



Image: Tretyakavo Valley, Kunashir Island

Tough Magnolias for tomorrow's urban forests: finding genotypes that will weather climate change in Northern Europe

A report on expeditions to Japan and Russia in 2018

Harry Watkins
University of Sheffield
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PhD supervisors

Professor James Hitchmough
Dr Ross Cameron
Dr Henrik Sjoman

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Research aims and context

We carried out two expeditions in 2018 to Japan and Russia to investigate wild populations of Magnolias and assess the range in functional traits that are displayed within different ecotypes. The over-arching purpose of the expeditions was to

- a) Identify the range of ecological niches that tree Magnolias in Japan and Russia occupy
- b) Identify genotypes that may be hardier or better suited to horticulture and urban forestry in the UK under climate change than those that have already been introduced, and
- c) Develop a methodology for the rapid screening of genotypes that can be applied to other genera in other ecotypes in later studies.

The target species (*M. kobus*, *M. obovata* and *M. salicifolia*) were chosen for three reasons:

- Their introductions to European horticulture have been sporadic and represent isolated examples of their natural genetic range,
- Early research suggested that these species might offer unexplored opportunities for urban forestry under climate change and in particular, the new designed environments that landscape architects are developing as part of SuDS schemes, and
- They represent a range of ecological strategies and are distributed across a wide range of environmental habitats.

We studied plant traits and habitat information at sites across a range of latitudes and altitudes to establish relationships between genotypes and the ecological niches they inhabit. By selecting sites that are separated by wide distances as well as environmental barriers such as mountain ranges and water bodies, we ensured that each population would be genetically distinct. Reviewing the literature in January 2018 (Figs 1a-c), we noted the reported distribution of three Magnolia species and identified 8 target sites for preliminary evaluation, shown in Fig 2:

- Target site 1: Shiiba Research Station, University of Kyushu, Kyushu Island. *M. salicifolia* and *M. obovata* present.
- Target site 2: Aburayama Forest Reserve, Kyushu Island. *M. kobus*, *M. obovata* and *M. salicifolia* present.
- Target site 3: Kaisho Forest, Aichi Prefecture, Honshu Island. *M. obovata* and *M. salicifolia* present.
- Target site 4: Takayama River Basin Research Station, Gifu University, Gifu Prefecture, Honshu Island. *M. obovata* and *M. salicifolia* present.
- Target site 5: Ogawa Forest Reserve, Honshu Island. *M. kobus*, *M. obovata* and *M. salicifolia* present.
- Target site 6: Shirakami Mountain Range. *M. kobus*, *M. obovata* and *M. salicifolia* present.
- Target site 7: Ashoro Research Station, Kyushu University, Hokkaido Island. *M. kobus* and *M. obovata* present.
- Target site 8: Kunashir Nature Reserve, Kunashir Island. *M. obovata* present.



Figs 1a-c. The natural distribution of *M. kobus*, *M. obavata* and *M. salicifolia*. Images taken from www.gbif.org, although it should be noted that numerous sources cite *M. kobus* as occurring on Kyushu Island.

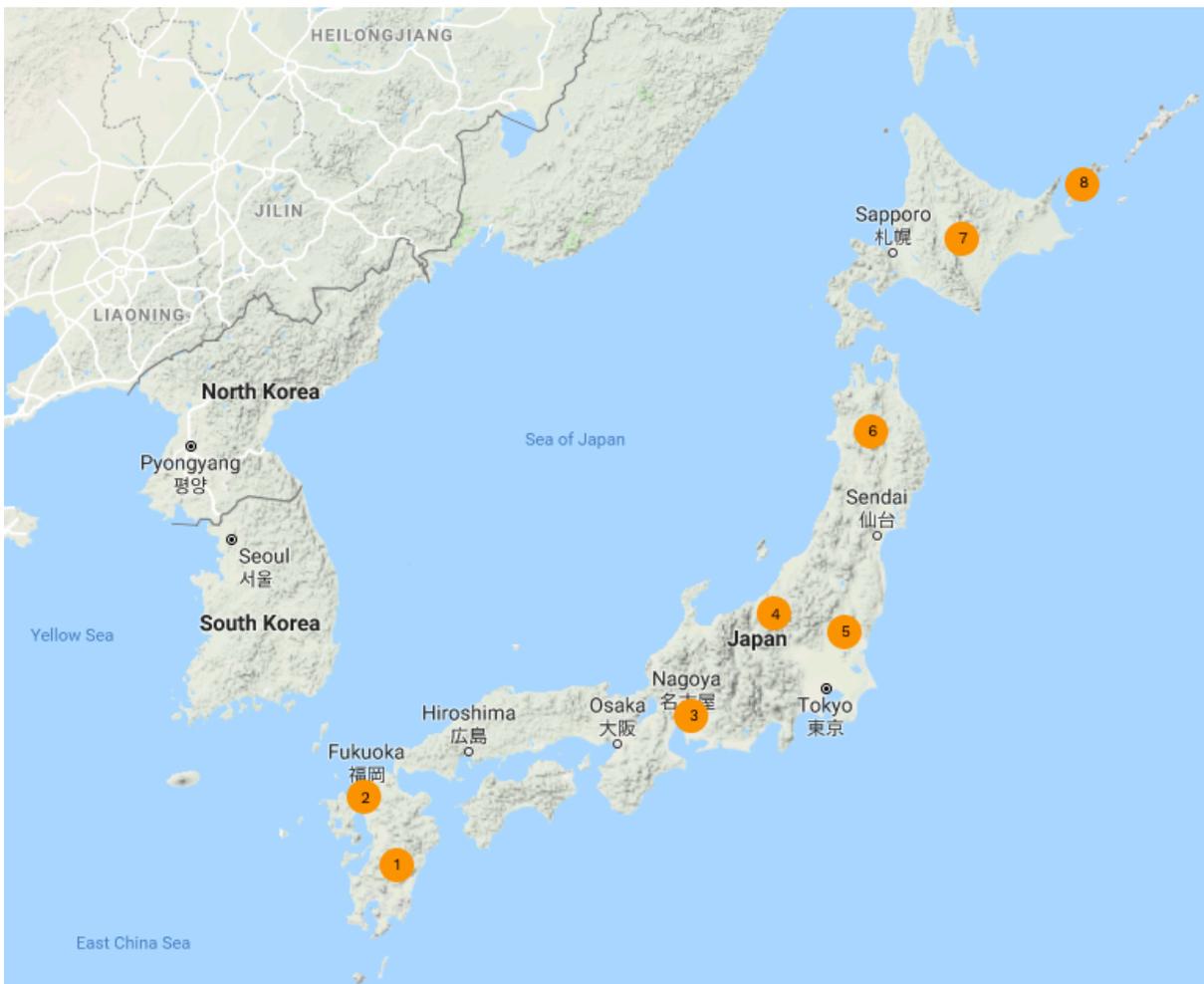


Fig 2. Study sites identified in January 2018

It should be emphasised that extensive research was carried out to identify target sites that were identified in other peer-reviewed studies, allowing us to compare the data we capture with data from other studies. In particular, we were interested in studying the populations of *M. obovata* that were recorded on Kunashir Island in Dr Polina Volkova's report to the Rufford Foundation (Volkova 2014). A well-used forestry tree in Japan, this population represents the most eastern and isolated gene pool of this species and has never been studied or introduced to UK horticulture. As such, it has promising potential for evaluation and may represent one of the hardiest populations of this species.

Having no connections with researchers in Japan, our objective on the first expedition was to establish links with botanic gardens and local teams, and then identify locations of wild-growing trees and record their locations with GPS, gathering baseline data on the habitat, allometry and condition of the candidate trees.

After this preliminary expedition, we reviewed the candidate trees and selected a small number for detailed assessment. During the first expedition, we noted that *M. kobus* occurred very rarely in our study sites- too rarely for robust sample sizes, whilst another interesting tree species frequently co-occurred with *M. obovata* and *M. salicifolia*, so we expanded the research project to include *Quercus mongolica* var. *grosseserrata* as it represents a different ecological strategy to the two Magnolia species.

During the second expedition we gathered detailed data for each tree, including:

- Specific Leaf Area,
- Leaf Dry Matter Content,
- Specific Stem Density,
- Vegetation structure, and
- Soil analysis (including slope gradient, oxygen availability, soil pH and soil texture)

This wide data set allowed for sophisticated statistical analysis of each suite of traits in order to test the wider hypotheses of the PhD.

Research questions

The core research question for the study is “How does climate affect functional strategies?”. It has long been hypothesised by Prof. Phil Grime (Grime 1977) that evolutionary processes select for three core strategies in plants and that these strategies should be affected by a range of climatic and environmental factors; this has been supported by recent research into model herbaceous plants (Vasseur et al. 2018; May et al. 2017) but has yet to be confirmed in woody plants. This research question was designed both to advance the status of ecological theory but also to apply these findings to recent guidance from the Forestry Commission in the UK that recommends that woody plant material in the UK should be selected from at least two degrees of latitude further south of the intended site for planting.

Key literature

This research was guided by some key texts:

- (Pierce et al. 2017), which describes a methodology for CSR ordination using soft traits
- (Albert et al. 2010), which examined intraspecific trait variability in relation to climate
- (Vasseur et al. 2018; May et al. 2017), which assessed CSR ordination along climate gradients in *Arabidopsis thaliana*
- (Grime & Pierce 2012; Mitchell & Bakker 2014), which argues that species functional strategies vary between phases of plant maturity
- (Chave et al. 2009), which demonstrates that wood density varies according to latitudinal gradients at a global scale

Methodology

Candidate sites were identified during desktop research and studied in reconnaissance fieldwork in April 2018 (Fig 2). At each site, a minimum of eight individuals of each species were selected and standardised protocols (Pérez-

Harguindeguy et al. 2013) were used to collect functional trait data, using a minimum of six leaves from each individual tree. The data was analysed in R, with median values of each trait calculated on each tree; these median trait values were then used to calculate CSR strategies for each tree using the methodology of Pierce et al. (2017). Site climate data was derived from Watkins et al 2019 (in review) and used to assess how CSR ordination was affected by Annual Rainfall and Warmth Index (Yim & Kira 1975) at each site. To assess the significance of these data, a correlation matrix was created to identify the strength and direction of the correlation between traits, functional strategies and climate.

A photographic journal was also recorded, and can be seen online at <https://medium.com/adventures-in-designed-ecology>

Parallel studies

We are carrying out three other research projects in parallel with this fieldwork. Firstly, to understand the range of climatic conditions that Magnolia species occupy, we surveyed the records of naturally-distributed Magnolia populations held in ex situ collections, herbariums and field reports and plotted these populations on graphs that assessed water availability (annual rainfall) against solar energy (warmth index). We found that species varied considerably in their distribution and that very often, these ranges were constrained by metabolic rates, opening the opportunity for target populations to be identified for further research and selection. A paper summarising this study was submitted to a peer reviewed journal in February 2019.

Secondly, common garden experiments of Magnolia seedlings are being carried out (Fig 3) to experimentally induce stresses that are found in urban environments and identify different abilities to tolerate stress within Magnolia species. Over the summer of 2019, fourteen Magnolia species will be subjected to drought, flooding and salt stress. Using functional traits (such as Specific Leaf Area, Leaf Dry Matter Content and biomass allocation), we will record both the ability of species to recover from stress and also the point at which this stress is terminal. By combining these research strands we have been able to link physiological processes from the literature, into fieldwork and then controlled trials.

Thirdly, studies of mature Magnolias growing in collections in northern Europe are being undertaken to assess a range of functional traits such as leaf turgor loss point, specific leaf area, leaf dry matter content and wood density. These functional traits are being assessed independently to rank the study species and then in combination to ordinate the species in CSR using the methodology of (Pierce et al. 2017) and to test the hypotheses set out by (Reich 2014).

Fieldwork team

A large number of researchers were involved in the fieldwork for this research, including:

Professor Masaaki Chiwa (Ashoro Research Station, Kyushu University)
Simon Hannus (SLU Alnarp)
Dr Takuo Hishi (Kyushu University)
Professor James Hitchmough (University of Sheffield)
Dr Liuba Kameneva (Vladivostok Botanic Garden)
Elena Linnik (Nature Reserve Kurilsky)
Dr Ayako Nagase (Chiba University)
Dr Takuma Nakamura (Ashoro Research Station, Kyushu University)
Ogawa-san (Aburayama Forest, Kyushu)
Dr Yoshitake Shinpei (Takayama Research Station, Gifu University)
Dr Henrik Sjöman (SLU Alnarp and Gothenburg Botanic Garden)

Dr Chie Sugizaki (Kaihso Forest Centre, Seto)
Harry Watkins (University of Sheffield)

Journal

(See Appendix 1 for a summary of woody plant species recorded).

- 5th March Prepare soils and seeds for sowing at Mount Stewart, Northern Ireland. Approximately 4,000 seeds of 19 species sown in a high-porosity peat-free soil.
- 8th April Simon Hannus and Harry Watkins flew Amsterdam – Tokyo, arriving 9th April.
- 9th April Connecting flight to Fukuoka and arrival at Hana Hostel in Fukuoka. In the afternoon we explored the city of Fukuoka, noting the tree species and planting details used in urban forestry. Many interesting trees noted including *Acer buergerianum* and *Fraxinus griffithsii*.
- 10-11th April Initial meeting with Ogawa-san, the forest reserve manager at Aburayama Forest, followed by four days of fieldwork. Working across altitude ranges between 150-450m we searched through *Cryptomeria japonica* forestry plantations (in mature and declining phases), paying particular attention to plantation edges, historic woodland with no history of clearance and secondary woodlands. We found a number of stands of *M. salicifolia* in disturbed or open positions where there was plenty of light and little competition, often in gravelly, high-oxygen soils. By contrast, *M. obovata* was much more widely distributed, occurring in locations from deep shade under *C. japonica*, through to woodland edges and as a climax species. We recorded details as per the methodology above and noted plant species that co-occurred with *M. obovata* and *M. salicifolia*, particular highlights included numerous *Arisaema* species in flower and *Lindera erythrocarpa*. *M. kobus* was seen planted along roadsides but it was interesting to note that this species did not naturally regenerate from these plantings, nor did occur anywhere on the mountain: a number of possible causes were suggested but no conclusive reason was found.
- 12th April Early morning departure to drive south through Kyushu Island to the Shiiba Research Station of Kyushu University high in the mountains in Miyazaki Prefecture. After an initial meeting with Dr Takuo Hishi we reconnoitred two forests at different altitudes (900m and 1,250m) that could be studied in more detail on a return visit. The fieldwork was highly productive, noting many interesting plants including a pink-flowered form of *M. salicifolia* and exceptional 25m tall *Stewartia monadelpha*.
- 13th April Early morning meeting with Dr Hishi to discuss fieldwork on our return in August, then return to Fukuoka in the afternoon.
- 14th April SH and HW flew from Fukuoka to Tokyo and then drove on to Daigo in Ibaraki Prefecture, arriving in the dark at 9pm.
- 15-17th April Research in Ogawa Forest Reserve. This location was based upon the numerous studies carried out in this plot but sadly after extensive searching, we were unable to locate any of the trees mentioned in the literature. As a consequence, we identified alternative study sites in Mt Ezimuro, Mt Yamizo, and Mt Asaki on the borders between Ibaraki, Fukushima and Gifu prefectures, working across altitudinal ranges from 400m to 1,000m. The mountains were predominantly given over to *Cryptomeria* plantations, although we identified target secondary and ancient

- woodland for study. *M. obovata* was widely distributed, with *M. kobus* occurring occasionally in clearings and *M. salicifolia* occurring only very rarely on riverbanks.
- 18th April Drove eight hours from Daigo to Seto, near Nagoya (Aichi Prefecture), stopping at a botanic garden en route to stretch our legs. Many interesting plants, including an astonishingly large and scented Wisteria, although most surprising were the loudspeakers, which played Auld Lang Syne at 17.00 to indicate that the gardens were closing.
- 19 and 20th April Recce expedition through Kaisho Forest, working up to 450m. The historic satoyama land management was interesting to note, creating habitats for beautiful gentians and *M. stellata*. Lunch on both days at the peak of the mountain, under the shade of a *Sorbus alnifolia*. *M. salicifolia* was very difficult to find and positively identify as the only locations we could find were places where it was naturally hybridising with *M. stellata* in river bottoms, although *Clethra barbinervis* again co-occurred with *M. salicifolia*, providing clues as to its location. *M. obovata* occurred widely in clearings, under Cryptomeria plantation, as a climax tree and in secondary woodland.
- 21st April A day off, and a trip into Seto to see a different side to Japan. Seto forms part of the Nagoya megacity, and whilst SH searched for presents to take home, I sat in a park and translated the protocols for visiting Kunashir Island from Russian into English using google.
- 22nd April Drove south through the Gamigori pass to Mt Atago.
- 23rd April Drove north from Seto to Matsumoto in Gifu Prefecture, via the eastern slopes of Mt Norikura.
- 24th April From our accommodation in a village on the western outskirts of Matsumoto we drove up to our study site, Gifu University's Takayama River Basin Research Station near Mt Norikura in the Japanese Alps. The study plot is secondary woodland, recovering from a clear fell approximately thirty years ago. *M. salicifolia* was observed in flower on the conifer-dominated northern slopes of the mountain between 900-1,100m, and we recorded many individuals of this species within the study plot. *M. obovata* was much more widely distributed from the valley floor (approx. 250m), along the road and up to the study plot (1,100m).
- 25th April Having had a successful day investigating the study site the previous day, we extended our search of the area to the Akasaura Natural Forest (a *M. sieboldii* site) in the heavy rain, finding *M. salicifolia*, *Rhododendron reticulatum* and Corylopsis species along the river. Many of the high mountain roads and trails were closed but nevertheless a productive day working across some large elevational gradients.
- 26th April To find the upper limits of *M. obovata* and *M. salicifolia* we visited the sub-alpine habitats of Komikochi and Taisho ponds. As expected, there were no Magnolia species present but we did find many interesting alder and willow species occurring in a rich variety of habitats and complex glacial ponds. A stunning landscape.
- 27th April A day off which we spent in the town of Takayama and visited a wasabi farm in Daio. We particularly enjoyed the local carpentry and needlepoint, as well as the wasabi ice cream.
- 28th April Our final day of fieldwork, climbing Mt. Norikura from a base of 1,450m. Amongst the woody species, it was interesting to note *Pachysandra terminalis* occurring in shaded marginal habitats,

- numerous *Helonopsis* species and extensive *Lysichiton camtschatcensis* in marginal habitats growing amongst birches and willows. In the evening we were invited by our hosts to attend a traditional spring festival that celebrated male fertility.
- 29th April Drove from Matsumoto back to Tokyo, returned the car and flew to Amsterdam.
- 2nd – 14th June Pricking out seedlings in Mt Stewart. A total of 2,000 plants set out in a polytunnel, using a peat-free, high porosity soil. Interested to note the influence of rooting volume on seedlings as they germinate (see Fig x): even at this early stage and in a short period, deeper pots seem to make a substantial difference.
- 15th June Visit to Mt Congreve, Ireland, to collect material. *M. liliiflora* in flower.
- 31st July HS and HW meet at Copenhagen airport to fly to Tokyo, arriving on 1st August, collecting a car and driving up to the Gifu University Takayama Research Station. We meet Dr Yoshitaki Shinpei late in the evening and prepare for fieldwork the following day.
- 2nd - 4th August Fieldwork begins. Accompanied by Dr Shinpei for the first hours on the 2nd, we identified specimens of the three species for detailed assessment, and then collected leaf and wood samples on the first day. The samples were measured on site and then taken to the laboratory at the research station, where they were placed in paper bags and dried at 40°C for 48 hours. Whilst the samples were drying, we undertook transect studies and recorded plants in the immediate and near vicinity, including *Miscanthus sinensis* glades, dells rich in many woody species common (or not so common to UK gardens) including *Clethra barbinervis*, *Hydrangea serrata*, *Lindera obtusiloba* and *Schizophragma hydrangeoides*. Evenings were spent working together in the library, taking advantage of the large whiteboard and reference books to assess our findings and plan the broader study.
- 5th August Drove back to Tokyo and flew to Fukuoka, where we picked up our car late in the evening and drove south to Shiiba, stopping overnight amongst the rice farms in the plains.
- 6th – 9th August Met Dr Hishi and his colleagues at the Kyushu University Shiiba Research Station early in the morning of the 6th, and drove up into the study site, an abandoned copper mine at 1,200m. On the first day we worked hard to collect plant and wood samples of the three species, processing them in the field and the lab before starting the transects on the second day. The work that the research team are doing there on habitat management allowed us to undertake additional transect studies, looking at species assemblages in open and closed woodland, in areas where deer are excluded and where they are not. Profound differences were recorded not only in species composition but also in soil stability; these results will be reported separately in a paper for a peer-reviewed journal. Dr Hishi and his colleagues were extremely welcoming and we could not have had a more productive time with such genial hosts; on the last evening we shared a barbeque with a research team from another university and studied herbarium and wood samples from their forests late into the evening.
- 10th August Drove north to Fukuoka through the Miyazaki mountains, into the plains and back into the city sprawl. Many lily species noted in the

- roadside rocks along the way. We found our accommodation in the city centre and had a Korean barbeque in the evening, a sweltering night.
- 11th – 13th August Fieldwork started early in the morning at Aburayama, meeting Ogawa-san on site. We found *M. salicifolia* already setting seed, although most were not yet fully ripe. By this stage we had a well-established process, collecting wood and leaf samples as early as possible before proceeding with habitat transects. Because we had no access to laboratory equipment here, we stored the plant materials until we could process them in Hokkaido. On the 13th I was able to find a particularly interesting *M. obovata* that we had seen in the spring, self-sown onto the top of a large concrete retaining wall- it seemed to be in good health, surprising given the high lime content of the soils and the exposed location in terms of sun and wind. Encouraging for urban foresters!
- 14th – 15th August We had planned to fly from Fukuoka to Nagoya and meet up with JH on the 14th but unfortunately typhoon season interfered, meaning that we had to spend an extra 48 hours in Fukuoka, a problem given our tight deadlines. We spent the additional time studying street trees (lots of *Zelkova serrata*) and coordinating with JH as he left China.
- 16th August Flew to Nagoya, picked up a well-rested JH, went to our accommodation in Seto and prepared for the compressed fieldwork we would have to do in Kaisho Forest the following day.
- 17th August Walking up through the *C. japonica* forestry plantations to find the *M. obovata* and *Q. mongolica* var. *grosseserrata*, we found many interesting trees, including *Carpinus laxiflora* and *Q. variabilis*, as well as plants that we were starting to see with great regularity such as *Hydrangea paniculata* and *Clethra barbinervis*. *M. obovata* was recorded in a range of habitats, from woodland edges at 450m down to river edges at 240m. Unfortunately due to the time constraints, *M. salicifolia* was impossible to determine with 100% confidence due to its extensive hybridising with the many *M. stellata* in the area, and it could not be included in our studies.
- 18th August Drove back into Seto, returned the car at Nagoya airport and flew to Hokkaido, arriving late in the evening to Sapporo.
- 19th August Picked up our car in the morning and drove north and east across the mountains, stopping en route to record woody and herbaceous species and arriving in Obihiro late in the evening. Whilst recording species, it was interesting to note the behaviour of invasive or highly competitive plants: North American *Oenothera* and *Rudbeckia* species were naturalised in large swathes along road edges, whilst native species of *Reynoutria* and *Sasa* formed large stands through which birches (*Betula ermanii*) grew. We spent
- 20th August Leaving Obihiro and driving towards Ashoro, we stopped to record plants we saw along the way. Again, many woody species to note including *Acer mono*, *Cercidiphyllum japonicum* (which to my mind showed characteristics of being intermediate with *C. magnificum*) as well as Japanese species of familiar herbaceous genera like *Aconitum*, *Campanula*, *Filipendula* and *Silene*- a reminder of the awesome diversity and range of plant life across the northern hemisphere. On arrival at the Kyushu University's Ashoro Research Station we met Professor Masaaki Chiwa and Dr Takuma Nakamura and went straight to site. The *M. obovata* and *Q. mongolica* var. *grosseserrata* both co-occurred, again with *C. barbinervis* and this time with *Acer palmatum* var. *matsumurae*, *Larix plantation*, and *M.*

- kobus* too- the only time that we saw *M. kobus* in any great number. The research team here felt confident in identifying these trees as *M. kobus var. borealis*, although unfortunately given the time of year there were not enough traits to base a confident determination of this upon.
- 21st August Having collected plant materials the previous day, we spent much of the 21st carrying out transects. *Sasa kurilensis* dominated the herbaceous layer, although this was replaced by *Miscanthus sinensis* in sunnier glades. Later in the day we had time to visit Daisetsuzan National Park, climbing a number of small peaks and driving very slowly to identify as many species as we could, noting the species composition gradients between wooded and open areas, and different aspects. Spectacular views from some of the higher mountain passes across the plateau.
- 22nd August Expedition to Lake Onnetoh and then a climb up to Mt. Akan-Fuji (1,476m). Around the lake there was lots of *Picea glehnii* plantation, with Rhododendrons underneath, and sub shrubs such as *Vaccinium* species and (unexpectedly), *Cornus canadensis*. Reaching the tree line through dense swathes of *Pinus pumila* to see the mountain ranges open up below us was a very moving moment, with rich wooded habitats ranging for miles in every direction to the horizon. This was also our closest encounter yet with bears, spotting a young bear scouting over the top of the *Pinus* about 40m away. Returning to the base of the mountain to the safety of the car park, we returned to Ashoro, stopping on the way to enjoy roadside ditches full of flowering *Lilium lancifolium*. In the evening it was a frantic spell to get all of the material we had collected in Aburayama Forest, Kaisho Forest and Hokkaido out of the ovens and then processed, as well as all the soils which were sieved, graded and tested for pH.
- 23rd August Early morning departure to return to Sapporo and say goodbye to James, before HS and HW flew to Yuzhno Sakhalinsk. An afternoon exploring the city and then met up with Dr Ilya Bogachyov and Dr Liubov Kameneva at Hotel Lenina on the edge of the town. In the morning we taxied to the port of Yuzhno Korsakov and boarded the ferry to Kunashir.
- 24th – 25th August The ferry to Kunashir was fairly uneventful, with cheering music piped into each of the cabins. The 36 hour journey gave us plenty of time to type up notes and enjoy plenty of meals in the cafeteria. We arrived in Yuzhno Kurilsk in the late afternoon, met up with Aleksandr (the nature reserve ranger) and prepared for the night at the Kurilsk Nature Reserve headquarters.
- 26th – 29th August Following our standard protocol, we gathered and processed plant material as soon as we could, focussing on *M. obovata* and *Q. mongolica var. grosseserrata*, forming a team of six that was led by Aleksandr and his Beretta pump action shotgun. Bears were a highly visible presence, with many signs of recent and close activity including discarded food, prints and scat. Luckily we did not see any in the flesh but it was hard not to think as we traversed along the shallow rivers through *Cardiocrinum* and *Fallopia* jungle that it would be some time before the rest of the group noticed that another was missing. Nevertheless, these four days of fieldwork were highly productive and we quickly completed the studies of Magnolias and Oaks, followed by the transects. This left time for us to study the region more widely, with several 20km treks across rocky and challenging terrain. Dr

Kameneva and Dr Bogachyov were superb identifiers of plants and translators between Elena and Aleksandr and us, negotiating meals and transport as well as the transfer of plants. On clear days it was just about possible to make out Hokkaido from our base in the village of Tretyakovo, and we hatched numerous plans together in the evenings over salmon from the stream and vodka flavoured with *Myrica* spp., comparing notes for working in academia in our respective organisations, the accessibility of journals and funding, as well as our broader research hopes. Our expeditions during these days covered the astonishing geological formations of western Kunashir, and working across gradients from the western shores of the island (with *Rosa rugosa* and *Lilium lancifolium* in the fixed dune), through the Tretyakovo Valley and up into the mountain ranges allowed us to study a large number of habitats and plant assemblages, truly a naturalist's paradise.

30th August

On the morning of the 30th we carried out our last piece of fieldwork to find a last *M. obovata* (apparently one of the largest on the island at 24m tall) and then left to catch our ferry back to Sakhalin.

1st– 3rd September

HS and HW caught an early flight from Sakhalin back to Sapporo, and then on to Tokyo, Copenhagen and finally Dublin and then by car to Northern Ireland.

Next steps

The next steps have been to analyse the functional traits that we recorded across the sites in August. Our preliminary findings suggest that whilst both *M. salicifolia* and *Q. mongolica* var. *grosseserrata* adjust their allocations of carbon and water between organs in response to climate, *M. obovata* does not: this poses a number of challenges to existing functional ecological theory and we hope to publish these results in articles in peer-reviewed journals in 2019. To address these results, we have identified the following questions to address in the discussion sections:

- Are variations in traits and CSR ordinations greater within or between populations?
- Can optimum trait values be identified within the species ranges?
- Are functional traits & functional strategies appropriate for this scale of investigation?

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Appendix 1 – Species recorded in August 2018.

Note – these species were recorded in transects and therefore represent a fraction of the species noted at each site. In many cases, species occur in sites outside the transects and are therefore not shown below. For example, *Schizophragma hydrangeoides* was noted in Ashoro Research Station and Takayama Research Station, but was only found in a transect in Shiiba Research Station.

Species	Sites
<i>Abies firma</i>	Takayama Research Station and Shiiba Research Station
<i>Abies sachalinensis</i>	Tretyakavo Valley
<i>Acanthopanax senticosus</i>	Ashoro Research Station
<i>Acer (unidentified snake bark maple spp)</i>	Takayama Research Station
<i>Acer crataegifolia</i>	Takayama Research Station, Shiiba Research Station and Kaisho Forest
<i>Acer mono</i>	Ashoro Research Station, Takayama Research Station
<i>Acer micrantha</i>	Shiiba Research Station
<i>Acer palmatum var. matsumurae</i>	Ashoro Research Station
<i>Acer pictum</i>	Tretyakavo Valley
<i>Acer pseudosieboldii</i>	Takayama Research Station
<i>Acer rufinerve</i>	Shiiba Research Station
<i>Acer sieboldianum</i>	Shiiba Research Station
<i>Acer sieboldii</i>	Takayama Research Station and Shiiba Research Station
<i>Acer spp</i>	Kaisho Forest
<i>Actinidia kolomikta</i>	Tretyakavo Valley
<i>Akebia spp</i>	Kaisho Forest
<i>Akebia trifoliata</i>	Aburayama Forest
<i>Aralia elata</i>	Shiiba Research Station and Tretyakavo Valley
<i>Araliaceae spp.</i>	Kaisho Forest
<i>Ardisia japonica</i>	Aburayama Forest
<i>Arisaema spp.</i>	Kaisho Forest
<i>Aucuba japonica</i>	Kaisho Forest
<i>Betula davurica</i>	Ashoro Research Station
<i>Betula ermanii</i>	Tretyakavo Valley
<i>Betula grossa</i>	Shiiba Research Station
<i>Betula platyphylla</i>	Ashoro Research Station, Takayama Research Station
<i>Blechnum sp.</i>	Kaisho Forest
<i>Callicarpa mollis</i>	Aburayama Forest
<i>Camellia japonica</i>	Kaisho Forest and Aburayama Forest
<i>Caprifoliaceae spp</i>	Kaisho Forest
<i>Carpinus japonica</i>	Takayama Research Station
<i>Carpinus laxiflora</i>	Shiiba Research Station
<i>Carpinus tschinoskii</i>	Shiiba Research Station
<i>Castanea crenata</i>	Takayama Research Station and Shiiba Research Station
<i>Castanopsis sieboldii</i>	Aburayama Forest
<i>Celastrus orbiculata</i>	Tretyakavo Valley

<i>Cercidiphyllum japonicum</i>	Ashoro Research Station, Takayama Research Station
<i>Cercidiphyllum magnificum</i>	Takayama Research Station
<i>Cephalotaxus harringtonia</i>	Aburayama Forest
<i>Cerasus jamasakura</i>	Shiiba Research Station
<i>Chamaecyparis sp.</i>	Kaisho Forest
<i>Chamaecyparis obovata</i>	Kaisho Forest
<i>Chengiopanax scadiophylloides</i>	Aburayama Forest and Shiiba Research Station
<i>Chengiopanax sp.</i>	Shiiba Research Station
<i>Cinnamorum camphora</i>	Aburayama Forest
<i>Cinnamorum pedunculatum</i>	Aburayama Forest
<i>Clerodendron trichotamum</i>	Kaisho Forest and Shiiba Research Station
<i>Clethra barbinervis</i>	Aburayama Forest, Kaisho Forest, Shiiba Research Station, Takayama Research Station
<i>Cocculus trilobus</i>	Aburayama Forest
<i>Cornus controversa</i>	Kaisho Forest and Shiiba Research Station
<i>Cornus kousa</i>	Kaisho Forest
<i>Cornus mcrophylla</i>	Shiiba Research Station
<i>Daphniphyllum macropodum</i>	Aburayama Forest
<i>Dioscorea japonica</i>	Aburayama Forest
<i>Dryopteris sp.</i>	Kaisho Forest
<i>Dryopteris erythro</i>	Kaisho Forest
<i>Eleagnus pungens</i>	Aburayama Forest, Kaisho Forest
<i>Epislemena spp</i>	Kaisho Forest
<i>Euonymus spp</i>	Kaisho Forest, Takayama Research Station
<i>Eurya sp.</i>	Shiiba Research Station
<i>Eurya japonica</i>	Aburayama Forest and Shiiba Research Station
<i>Fagus crenata</i>	Kaisho Forest
<i>Ficus erecta</i>	Aburayama Forest
<i>Frangula crenata</i>	Shiiba Research Station
<i>Fraxinus manschurica</i>	Ashoro Research Station
<i>Fraxinus sieboldii</i>	Takayama Research Station
<i>Gamblea innovans</i>	Shiiba Research Station
<i>Hamemmelis japonica</i>	Takayama Research Station
<i>Hulbolia sp.</i>	Kaisho Forest
<i>Hydrangea luteovenosa</i>	Aburayama Forest and Shiiba Research Station
<i>Hydrangea paniculata</i>	Ashoro Research Station, Shiiba Research Station, Takayama Research Station and Tretyakavo Valley
<i>Idesia spp.</i>	Kaisho Forest
<i>Ilex crenata</i>	Aburayama Forest, Kaisho Forest, Shiiba Research Station, Takayama Research Station
<i>Ilex macrantha</i>	Shiiba Research Station
<i>Ilex macropodum</i>	Shiiba Research Station, Takayama Research Station
<i>Ilex pedunculosa</i>	Aburayama Forest and Shiiba Research Station
<i>Illicium anisatum</i>	Aburayama Forest, Kaisho Forest, Shiiba Research Station
<i>Juglans ailanthifolia</i>	Ashoro Research Station

<i>Kalopanax pictus</i>	Ashoro Research Station
<i>Kalopanax septemlobus</i>	Shiiba Research Station, Takayama Research Station, Tretyakavo Valley
<i>Koelreuteria type</i>	Kaisho Forest
<i>Lespedeza bicolor</i>	Ashoro Research Station
<i>Ligustrum japonicum</i>	Aburayama Forest
<i>Ligustrum spp</i>	Kaisho Forest
<i>Lindera erythrocarpa</i>	Aburayama Forest, Shiiba Research Station
<i>Lindera obtusiloba</i>	Takayama Research Station
<i>Lindera triloba</i>	Shiiba Research Station
<i>Litsea spp</i>	Kaisho Forest, Takayama Research Station
<i>Lonicera chrysantha</i>	Ashoro Research Station
<i>Lonicera spp</i>	Takayama Research Station
<i>Lyonia ovalifolium</i>	Kaisho Forest
<i>Maackia amurensis var. buergeri</i>	Ashoro Research Station
<i>Maackia spp</i>	Takayama Research Station
<i>Machilus thunbergii</i>	Aburayama Forest
<i>Magnolia obovata</i>	Aburayama Forest, Ashoro Research Station, Kaisho Forest, Shiiba Research Station, Takayama Research Station, Tretyakavo Valley
<i>Magnolia salicifolia</i>	Aburayama Forest, Kaisho Forest, Shiiba Research Station, Takayama Research Station
<i>Malotus japonica</i>	Aburayama Forest
<i>Neolitsea sericea</i>	Aburayama Forest
<i>Oplismenus undulatifolius</i>	Aburayama Forest
<i>Osmanthus heterophylla</i>	Kaisho Forest
<i>Osmunda spp</i>	Kaisho Forest
<i>Ostrya japonica</i>	Ashoro Research Station
<i>Phellodendron amurense</i>	Ashoro Research Station, Tretyakavo Valley
<i>Picea jezoensis</i>	Tretyakavo Valley
<i>Pieris japonica</i>	Kaisho Forest and Shiiba Research Station
<i>Pinus densiflora</i>	Shiiba Research Station
<i>Pinus parviflora</i>	Takayama Research Station
<i>Pittosporum spp</i>	Kaisho Forest
<i>Populus tremula subsp sieboldii</i>	Takayama Research Station
<i>Prunus grayana</i>	Takayama Research Station
<i>Prunus koreana</i>	Takayama Research Station
<i>Prunus maximowiczii</i>	Ashoro Research Station
<i>Prunus sargentiana</i>	Ashoro Research Station, Kaisho Forest
<i>Prunus spinulosa</i>	Aburayama Forest
<i>Pterostyrax corymbosa</i>	Shiiba Research Station
<i>Quercus acuta</i>	Shiiba Research Station
<i>Quercus mongolica var. grosseserrata</i>	Aburayama Forest, Ashoro Research Station, Kaisho Forest, Shiiba Research Station, Takayama Research Station, Tretyakavo Valley
<i>Quercus glauca</i>	Aburayama Forest
<i>Quercus salicia</i>	Shiiba Research Station

<i>Quercus spp</i>	Kaisho Forest
<i>Quercus stenophylla</i>	Aburayama Forest
<i>Quercus variabilis</i>	Kaisho Forest
<i>Rhododendron reticulatum</i>	Shiiba Research Station
<i>Rhus japonica</i>	Shiiba Research Station
<i>Rhus trichocarpa</i>	Ashoro Research Station
<i>Rubus pvp</i>	Shiiba Research Station
<i>Schizophragma hydrangeoides</i>	Shiiba Research Station
<i>Skimmia japonica</i>	Shiiba Research Station
<i>Smilax china</i>	Aburayama Forest and Shiiba Research Station
<i>Sorbus commixta</i>	Tretyakavo Valley
<i>Staphylea bumalda</i>	Ashoro Research Station, Shiiba Research Station
<i>Stauntonia hexaphylla</i>	Aburayama Forest
<i>Stewartia monodelpha</i>	Shiiba Research Station
<i>Styrax japonica</i>	Aburayama Forest, Kaisho Forest, Shiiba Research Station
<i>Styrax ob</i>	Takayama Research Station
<i>Symplocos koreana</i>	Takayama Research Station
<i>Symplocos kuroki</i>	Aburayama Forest
<i>Symplocos myrtaea</i>	Aburayama Forest and Shiiba Research Station
<i>Symplocos spp</i>	Kaisho Forest
<i>Syringia reticulata</i>	Ashoro Research Station
<i>Tilia japonica</i>	Ashoro Research Station
<i>Tilia maximowicziana</i>	Ashoro Research Station
<i>Toxicodendron radicans</i>	Shiiba Research Station
<i>Toxicodendron septemlobus</i>	Kaisho Forest, Shiiba Research Station
<i>Toxicodendron trichitomum</i>	Takayama Research Station
<i>Trachelospermum asiaticum</i>	Aburayama Forest
<i>Trachelospermum spp</i>	Kaisho Forest
<i>Tripterospermum japonicum</i>	Aburayama Forest
<i>Tripterygium regelii</i>	Shiiba Research Station
<i>Tsuga sieboldii</i>	Shiiba Research Station
<i>Ulmus japonica</i>	Ashoro Research Station, Tretyakavo Valley
<i>Viburnum erosum</i>	Shiiba Research Station
<i>Viburnum wrightii</i>	Takayama Research Station
<i>Weigelia japonica</i>	Shiiba Research Station
<i>Wisteria brachybotrys</i>	Aburayama Forest
<i>Wisteria japonica</i>	Aburayama Forest, Kaisho Forest
<i>Zanthostylem schinfolium</i>	Shiiba Research Station