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## Research

### Legacies of historic charcoal production affect the forest flora in a Swedish mining district

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Iron production was historically associated with major impacts on forests worldwide, as vast amounts of wood were harvested to produce the charcoal needed for heating the furnaces and reducing iron oxides in the ore to iron. This impact has left abundant legacies which potentially may remain in the present-day vegetation. We investigated how remains of historic charcoal production, mainly from the 18th to the early 20th century, at still remaining charcoal kiln platforms (CKPs), affect the current species richness, species occurrences and cover of vascular plants in the ground vegetation in a Swedish mining district located in the boreo-nemoral forest zone. CKPs have a significantly higher species richness than the surrounding forest, and they also affect cover (negatively) for ericaceous species typically dominating the forest ground vegetation. Several forest species are more frequent at CKPs, and these also harbor significantly more uncommon species, of which many are typical for traditionally managed grasslands. These latter species are likely to represent remnants in present-day forests reflecting former land-use such as livestock grazing. The soil chemistry at CKPs is strongly deviating from the surrounding forest, and this, together with a lower cover of ericaceous shrubs, are the most likely mechanisms behind the higher species richness. CKPs represent conspicuous and abundant historic anthropogenic habitats in the forest vegetation. As far as we are aware, the flora at CKPs in boreal and boreo-nemoral forests has not previously been investigated in detail, and they deserve more attention, both from a biological and a cultural–historical perspective.

Keywords: biological cultural heritage, boreo-nemoral forests, charcoal kiln platforms, relict charcoal hearths, remnant populations, species richness

#### Introduction

Anthropogenic impacts on present-day vegetation are ubiquitous, as most of the Earth's land surface is more or less transformed by humans (Ellis and Ramankutty 2008). Some of these impacts are due to human activities and land use that are no longer occurring. In the ecological literature, remaining traces of past impacts are usually referred to as historical land-use legacies (Perring et al. 2016), and there is an extensive literature describing such legacies, for example in grasslands (Poschold and WallisDeVries 2002, Eriksson and Cousins 2014) and in forests (Bellemare et al.



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2002, Hermy and Verheyen 2007). Some of these legacies are valued as part of cultural heritage (Rotherham 2015, Eriksson 2018), and some are recognized due to their relevance for conservation biology (Foster et al. 2003, Plieninger et al. 2015), but it is likely that a considerable fraction of detectable legacies of past human actions and land use are simply overlooked, and not heralded as heritage, cultural or biological, or as important for conservation biology. Still, if a general aim of plant ecology is to understand current patterns of species distribution and plant community composition, a perspective of historic influence of past land-use should not be neglected. The time frame for historical legacies in vegetation, if these are defined as remains of no longer occurring activities and land use, varies. They may for example reflect a very recent abandonment of a pasture or a meadow, where species dependent on the former land-use naturally remain for some period. However, some legacies of abandoned grasslands may be detectable in present-day forests after more than a century (Herben et al. 2006), even if the land has been transformed into production forest and has passed cycles of clear-cuts (Jonason et al. 2014, Milberg et al. 2019). In exceptional cases, the time-frame may even be millennia, as remaining legacies have been found which reflect land use over 2000 years ago (Dambrine et al. 2007, Plue et al. 2008).

In boreal and boreo-nemoral Sweden (Sjörs 1999) large areas currently covered with forest (mostly coniferous production forest), and where very few people live permanently today, were for not so long time ago (less than 100 years) populated by lots of people. These were crofters and small-scale farmers, who in addition to maintain their livelihood by some crop production, gardening and keeping a few livestock, worked at larger manors, mines, mills, iron-works etc. What is today production forest for pulp and timber, at that time served manifold purposes, for example for production of charcoal, tar and potash (Emanuelsson 2009). Furthermore, livestock was grazing in the forests (Kardell 2016). As a consequence, forests were previously much more open. Another consequence of the former use of forests is that boreal and boreo-nemoral forests contain a plethora of botanical legacies (Ljung et al. 2015, Eriksson 2018). Some of these have been subject to detailed studies, for example legacies of livestock forest grazing (Oldén et al. 2016) and former crofts (Eriksson and Glav Lundin 2020). However, in comparison with the much more researched topic of historical effects on still existing pastures and meadows, the legacies of former land-use in forests are much overlooked (Eriksson 2018).

One of the globally most common human activity that had extensive impacts on forests was iron production, through its associated production of charcoal (reviewed by Iles 2016). Iron production has a long history in Sweden (National Atlas of Sweden 2011, Hjärthner-Holdar et al. 2018). After the invention of the blast furnace in the 12th century, iron ore mining (mainly magnetite and hematite) expanded in several mining districts in Sweden. From the 17th century and through the following centuries, Sweden was one of the major exporters of iron in Europe (National Atlas of Sweden 2011).

In addition to the iron ore, charcoal was a necessary resource for iron production. Charcoal serves two main functions in iron production. It heats the furnace, and carbon is needed for reducing the iron oxides in the ore to iron. Until the introduction of other carbon sources, for example coke, the demands for charcoal was enormous and the charcoal production demanded a rich supply of wood (Arpi 1951, Hammersley 1973, National Atlas of Sweden 2011, Crew and Mighall 2013). Large areas of forests surrounding the iron-works in Sweden were allocated for charcoal production. As an example, between 1850 and 1885, 20–25% of all wood harvested in Sweden was used for producing charcoal (Arpi 1951, p. 46), and the wood supply may have been a limiting factor for iron production, at least locally (Hedström 2005).

Hennius (2018) gives an overview of historic charcoal production and its material remains in Sweden. To produce charcoal, wood was burned with limited oxygen supply. Charcoal has been produced since the early Iron Age, and initially this was conducted in pits, but from the Middle Ages the production was made more efficient by making above-ground constructions. The terminology for these constructions varies in the literature. The actual structure used for charcoal production was the charcoal kiln, or charcoal hearth. The remains of the kiln/hearth (Swedish: 'kolbotten') are variably termed charcoal kiln platforms (Carrari et al. 2016a), pre-historic charcoal kilns (Hardy et al. 2016) or relict (or historic) charcoal hearths (Hirsch et al. 2017, 2018). Henceforth in this paper, we use the term charcoal kiln platform, abbreviated CKP.

Wood was harvested in the vicinity of the production site, resulting in a clear-cut, in boreo-nemoral forests typically sized about a hectare (Hedström 2005). The harvested wood was left for drying, and thereafter a charcoal kiln was raised (Fig. 1A). The kiln was sealed, for example with turf, litter or pulverized charcoal from previous kilns. The kiln was ignited, allowed to burn under strictly controlled oxygen supply, and after a few weeks (Hennius 2018) the charcoal was ready to be removed (Fig. 1B). The remains of the kilns are visible, more or less conspicuously, as a circular area (diameter ca 10–15 m) delineated by a low wall and sometimes a shallow depression outside the wall, a CKP (Fig. 1C).

There are around 33 000 CKPs in Sweden registered by the Swedish National Heritage Board, but this figure is probably a great underestimation of their true number (Hennius 2018). Their age (here meaning when the last charcoal kiln was raised) is typically from the 15th century onwards until the early 20th century. The majority of the known CKPs are remains of charcoal kilns of the type shown in Fig. 1A, which was the most common during the later phase of charcoal production.

Considering the ubiquity of charcoal production, all over the world, for example in Europe (Crew and Mighall 2013), North America (Raab et al. 2017) and Africa (Eichhorn et al. 2013), there are surprisingly few studies of the remaining traces of charcoal production in the present-day flora. Most studies concern charcoal production technology (Crew 1991), the organization of charcoal production (Groenewoudt and van Nie 1995) or the environmental



Figure 1. (A) A charcoal kiln before ignition, and (B) when charcoal production is completed. (C) An example of a charcoal kiln platform in a boreo-nemoral forest. (A) and (B) are from the museum at the Skottvång iron mine in the study area, where a charcoal kiln is raised for demonstration every year. The use of a chimney as shown in (B) was an invention introduced during the early 20th century. Photos: the authors.

impacts on landscapes (Fyfe et al. 2013) and forest structure (Pélachs et al. 2009, Deforce et al. 2013, Paradis-Grenouillet et al. 2015). Some studies focus on the impacts of the charcoal kilns on soil chemistry (Criscuoli et al. 2014, Hardy et al. 2016, Hirsch et al. 2017). Specifically, carbon affects several aspects of boreal soil function such as nutrient retention (Hart and Luckai 2013). Only a handful of studies, as far as we are aware, have dealt explicitly with still visible traces in the vegetation (Mikan and Abrams 1995, Young et al. 1996, Carrari et al. 2016a, Pedrotti and Gafta 2017, Máliš et al. 2021), and none of these have been conducted in Sweden. However, several Swedish authors have remarked that the vegetation at CKPs often deviates from the surroundings (Hennius 2018), for example with a conspicuously high density of stunted Norway spruce *Picea abies* (Ljung 2017).

The aim of this study was to investigate whether the current vegetation at CKPs deviates from the surrounding forest, specifically with regard to species richness of vascular plants, and occurrences and cover of single species. As the study was conducted in forest which during the last 70–90 years have been used mainly as production forest, the main focus was on the ground vegetation, although some records were also made for trees. We also compared the soil chemistry of CKPs with the surrounding forest soil. We place the results in the context of biological cultural heritage, and conservation biology.

## Study area

This study was conducted in Åkers mining district, one of the smallest mining districts in Sweden (National Atlas of Sweden 2011), located in the Province of Södermanland, just south of the lake Mälaren (Fig. 2). During the 17th century, there were 12 iron-works with blast furnaces in this district (Haggrén et al. 2016). During the centuries that followed, the number of iron-works declined, and in the 19th century there were only few left, among which one, Åkers styckebruk (founded 1580), became the dominating (and after 1875 the only one).

The forest area south of the iron-works at Åkers styckebruk was largely used for charcoal production (Fig. 3). The area was what in Swedish was termed ‘rekognitionskog’, a forest area for which the iron-works, based on an agreement with the State, had permission to use wood for production of charcoal (Arpi 1951, page 55). The forest area has a density of ca 6.6 CKPs per km<sup>2</sup>. Of the 230 CKPs shown in Fig. 3, 50 were used in this study. Overall, there are hundreds more CKPs in the neighboring forest areas.

Also iron ore was produced locally. Until the early 20th century, there were three local mines delivering iron ore to Åkers styckebruk: Bredsjönäs, Älgsjöbacken and Skottvång (Fig. 3), the latter being preserved as a museum. The forest area is today mostly used as production forest, but is also much visited by people, for leisure, hiking, canoeing and fishing. Few people live in the forest area. This is in contrast to

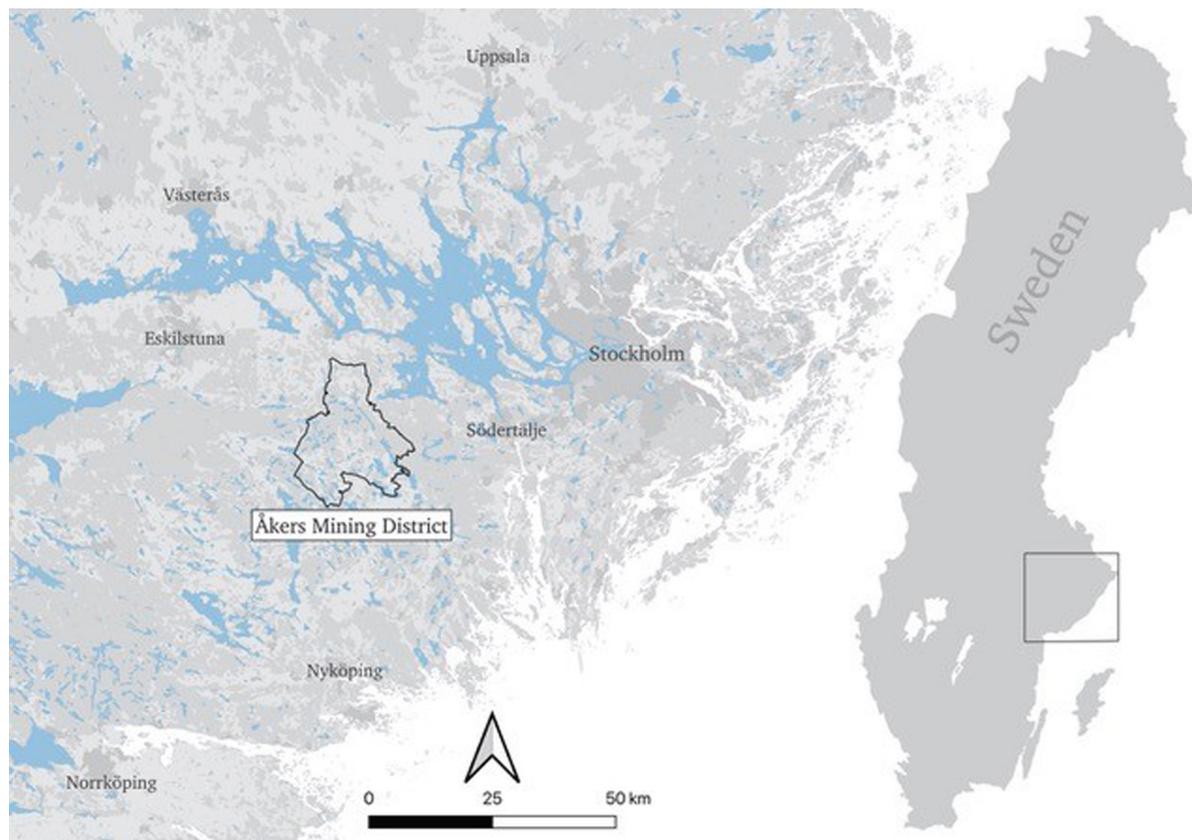


Figure 2. A map of the study area Åkers mining district, and its location in Sweden.

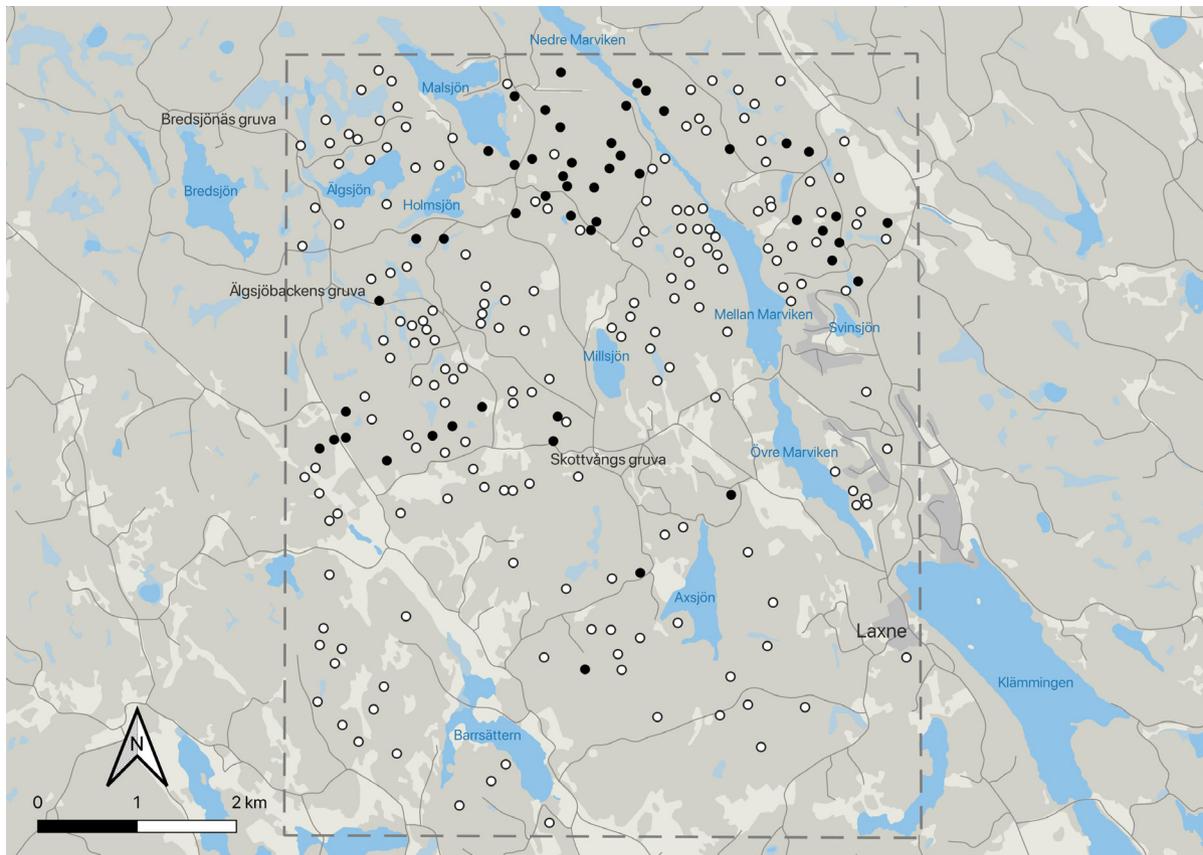


Figure 3. A map showing the distribution of charcoal kiln platforms (CKPs) in the study area (inside the hatched lines). The 50 investigated CKPs are those with filled circles.

the time up until the early 20th century, when mining and charcoal production was still active (Karlsson 2018). While the area today is mostly covered by forest, we should image it as much more open just a century ago. Karlsson (2018, p. 20) refers a note made on a map from 1719 stating that the area between Åkers styckebruk and Skottvång mine (a distance of ca 8 km) barely had any trees at all due to charcoal production. In addition, livestock were at that time grazing in the semi-open forests, and there was land used as pasture or hay-meadows, i.e. ‘semi-natural grasslands’ (Eriksson and Cousins 2014). These grasslands have now mostly disappeared, being replaced with forest. Overall, the total area of semi-natural grasslands in the Province of Södermanland has decreased with over 96% during the 20th century (Cousins et al. 2015).

The study area is located within the boreo-nemoral zone, i.e. the transition zone between the southern nemoral zone and the boreal zone (Sjörs 1999). The bedrock is mostly gneiss and granite, and open bedrock is common at higher elevations. The soil is mostly formed by glacial deposits, i.e. morainic till, with stones and gravel and embedded in sand or silt. A characterized feature of the landscape is deep fissure valleys, creating a lake system in the NW–SE direction. There are lots of small wetlands, bogs and mires, and several small lakes. The average temperature in the region is  $-4^{\circ}\text{C}$  (January) and  $16^{\circ}\text{C}$  (July), and the average yearly precipitation is ca 600 mm (Cousins et al. 2015). *Picea abies* and *Pinus*

*silvestris* dominate the forests, but with deciduous species such as *Betula* spp., *Populus tremula*, *Alnus glutinosa*, *Sorbus aucuparia*, *Salix caprea*, *Acer platanoides* and *Quercus robur* commonly occurring. Some giant oaks are still present, reminding of the formerly more open landscape. The ground flora is generally quite poor. Typically, the dominating field layer species are *Vaccinium myrtillus*, *V. vitis-idaea*, *Calluna vulgaris*, and the grasses *Deschampsia flexuosa* and *Calamagrostis arundinacea*. There are also abundant bryophytes on the forest floor, e.g. *Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium crista-castrensis*, *Dicranum* spp. and *Polytrichum* spp., and, especially where there is open bedrock, lichens such as *Cladonia* spp. and *Cetraria islandica*.

## Methods

The field studies were conducted during the summer 2020. Based on field maps where CKPs are indicated, 50 CKPs were selected (Fig. 3). In general, the CKPs were easy to locate. Only in a few cases the CKP was not immediately found, and a more thorough search was necessary. We used a pairwise design, with a control for each individual CKP. Each CKP was delineated and its size measured. As CKPs are approximately circular, we used the diameter as a size measure. Soil cores sampled from 3 to 5 places within the CKP were

examined for remains of charcoal (Supporting information), and if present, confirming that the site actually is a CKP. Within the area covered by each CKP, all vascular plant species were recorded. In addition, a 2 × 2 m quadrat was placed in the center of the CKP, in which the cover of each species in the ground vegetation was recorded, using a four-graded scale: single occurrence, < 10, 10–50 and > 50%. For each CKP, a similarly sized control area was subjectively selected, with its outer boundary approximately 10–15 m from the focal CKP. Absence of visible remains of charcoal confirmed that the control is not a CKP. The species survey of the control was made exactly similarly as for the CKP.

A few taxa were distinguished only at the genus level. We encountered specimens of *Carex* which could not be identified to species, and the same holds for one specimen of *Prunus*. Some apomictic *Hieracium* species were only identified to genus. These three taxa were counted as one species each.

At 12 CKPs and their respective control, soil samples were gathered for soil analysis. After removing the litter layer, soil (down to 10–15 cm depth) was gathered from 10 places within each CKP, and mixed into one sample. The procedure was repeated for the control. The samples were kept dark and cold, and immediately after the field sampling sent to an accredited laboratory for soil chemical analyses, Eurofins (<[www.eurofins.se](http://www.eurofins.se)>), where analyses were made for pH, P, K, Mg, Ca, NH<sub>4</sub>-N and NO<sub>3</sub>-N, using standard methods.

When examining the flora and vegetation at CKPs, it would have been useful to know the age of each CKP, i.e. when the last charcoal kiln was raised. Unfortunately, we do not have this information. Charcoal was produced in the area until the 1940s, but considering the expansion of the iron-works at Åkers styckebruk during the 19th century, and the introduction of other means of reduction of iron oxides, mainly coke, from the early 20th century, a qualified guess is that the investigated CKPs have an age distribution mainly spanning from the late 18th century, peaking during the 19th century and up to the early 20th century, and with a few CKPs probably being slightly younger.

The analyses for comparing the total species richness, and soil chemistry in CKPs and control were made by t-test (paired samples). In order to examine if some species occurred more often at CKPs, or controls, respectively, we used  $\chi^2$  – test, including all species which occurred in at least 10 sites (a CKP and its control). Sign test was used to examine if species with few ( $\leq 9$ ) occurrences were disproportionally distributed among CKPs and controls. The analyses of difference in cover for each species, in CKPs versus controls, were made for field layer species which occurred in at least 20 sites (many species which were recorded at CKPs/controls did not occur in the 2 × 2 m plot used for estimating cover). As the cover estimate was based on four cover classes, we decided to assess, for each of the pairwise comparison for each species (CKP versus control) whether the focal species had higher, or lower, cover in the CKP as compared with the control. The resulting tabulation for each species was examined using sign-test.

The nomenclature follows the flora provided by the Swedish Museum of Natural History (<<http://linnaeus.nrm.se/flora/>>).

A list of all species and a summary of occurrence data is available in the Supporting information.

## Results

For all 50 sites with a CKP and a control, the identity of the CKPs was confirmed by the presence of a black layer of coal in the soil, and a corresponding lack of such a layer in the control. The coal layer ranged 4–25 cm in depth (median: 10 cm). In only one case, the charcoal layer was difficult to detect, but instead the abundance of pieces of charcoal confirmed the presence of the CKP. The CKPs were approximately circular, with a diameter in the range 7–16 m (median: 11 m).

In all, 127 species of vascular plants were recorded in the surveys of the 50 sites with CKPs and controls (Supporting information). Two species occurred at all 50 sites, *Picea abies* and *Vaccinium myrtillus*, and with *Pinus sylvestris*, *Sorbus aucuparia*, *Vaccinium vitis-idaea*, and the graminoids *Luzula pilosa* and *Deschampsia flexuosa* occurring at  $\geq 45$  sites. Accordingly, the dominating flora in CKPs is generally a reflection of the dominant species in the forest vegetation. The subjective assessment (mentioned in the introduction) that CKPs are characterized with a conspicuous and from the surroundings clearly deviating high density of stunted Norway spruce was noted during the survey (Fig. 4), but clearly so in only three of the 50 CKPs.

The number of species recorded in CKPs was higher than in the controls (Fig. 5). At 34 of the 50 pairwise comparisons, the number of species was highest at the CKP. Even though the average number of species is just ca 17% higher at CKPs as compared to controls ( $21.7 \pm 8.2$  versus  $18.6 \pm 7.8$ ), the difference was highly significant ( $t=3.41$ ,  $p=0.0013$ ). Figure 5 shows that there was a positive correlation between the species richness at the CKPs and their respective controls ( $r=0.68$ ,  $p < 0.001$ ). Generally, at sites where the control was rich in species, also the CKP was rich in species. Note the hatched line in Fig. 5, indicating a 1:1 ratio of number of species at each of the CKPs and their respective controls. Most dots are above the line, showing that there was generally a slightly higher number of species at the CKP.

Five species occurred significantly more often at CKPs, and two species occurred close to significantly more often at CKPs (Table 1A). The clearest cases were *Fragaria vesca*, *Frangula alnus*, *Luzula pilosa* and *Sorbus aucuparia*. Also the records of *Hieracium* spp., not determined to species, were more common at CKPs. However, considering that these represent an unidentified ensemble of apomictic forms, we would not stress this result. Two species, *Oxalis acetosella* and *Orthilia secunda*, showed a tendency to occur more commonly at CKPs. The only species with a significantly higher occurrence on controls was *Calluna vulgaris*.

Among the 127 recorded species, 63 (50%) were recorded at  $\leq 2$  sites (Supporting information). Out of these 63 species, 34 (54%) occurred only at CKPs, while 16 (25%) occurred only at controls. The remaining 13 species were recorded once at a CKP and a control, respectively. Thus, uncommon species in the forest environment tended to significantly



Figure 4. In the literature, it has been noted that there are often dense stands of stunted Norway spruce *Picea abies* at charcoal kiln platforms (CKPs). The border of the CKP is indicated with a red line. The photo shows one such case. However, they are rather exceptions than a characteristic feature of CKPs. Photo: the authors.

more often occur at CKPs ( $Z=2.54$ ,  $p=0.011$ ). For species with 3–9 occurrences, 13 out of 21 were more often found at CKPs, whereas three species were more often found at controls (the remaining five species were equally common at

CKPs and controls). The higher occurrence of these species at CKPs was significant ( $Z=2.5$ ;  $p=0.012$ ).

Including cases of close to significance ( $p \leq 0.1$ ), there were three field layer species which had a higher cover at CKPs

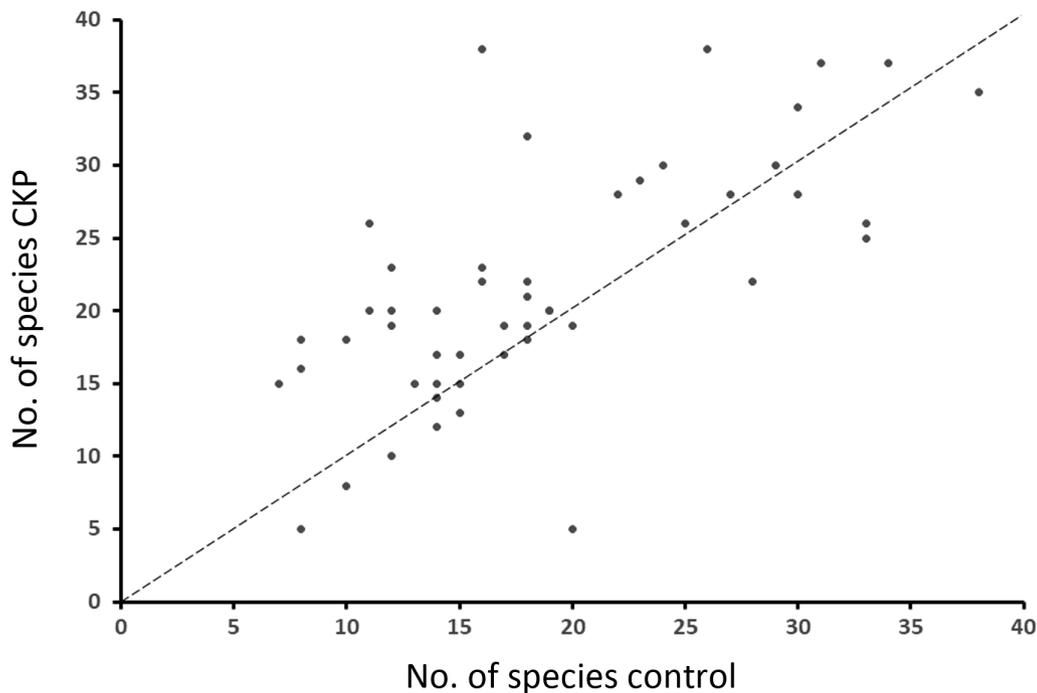


Figure 5. The species richness of vascular plants on charcoal kiln platforms (CKPs) and controls. Each dot represents the number of species at a site consisting of pairs ( $n=50$ ) of a CKP and its control. The hatched line illustrates the 1:1 relationship, i.e. when the number of species is equal between CKPs and controls.

Table 1. Species occurrences (A) and species cover (B) at charcoal kiln platforms (CKPs) versus controls (n=50). The listed species are those with significant ( $p < 0.05$ ) or close to significant ( $p \leq 0.1$ ) differences in (A) occurrences between CKPs and Control, and (B) cover in a  $2 \times 2$  m plot in CKPs and Control. Information on occurrences for all species is found in the Supporting information. Note that difference in cover only considered the comparison higher versus lower, based on four cover classes. No absolute figure of cover for the species is presented.

(A) Occurrences	No. of occurrences at:		p
	CKP	Control	
More common at CKP			
<i>Fragaria vesca</i>	20	5	< 0.001
<i>Fragula alnus</i>	23	10	0.006
<i>Hieracium</i> spp.	33	19	0.005
<i>Luzula pilosa</i>	41	29	0.009
<i>Sorbus aucuparia</i>	42	30	0.008
<i>Oxalis acetosella</i>	23	14	0.06
<i>Orthilia secunda</i>	11	5	0.1
More common at Controls			
<i>Calluna vulgaris</i>	12	27	0.004
(B) Cover			
Higher at CKPs		Lower at CKPs	
<i>Fragaria vesca</i> (p=0.034)		<i>Vaccinium vitis-idaea</i> (p=0.003)	
<i>Luzula pilosa</i> (p=0.072)		<i>Veronica officinalis</i> (p=0.034)	
<i>Viola riviniana</i> (p=0.074)		<i>Vaccinium myrtillus</i> (p=0.072)	
		<i>Calluna vulgaris</i> (p=0.095)	

than at controls, and four species which had higher cover at controls (Table 1B). Most notable was that the two dominating species of the forest ground vegetation, *Vaccinium myrtillus* and *V. vitis-idaea*, both had higher cover at controls.

The soil chemistry analyses showed that the soil at CKPs deviates from the surrounding forest soils (Table 2). CKPs have higher concentrations of phosphorous, potassium, magnesium and calcium, and a close to significantly higher pH. Concentrations of soil nitrogen ( $\text{NH}_4 - \text{N}$ ) was close to significantly higher at controls.

## Discussion

It is generally well-known that the current composition and diversity in boreal and boreo-nemoral forests is influenced by their history, i.e. how forests were used and managed before the introduction of modern forestry (Östlund et al. 1997,

Table 2. Soil chemistry at charcoal kiln platforms (CKPs) and Controls (n=12). Analyses were performed at the accredited laboratory Eurofins (<www.eurofins.se>). Except for pH all measures are as mg/100 g dry soil (mean  $\pm$  SD).

	CKP	Control	p
Soil pH	5.0 (4.5–5.5)	4.7 (4.3–5.1)	0.058
Phosphorous	4.0 $\pm$ 1.9	1.8 $\pm$ 1.1	0.003
Potassium	8.0 $\pm$ 1.8	4.8 $\pm$ 1.8	0.002
Magnesium	10.7 $\pm$ 2.4	5.1 $\pm$ 1.7	< 0.001
Calcium	64 $\pm$ 24	21 $\pm$ 12	< 0.001
Nitrogen – $\text{NH}_4$	0.26 $\pm$ 0.11	0.42 $\pm$ 0.22	0.066
Nitrogen – $\text{NO}_3$	< 0.06	< 0.06	–

Lindbladh and Bradshaw 1998, Ericsson et al. 2000, 2005), including human interventions in the forest's fire dynamics (Lindbladh et al. 2003, Granström and Niklasson 2008, Rolstad et al. 2017). Despite this recognition of the importance of history, no previous study has, to our knowledge, specifically examined biological legacies from the remains of the charcoal production sites, the CKPs, in boreal and boreo-nemoral forests. Until the early 20th century, charcoal production was a dominating use of forests in Swedish mining districts. Due to the varied use of charcoal for other purposes than iron production, CKPs also occurred outside the mining districts. There are tens of thousands CKPs in Swedish forests (Hennius 2018). Thus, it seems highly motivated to examine biological legacies from charcoal production.

Our main result is that CKPs have a significantly higher species richness of vascular plants than the nearby surrounding forest. The difference, in quantitative terms, was not very large (ca 17%), but it is consistent across the occurring range of variation of species richness among forest sites. The CKPs generally contain a slightly higher number of species than the controls. This pattern may depend partly on minor differences in frequency of species occurrences, which if analyzed for single species are not detected as significant. However, a group of five (or seven if  $p \leq 0.1$  is accepted) species has a significantly higher frequency of occurrence at CKPs. Only one species was more frequent outside CKPs. A first conclusion is that all these species (Results) exhibiting significant differences in frequency are typical members of the boreo-nemoral forest flora.

In addition, species which are not common in the survey tend to occur disproportionately often at CKPs. For example, a significantly higher fraction of the species with very few ( $\leq 2$ ) occurrences is only recorded at CKPs. Of the 34 species with this occurrence pattern, ca 65% are listed by Ekstam and Forshed (1992) as open habitat species declining after abandonment of management, such as grazing or mowing of 'traditionally' managed semi-natural grasslands. Examples include *Achillea millefolium*, *Danthonia decumbens*, *Hypericum maculatum*, *Lathyrus pratensis*, *Leucanthemum vulgare*, *Lotus corniculatus* and *Polygala vulgaris* (Supporting information). In a previous study conducted in boreo-nemoral forests, these seven species were all found as remnant populations in present-day forests which 70–110 years ago were land managed as pasture or meadow (Johansson et al. 2011). 'Remnant populations' imply that populations remain for long periods of time, despite having a negative population growth rate (Eriksson 1996). It thus seems that CKPs provide refuges for a flora that was much more abundant historically, at the time (19th and early 20th centuries) when the studied forest area included semi-natural grasslands, and also lots of people and livestock contributing to promote seed dispersal (see the section Study area). This conclusion is in line with the findings by Jonason et al. (2014) and Milberg et al. (2019), that present-day production forests, and even clear-cuts, on former land managed as pasture or meadow has a considerably higher species richness of species typical for open grasslands. Our results indicate that the CKPs contribute to biological

legacies of former land-use, remaining in the forest flora for at least a century, perhaps longer, even in forests which have been transformed by modern production forestry.

Our results are consistent with a study from Tuscany (Italy), where Carrari et al. (2016a) found a higher diversity of understory plants at CKPs, and that the occurrence of several species differed between CKPs and controls. In their study, one species was more common at controls (*Anemone nemorosa*), whereas 12 species were more common on CKPs. Three of them (as well as *A. nemorosa*) are included in our data (*Dactylis glomerata*, *Poa trivialis* and *Prunella vulgaris*), but none of them showed any response to CKPs in our study. However, one species found by Carrari et al. (2016a) to be more common on CKPs in Tuscany, *Luzula forsteri*, is closely related to *L. pilosa* which in our study was over-represented on CKPs. We know of only one more study that has quantified species richness on CKPs. Young et al. (1996) conducted a study in the Appalachian mountains (USA) and they found that understory density and species richness were consistently, although not significantly, lower on CKPs. Thus, the effects of CKPs on species richness is likely to be dependent on context, for example the composition and requirement of the species in the regional species pool, and aspects of the charcoal kiln technology, such as the extent of litter raking for construction of the kilns (Krebs et al. 2017, Vild et al. 2018). We suggest that the results we obtain on a positive effect of CKP on species richness is contextually dependent on these forest's previous history as land partly used for livestock grazing, and with specific areas used as hay-meadows.

Furthermore, not only species occurrences differ between CKPs and control, but also, for some species, their cover. For three of the species the difference in cover was congruent with the difference in frequency, *Fragaria vesca* and *Luzula pilosa* (higher at CKPs), and *Calluna vulgaris* (lower at CKPs). In addition to *Calluna*, we also found that the two dominating *Vaccinium* species had lower cover on CKPs. The only direct comparison in the literature is Mikan and Abrams (1995) who also found a lower cover of *Vaccinium* shrubs at CKPs. A tentative generalization is that the ericaceous shrubs, which are typical dominants in boreo-nemoral forests, have some disadvantage at CKPs. This may reflect that they are acidophilous, and that they are disfavored by the destruction of the raw humus layer associated with burning of the charcoal kilns.

It is also relevant to compare our results with studies not specifically of CKPs, but of general effects of forest fires on the boreo-nemoral flora. Forest fires are common in this vegetation, both as part of a natural fire dynamics, and as a result of intentional burning, historically conducted to promote grazing conditions for livestock (Granström and Niklasson 2008). Among plant species considered to be promoted by forest fires, several are included in our dataset, for example *Calamagrostis arundinacea*, *Deschampsia flexuosa*, *Chamenerion angustifolium* and *Rubus idaeus* (Groven and Niklasson 2005, Gustafsson et al. 2019). None of these species turned out to exhibit differences in frequency or cover between CKPs and controls. The most reasonable explanation

is that the direct effects of forest fires detected in the abundance of these species disappear after some time, and that any effect on these species are long gone among the investigated CKPs. We also note that *Pteridium aquilinum*, which according to Oinonen (1967) maintains stands many centuries after intentional fires, was not prevalent specifically on CKPs.

So what are the mechanisms promoting some species, such as *Fragaria vesca* and *Luzula pilosa*, and a whole group of low-frequent grassland species, at CKPs? Experiments (Carrari et al. 2018) would have been necessary to identify these mechanism, but the most likely explanation is that the strongly deviating soil conditions at CKPs play an important role. As our soil profiles show (Supporting information), and as confirmed by many other studies (Mikan and Abrams 1995, Criscuoli et al. 2014, Carrari et al. 2016a, Hardy et al. 2016, Hirsch et al. 2017, 2018), CKP soil is heavily enriched with charcoal remains, and charcoal has many effects on boreal forest soils (Hart and Luckai 2013). There are large stocks of carbon stored in forest soils as remains of historic charcoal production (Mastrolonardo et al. 2018, Bonhage et al. 2020). The residence time in soil for carbon added via charcoal has been found to be around 600 years ( $650 \pm 139$  years) (Criscuoli et al. 2014). Furthermore, as in our study (marginally significant), the pH is typically higher at CKPs (Mikan and Abrams 1995, Young et al. 1996, Hardy et al. 2016, Carrari et al. 2016a). For other nutrients, results from other studies vary. In contrast to our results, Hardy et al. (2016) found that soil at CKPs were depleted in potassium and phosphorous, and Hirsch et al. (2018) found no clear differences at all in soil chemistry between CKPs and controls. Young et al. (1996) found accumulation of calcium at CKPs, but depletion of phosphorous. Two studies, however, are fully congruent with our results. Criscuoli et al. (2014) documented enrichment at CKPs of phosphorous, potassium, calcium and magnesium, and Mikan and Abrams (1995) found enrichment of potassium, calcium and magnesium at CKPs. Although we did not investigate this, there might also be other soil conditions specific to CKPs, e.g. enrichment of various aromatic carbon compounds (Hirsch et al. 2017) and effects on water availability (Schneider et al. 2018). Wardle et al. (1998) highlighted that fire-produced charcoal may adsorb various secondary metabolites and humus phenolics, especially from ericaceous shrubs, possibly promoting seedling recruitment (and spore recruitment in ferns) of several species.

Even though our study was not experimental, and we therefore cannot identify the acting mechanisms, it is reasonable that the deviating soil conditions contribute to the overall pattern that generally more species inhabit CKPs than the neighboring surrounding forest. One contributing factor may also be that the typically dominating ericaceous species (*Vaccinium* and *Calluna*) have less cover at CKPs. Furthermore, as is evident from Fig. 5, the slightly higher species richness at CKPs occurs along the gradient of local species richness of the investigated sites, ranging from 7 to 38 species, recorded in the controls. This can be interpreted in two ways. It may be that there is an underlying environmental

variation affecting species richness in both the CKPs and their respective controls. Furthermore, the species richness in the forest close to each CKP may affect the colonization rate at the CKP. More species in the neighborhood implies that more species could colonize the CKP after the last kiln was completed, i.e. an effect of the size of the local species pool (Zobel 2016). Unfortunately, we have no data enabling us to distinguish between these mechanisms, but a fair guess is that they are complementary rather than alternative.

There may be a succession process that we have not detected, from when the last charcoal kiln was completed at each site and until the present. As mentioned in the Methods section we have no data on the age of the CKPs (i.e. when the last charcoal kiln was raised), but we may speculate that there is a hidden pattern in the data reflecting a successional development of the flora at a CKP, from the first colonizers until the species composition we see today. Perhaps this process is manifested in the few cases where there was a conspicuously low species richness at the CKPs as compared with controls (i.e. dots well below the hatched line in Fig. 5). Before the field survey, we expected that CKPs with particularly dense stands of *Picea abies*, which have been remarked to characterize CKPs in Sweden (Fig. 4), would represent relatively young CKPs, which then would contain unusually few species. In that case, *P. abies* would be an initial colonizer, and only after thinning of the dense stand (due to mortality) many other species may colonize. However, although we cannot conclude anything about the CKPs age, the three CKPs we found that most obviously conformed to the description with dense and stunted *P. abies*, contained 8, 26 and 28 species, respectively. Thus, the idea that these only included a few early colonizers was not supported. The finding that only three of our 50 CKPs actually looked like this, is rather in line with some other studies suggesting that for woody species, CKPs inhibits recruitment (Mikan and Abrams 1996, Carrari et al. 2016b, 2018).

Historic charcoal production has left plenty of legacies in forests, not only in Sweden, but in many parts of the world. The most obvious remains, the CKPs, are often scattered densely in present-day forest. However, the density of CKPs in our study area (ca 6.6 per km<sup>2</sup>) is actually low compared with other studies. In Connecticut, USA, Hirsch et al. (2017) reported ca 17 CKPs per km<sup>2</sup>, and the figures presented by Bonhage et al. (2020) for Brandenburg, Germany, and Carrari et al. (2017) for Tuscany, Italy, are considerably higher, 3 and 5.5 CKPs per hectare, respectively. Indeed, the density of CKPs generally seem to be highest in Mediterranean forests, even up to 40 CKPs per hectare (Blondel 2006). This large variation in CKP density probably reflect differences in production technology, for example the size of the charcoal kilns, and also whether each kiln site was used at a single occasion or repeatedly. It may also reflect variation in the forest productivity. In any case, it is evident that CKPs represent abundantly occurring cultural traces from historic charcoal production in many forest areas. As our study (and also Carrari et al. 2016a) shows, the CKPs harbor a deviating flora compared with the surrounding forest,

which is still detectable long after the charcoal production has ceased. CKPs are thus manifesting biological features associated with the cultural history of previous forest use and management. This conclusion adds to a growing awareness of the hitherto much neglected biological cultural heritage in forests (Agnoletti and Santoro 2015, Eriksson 2018).

Although the species recorded in our study as favored by the environment at CKPs did not contain any conspicuously 'rare' species, or species considered to be threatened, the results clearly shows that the CKPs contribute to heterogeneity and diversity of boreo-nemoral forests, which indirectly may favor even other species than those recorded by us. Other studies have reached the same conclusion (Carrari et al. 2016a, Máliš et al. 2021). In their study from Italy, Carrari et al. (2016a, p. 494) concluded that '(...) abandoned charcoal kiln platforms represent stable anthropogenic microhabitats that can increase the diversity, (...) and compositional variability of different types of forest understories (...)'. We concur with this conclusion. Charcoal kiln platforms are not only interesting physical remains of a historic use of boreal and boreo-nemoral forests, which, at least regionally, was dominating just a century ago and engaged lots of people, they also represent abundant but easily overlooked anthropogenic environments, contributing to the biological diversity in these northern forests. Being the perhaps most conspicuous historic legacies in boreo-nemoral forests manifested also biologically, charcoal kiln platforms deserve more attention in research.

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## Author contributions

**Ove Eriksson:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Linnea Glav Lundin:** Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (supporting); Visualization (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

## Data availability statement

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.rn8pk0p9q>> (Eriksson and Glav Lundin 2021).

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