemporary lack of regeneration. Fortunately it appears that modern cattle are helping to fulfil the role as regeneration agent is upland wood pastures; though the historic switch from cattle to intensive sheep rearing has almost certainly been detrimental to wild apple. The fact that hawthorns is such a frequent co-associate with wild apple (see table 4) suggests that both species benefit from similar regeneration conditions.

The dispersal of apples by water, is implicated by the population of trees at high water mark on the islands of Loch Lomond. We also observed apples dispersing down watercourses, and wonder if this is linked to their occurrence in upland gulley woodlands.

4.4 Conservation status and ecological value

Wild apple is regarded as threatened in several European countries (IUCN 2011), though IUCN's overall assessment for Europe is that the species is "data deficient". The lack of understanding of its distribution in

Scotland reported in the paper is a good example of that data deficiency. The main threat reported by IUCN is that of hybridization, though threats from woodland management are also mentioned. The main conservation requirement is research to determine the effect of hybridization and efforts to establish *ex situ* conservation collections.

Wild apple is a relatively rare tree in most (but not all) woods we encountered. It hits the sweet spot between being common enough to be ecologically meaningful and rare enough to be notable when you find one (rather like aspen). As with other rare plants it is hard to figure out why it should be rare; especially given its prolific fruiting. When collecting seed for the germination studies there was some evidence that isolated trees produced fewer apples, and those apples had fewer seeds in them, suggesting that isolation inhibits pollination and therefore seeding. This could be a mechanism contributing to the apparent scarcity in areas like the Western Highlands, where it is possible that land use pressures led to the reduction of woodland cover to the point that pollination distances became so large that this contributed to regeneration failure.
Their most obvious ecological value would appear to be the prolific flowering as a source of pollen and nectar for pollinating insects; so this is a species to promote in the context of our threatened pollinators. The status of apples as food for animals points mainly in the direction of animals now extinct in the Scotland; wild boar, bears and wild cattle / auroach; and highlight the difficulties of properly managing wild apple with these animals missing. The useful association between cattle and wild apple hinted at in this study suggests that controlled cattle grazing may be a key for establishing regeneration.

Wild apple is recorded as having quite a high number of associated invertebrates i.e. 93 species and 7th out of 30 tree and shrub species listed (http://www.countrysideinfo.co.uk/woodland_manage/tree_value.htm). There appears to be little easily available information on the species of mammals, bird and epiphytic plant associated with wild apple and more research of this would clearly be useful.

4.5 Landscape value

Wild apple trees are almost without exception characterful and impressive; and a veteran wild apple at flowering time is as spectacular as it comes (fig 22). This is equally true of many of the older hybrid apples we found too. Planted singly or in small clumps at the edges of woods or near clearings, or in wood pasture, wild apple gives outstanding value.

Figure 22 A wild apple in flower in Borrowdale, Lake District

4.6 History, uses and cultural associations

Wild apple appears to have been a fruit that was used by people for millennia, but evidence is scarce. Its pollen cannot easily be distinguished from some other trees of the *Rosaeceae* in historical pollen studies. It is listed from sediments in Yorkshire from 10,500 years ago, and it is recorded as burnt timber or food remains from the late Neolithic and early bronze age from a few sites in Scotland, and rather more in England (Dickson and Dickson 2000). Twenty-one fragments of wild apple (seeds and fruit parts) were recorded at a Mesolithic site on Colonsay (along with 30,000 to 40,000 hazel nuts). During the Neolithic, fruits have been found halved and quartered, then dried for later consumption in lakeside villages in Switzerland and Italy (Dickson and Dickson 2000). Fifty four wild apples were found in a bucket in a viking ship in Norway dating from 820, suggesting considerable status as food[2] in the dark ages. It is easy to store and increases in palatability as time progresses. There is an intriguing references to wild apples in the medieval period, from the town of Egremont in Cumbria, where a "crab fair" was first held in 1267 and continues to the present. There are written accounts from Scotland and Norway from 1500-1780 of wild apples being used for juice and vinegar[3]. Whether use of wild apples was casual, or involved cultivation is unknown. In this survey we found evidence that wild apple is a common component of wood pastures; and we wondered if this was a sign of it being favoured as a tree for pollarding for winter feed. We also looked for evidence of wild apples being planted close to old farms as has historically been the case with wild cherry, rowan and sycamore; but it was conspicuously absent. Presumably its place was gradually taken by domestic apple grown in orchards and gardens; with orchards known to have been present in Scotland as early as 1100 (Roberston 2007, Hayes 2016). Recent inventories of historical orchards in Scotland suggest they were fairly extensive, with about 1800 recorded across Scotland at the time of the first ordnance survey maps, covering some 700 hectares. So wild and domestic apple have both been present for at least 1000 years.

In modern times "crab apple" has maintained a tenuous place in the public consciousness because of its use as a means of setting jams and making crab apple jellies; and this makes apples one of the more useful "non-timber forest products". It is still used as an effective pollinator of domestic apples in both orchards and gardens; and the myriad cultivars of foreign crab apple are popular as decorative garden trees. It also appears in mixes for hedging. Wild apple can clearly be of use in the future in efforts to help support our populations of threatened pollinator insects (e.g. Scottish Government 2017). In Europe it is considered a "noble hardwood" capable of small scale production of decorative timber. Although that is a distant prospect in Scotland, it would be useful if foresters were more widely aware that an apple log might be a saleable item.

Wild apple suffers from an "image problem". The common name, "crab apple" and its colloquial equivalent "scroggie", derives from words meaning small, untidy and scrubby. It genus name *Malus*, means "evil-one" - think of mal-words like *malformed, malice, malaria* and *dismal;* because the apple was the evil fruit that tempted Eve and led to mankind's expulsion from the Garden of Eden; with the apple appearing in some Christian art as a symbol for sin. On the other hand apples have several positive cultural connotations; for example the term "apple of my eye" is of biblical origin; the apple is sacred in Norse mythology and has featured in several cultures a symbol of fertility and good luck. The apple fruit as an image is universally known and obviously appealing; think of Newton's apple, New York as "The Big Apple", Apple the recording label and nowadays of course, the Apple Iphone. It shouldn't be a hard sell, therefore to reinstate our wild apple as a tree foresters, ecologists and the wider public value, appreciate and work to look after.

5. Recommendations

Rehabilitating the wild apple as a more prominent and valued member of Scotland's native trees and woods will take a little deliberate effort on all our parts. So where next ? The priorities are as follows:

[3] http://consideratecandidum.com/villepler/historikk_og_bruk.html

1. Our professional and popular literature on native woodland should feature wild apple with the same prominence as other tree species.
2. The main populations of more or less pure wild apple in native woodland and wood pasture should be catalogued, and owners, managers and agencies made aware of their existence and value. These areas will include Loch Lomond / Trossachs, Galloway, Highland Perthshire and the Lake District, as well as smaller areas further north and west. It would be useful to continue searching for wild apple in western Scotland to complete our inventory of the species.
3. In areas with frequent wild apple, owners should be encouraged to establish a new generation of trees by protecting existing saplings wherever they can be found; and by planting small numbers of genuine wild apple. Planting of other apple species in the wild should only take place with good reason.
4. Elsewhere across Scotland, small admixtures of wild apple should be planted as part of new native broadleaved woodland on suitable sites, with trees numbering in the tens at most, and planted as a component of shrub areas, in clearings and on woodland edges.
5. Seed collections from known more or less pure populations should be encouraged and seed orchards set up using known wild apple parents from across Scotland for Regions of Provenance 10 and 20. Nurseries wishing to sell hybrid apples should label and market them accordingly and make customers aware of the differing conservation value of wild and hybrid apples.
6. Research needs to be undertaken to clarify the invertebrate, plant and fungal associates of wild apple, its regeneration biology and its adaptive genetic variation.

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