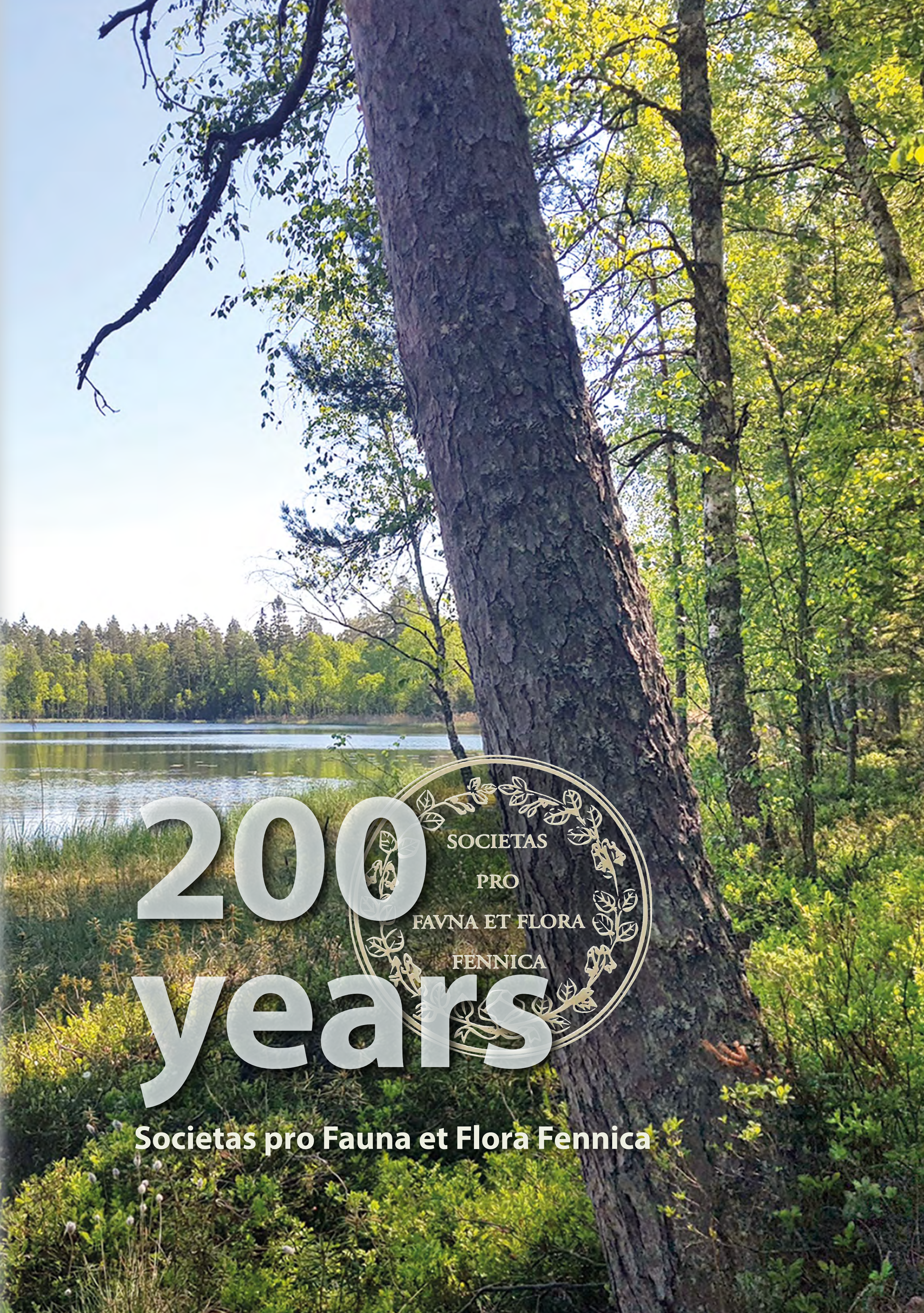

200 years

Societas pro Fauna et Flora Fennica

In 2021, Societas pro Fauna et Flora Fennica's 200th anniversary was celebrated in the Finnish House of Nobility, Helsinki. Photograph by Daniel Torsell / Epific.

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Cover photo
In honor of the 200th anniversary celebrations of the *Societas pro Fauna et Flora Fennica*, a fundraising was organized to acquire an old Finnish forest for protection in collaboration with the Finnish Natural Heritage Foundation. The landscape in Laipansalo is particularly beautiful, and its forest retains a strong feeling of an old-growth forest in its natural state. The terrain varies from light, rocky pine woods dotted with *Cladonia stellaris*, a type of reindeer lichen, to spruce-dominated forests where fallen decayed trees covered in bracket fungus which shows how untouched the area has remained. In the glades of the forest, the wetlands covered in peat moss stand out as shining green spots among the dark surrounding spruce woods. The long shoreline of the small lake hidden in the forest is especially charming. As a conservation area, the natural state of the wild forest will increase over the coming decades, and the habitats will become more and more suitable for species that live in old-growth forests. – Finnish Natural Heritage Foundation, photograph by Heini Koivuniemi.

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Societas pro Fauna et Flora Fennica 200 years

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Photograph by Sonja Still

Panel on The future of Flora and Fauna in Finland. Participants from the left: Docent Aleksi Lehikoinen, Docent Maria Hällfors, Prof. Mikko Mönkkönen and Prof. Erik Bonsdorff, hosted by Heidi Björklund and Tobias Tammelander.

Honorary chairman Carl-Adam Hægström gave his presentation remotely.

Photograph by Sonja Still

Societatis pro Fauna et Flora Fennica 200 years

5. November 2021
Finnish House of Nobility, Helsinki

Program

Symposium
9.00 Welcome words
Docent Mikael von Numers, the chairman of the Society
9.10 What do birds tell us about recent changes in the environment?
Docent Aleksi Lehikoinen, University of Helsinki
9.40 The impact of climate change on species in Finland
Docent Maria Hällfors, University of Helsinki

Break

10.40 The changing fauna and flora of Finland – discovering the bigger picture through long-term data,
Prof. Tomas Roslin, SLU Uppsala, University of Helsinki
11.10 What can the long-term ecological monitoring of the Åland islands meadow network tell us about changes in Finnish nature?
Prof. Marjo Saastamoinen, University of Helsinki

Break

12.45 More wood but less biodiversity in forests in Finland: a historical evaluation
Prof. Mikko Mönkkönen, University of Jyväskylä
13.15 Rethinking research: the role of tradition in the study of marine invertebrates
Prof. Erik Bonsdorff, Åbo Akademi University

Break

14.15 The nature loss is still going on – should we look beyond the borders of our country?
Prof. Ilari Sääksjärvi, University of Turku

15.00 Panel: The future of Flora and Fauna in Finland
Participants Prof. Erik Bonsdorff, Docent Maria Hällfors, Docent Aleksi Lehikoinen and Prof. Mikko Mönkkönen

16.15 Societas pro Fauna et Flora Fennica – 200 years – a survey of the activities 1997–2021
Prof. Carl-Adam Hæggström

19.00 Dinner

Music by Ainoa Quartet
Isa Halme, Auroora Kiiski Touizrar & Iisa Kostiainen (violin), Kristiina Hirvonen (cello)

Greeting words


Photograph by Daniel Torsell / Epific

People are named in the pictures from left to right. Stephen Venn, Tapani Veistola, Maria Hällfors, Juho Paukkunen.

Heidi Björklund, Sonja Still, Ulrika Candolin.


Photograph by Daniel Torsell / Epific

Welcome words

Honoured members, ladies and gentlemen

Mikael von Numers

Photo: Video screenshot / RajuLive.fi

In 1921, *Societas pro Fauna et Flora Fennica's* 100th anniversary was celebrated in the Ceremonial Hall of the University of Helsinki. The chairperson was Alvar Palmgren, who would soon become professor of Botany at the University of Helsinki. Palmgren could then look back on a hundred years of activity since the *Society* was founded in Turku on November 1, 1821. The founders were Professor Carl Reinhold Sahlberg together with nine other natural scientists and students. This took place only 43 years after Linnaeus' death and 38 years before Darwin's *The Origin of Species* was published. Finland had a population of about 1 million. Knowledge of the animals and plants of Finland was limited. For example, only 600 of Finland's vascular plant species were known. The primary purpose of the *Society* was unequivocal: to compile a complete collection of the animals and plants of Finland.

During the first one hundred years, some events were crucial for the *Society*. Virtually all of the *Society's* collections and documents were destroyed in the Turku fire in 1827. After the fire, the *Society* moved with the University to Helsinki, and operations were re-established. The number of members increased gradually. In 1827, the *Society* had 119 members. At the turn of the century, the number approached 1 000. The number of members has remained at the same level, and it still is a little over a thousand. The first female member, Minna Sahlberg, was enrolled in 1878. Among the *Society's* chairpersons were noteworthy scientists, such as the botanist Professor Wilhelm Nylander and the zoologist Professor Johan Axel Palmén.

At an early stage, the *Society* set up a "standing fund" that would form the basis for scholarships and for financing expeditions. As early as 1838 money was, for example, allocated for scientific expeditions in Finland and its surrounding areas.

The *Society's* publishing activities began on a small scale in the 1830s, but it expanded rapidly. In 1921, the number of printed pages in the *Society's* journals already amounted to 37,000. It can rightly be said that the *Society's* publications well into the 20th century played a central role in increasing scientific knowledge about Finland's fauna and flora. Today, *Memoranda Societatis pro Fauna et Flora Fennica* (*Memoranda*) remains as the scientific journal of the *Society*.

In 1858, the *Society's* biological collections were merged with the collections of the university, and they thus form the basis for the current collections at the Finnish Museum of Natural History. From 1876, the *Society's* statutes were written in both Swedish and Finnish, and the *Society* became bilingual.

The focus of the activity of the *Society* shifted early from pure collection of species to botanical and zoological research in a broader sense. Alvar Palmgren declared in his speech 100 years ago, that the *Society* should promote zoological and botanical research of Finland in all its extent.

This is how it has remained. Today, the *Society's* most important tasks are to support graduates and doctoral students with scholarships, to publish *Memoranda* and to maintain Nåtö biological station together with the Government of Åland. In addition, the *Society* arranges meetings and symposia.

Now, back to Palmgren 100 years ago! This is how he ended his speech (somewhat shortened): ”Today the members of *Societas pro Fauna et Flora Fennica* gather to pay tribute to the past one hundred years of work. We pay tribute to you, who a hundred years ago with foresightedness built the foundation for the zoological and botanical exploration of our motherland, the founders of the *Society*. In the last hundred years Natural Science has made tremendous progress. The naturalist is thrilled to speculate what the next hundred years will testify to the history of life. May you, biologists of the future, see fulfilled the promises, which for us begin to appear above the horizon in the land of science! Future generations in *Societas pro Fauna et Flora Fennica*, may you see the plant and animal world of our motherland depicted with near totality; may its structure emerge in the light of laws, which we have merely sought! You, who a hundred years in the future, make up this *Society*, take our greeting through the century that separates us! Pass it on to those who will hereafter gather in the name of Finland's zoological and botanical research!”

So now, one hundred years later, we have received the greeting. Thank you Alvar Palmgren!

As we all know, developments in all areas of Biology have been breathtaking since Palmgren gave his speech. On the other hand, the development, or should we say the state of the object of biological research, has not been so. For nature itself and for the species, conditions have deteriorated.

Nature and species protection were already relevant a hundred years ago. For example, one can read in the *Society's* journals that the capercaillie had disappeared as a breeding bird from Drumsö in Helsinki just a few years before the 100th anniversary. The scale and extent of the decline in biodiversity is now, unfortunately, completely different from how it was then.

Today we know much more about what is needed to keep ecosystems functioning and to keep populations viable. We can create models and make forecasts. Statistics and methods of analysis have developed tremendously. Today we have a world that is increasingly depleted of both biotopes and species. In theory, we know what should be done to be able to maintain species diversity. Now measures and actions are needed. What the *Society* originally stood for is still relevant: knowledge of the species, their distribution and biology still holds a key position when it comes to ensuring that a sustainable nature is maintained.

Therefore, we have every reason to look ahead: we can now do as Palmgren did a hundred years ago.

You who in a hundred years (in 2121) make up this *Society*, take our greeting through the century that separates us! The challenge of the future, as we now see it, is to be able to preserve functioning, diverse and species-rich ecosystems of Finland and of the earth. We ask you to convey the greeting to all those who will in future come together in the name of Finland's zoological and botanical research!

In honor of the 200th anniversary celebrations, a collection was organized to acquire an old Finnish forest for protection in collaboration with the Finnish Natural Heritage Foundation.

Välkomstord

Ärade festpublik, mina damer och herrar

Mikael von Numers

Photo: Video screenshot / RajuLive.fi

År 1921 firades *Societas pro Fauna ett Fennicas* 100-årsjubileum i Helsingfors universitets solennitetssal. Ordförande var Alvar Palmgren som snart skulle bli professor i botanik vid Helsingfors universitet. Palmgren kunde då blicka tillbaka på 100 år av verksamhet sedan *Societas* grundades i Åbo den 1 november år 1821. Grundarna var professor Carl Reinhold Sahlberg tillsammans med nio andra naturforskare och studenter. Detta hände alltså bara 43 år efter Linnés död och 38 år före Darwins *Om arternas uppkomst* utkom. Finland hade en befolkning på ungefär en miljon. Kunskapen om Finlands djur- och växtvärld var mycket begränsad. Exempelvis kände man till endast 600 av Finlands kärlväxtarter. *Societas* primära syfte var entydigt: att sammanställa en fullständig samling av Finlands djur och växter.

Under de första hundra verksamhetsåren inträffade några händelser som var avgörande för *Societas*. I stort sett alla *Societas* samlingar och dokument förstördes i Åbo brand år 1827. Efter branden flyttade *Societas* med universitetet till Helsingfors och verksamheten återupprättades. Medlemsantalet steg efter hand. Vid sekelskiftet närmade sig antalet medlemmar 1 000. Sedan dess has *Societas* medlemsantal etablerats kring en bit över tusen. Den första kvinnliga medlemmen, Minna Sahlberg, skrevs in år 1878. Bland *Societas* ordförande märks betydande forskare, såsom botanisten Wilhelm Nylander och zoologen Johan Axel Palmén.

Societas anlade tidigt en ”stående fond” som skulle utgöra grunden för framtida stipendiemedel och finansiering av expeditioner. Redan år 1838 anslogs exempelvis pengar för att göra vetenskapliga expeditioner i Finland och dess närområden.

Societas publiceringsverksamhet började i liten skala på 1830-talet, men den utökades snabbt. År 1921 uppgick antalet tryckta sidor i *Societas* serier redan till 37 000. Man kan med fog påstå att *Societas* publikationer långt in på 1900-talet spelade en central roll då det gällde att öka den vetenskapliga kunskapen om Finlands fauna och flora. Idag återstår *Memoranda Societatis pro Fauna et Flora Fennica* (*Memoranda*) som *Societas* vetenskapliga serie.

År 1858 förenades *Societas* biologiska samlingar med universitetets samlingar, och de utgör därmed grunden för de nuvarande samlingarna vid Naturvetenskapliga centralmuseet. Från 1876 skrevs *Societas* stadgar på både svenska och finska, och Sällskapet blev med detta tvåspråkigt.

Tyngdpunkten för verksamheten flyttades redan tidigt från rent samlande av arter till botanisk och zoologisk forskning i en vidare bemärkelse. För 100 år sedan deklarerade Alvar Palmgren i sitt tal att *Societas* skulle vara ett sällskap för fäderneslandets zoologiska och botaniska forskning i hela dess vidd. Så har det förblivit. Idag är *Societas* viktigaste uppgifter att med stipendier understöda graduister och doktorander, att utge *Memoranda* och att ha hand om Nåtö biologiska station tillsammans med Ålands landskapsregering. Dessutom ordnas möten och symposier.

Nu tillbaka till Palmgren för 100 år sedan! Så här avslutade han sitt föredrag (förkortat och aningen moderniserat): ”Så samlas *Societas pro Fauna et Flora Fennica* i dag att bringa gångna hundra års arbete sin hyllning. Ni som för hundra år sedan med framsynt blick byggde grunden för fosterlandets zoologiska och botaniska utforskande, tag vår hyllning! De senaste hundra årens naturforskning har skådat ett bevingat framåtskridande. Naturforskaren står hänryckt undrande vad kommande hundra år skola vittna om livets historia. Kommande generationer i *Societas pro Fauna et Flora Fennica*! Må ni se fäderneslandets växt- och djurvärld i möjlig fulländning tecknad; träde dess byggnad fram i ljuset av lagar, dem vi blott sökt! Ni som hundra år härefter utgör detta sällskap! Ta vår hälsning genom det skiljande seklet! För den vidare till alla dem som samlas i namn av Finlands zoologiska och botaniska forskning!”

Vi har alltså nu 100 år senare tagit emot hälsningen. Tack Alvar Palmgren!

Som vi vet har utvecklingen inom alla biologins områden varit hisnande sedan Palmgren höll sitt tal. Däremot har tillståndet för föremålet för den biologiska forskningen inte varit det. För själva naturen och för arterna har det gått mot det sämre. Natur- och artskydd var aktuella redan för 100 år sedan. Exempelvis kan man i sällskapets serier läsa att tjädern försvann som häckfågel från Drumsö i Helsingfors bara några år före 100-årsjubileet. Skalan och omfattningen av minskningen i den biologiska mångfalden är idag självfallet en helt annan än då.

Idag vet vi mycket mer om vad som behövs för att hålla ekosystem fungerande och för att hålla populationer livskraftiga. Vi kan modellera och göra prognoser. Statistiken och analysmetoderna har utvecklats enormt. Dagens värld är allt mer utarmad på både biotoper och arter. I teorin vet vi vad som bör göras för att bibehålla artmångfalden. Nu är det åtgärder och handling som behövs. Det som sällskapet ursprungligen stod för är fortfarande aktuellt. Kännedomen om arterna, deras utbredning och biologi är i en nyckelställning då det gäller att försäkra sig om en fortsatt livskraftig natur.

Vi har alltså all orsak att blicka framåt: vi kan nu göra som Palmgren gjorde för hundra år sedan.

Ni som hundra år härefter år 2121 utgör detta sällskap! Ta vår hälsning genom det skiljande seklet! Framtidens utmaning, som vi nu ser det, är att kunna bevara Finlands och jordens ekosystem fungerande, mångformiga och artrika. För hälsningen vidare till alla dem, som i framtiden kommer att samlas i namn av Finlands zoologiska och botaniska forskning!

200-årsjubileet till ära anordnades i samarbete med Stiftelsen för naturarvet i Finland en insamling för att skydda ett område gammelskog.

Tervetuliaissanat

Arvoisa juhlayleisö

Mikael von Numers

Photo: Video screenshot / RajuLive.fi

Vuonna 1921 *Societas pro Fauna et Flora Fennica* vietti satavuotisjuhlapäivää Helsingin yliopiston juhlasalissa. Puheenjohtajana toimi yliopiston tuleva kasvitieteen professori Alvar Palmgren. Tuolloin Palmgren muisteli 100-vuotista toimintaa sen alusta lähtien. Seura perustettiin Turussa 1. marraskuuta 1821. Perustajina olivat professori Carl Reinhold Sahlberg yhdessä yhdeksän muun luonnontieteilijän ja ylioppilaan kanssa. Tämä tapahtui vain 43 vuotta Linnén kuoleman jälkeen, ja 38 vuotta ennen Darwinin *Lajien synnyn* julkaisemista. Suomen asukasluku oli noin miljoona. Suomen eläimistön ja kasviston tuntemus oli hyvin vähäistä. Esimerkiksi putkilokasveja tunnettiin ainoastaan 600 lajia. Seuran ensisijainen tarkoitus oli selkeä: koota täydellinen kokoelma Suomen eläimistä ja kasveista.

Seuran ensimmäisen sadan toimintavuoden aikana oli useita seuran kannalta merkittäviä tapahtumia. Lähes kaikki sen kokoelmat ja kirjoitukset tuhoutuivat Turun palossa vuonna 1827. Palon jälkeen *Societas* muutti yliopiston mukana Helsinkiin, jossa toiminta aloitettiin uudelleen. Jäsenmäärä kasvoi vähitellen. Vuosisadan vaihteessa se lähestyi tuhatta. Sittemmin seuran jäsenmäärä on vakiintunut vähän yli tuhannen paikkeille. Ensimmäinen naisjäsen, Minna Sahlberg, valittiin seuraan vuonna 1878. Seuran puheenjohtajien joukosta löytyy huomattavia tutkijoita, kuten kasvitieteilijä Wilhelm Nylander ja eläintieteilijä Johan Axel Palmén.

Societas perusti varhain ”pysyvän rahaston”, joka muodostaisi perustan tuleville stipendien myöntämisille ja tutkimusmatkojen rahoituksille. Jo vuonna 1838 myönnettiin rahaa tieteellisten tutkimusretkien toteuttamiseen Suomessa ja sen lähialueilla.

Seuran julkaisutoiminta alkoi pienimuotoisesti jo 1830-luvulla, mutta laajeni nopeasti. Seuran 100-vuotispäivänä julkaisujen sivumäärä oli jo noin 37 000. On perusteltua sanoa, että Seuran sarjoilla oli keskeinen asema tieteellisen tiedon lisäämisessä Suomen eläimistöstä ja kasvistosta pitkälle 1900-luvulle. Nykyisin *Societas* julkaisee tieteellistä sarjaa *Memoranda Societatis pro Fauna et Flora Fennica* (*Memoranda*).

Seuran sekä yliopiston eläin- ja kasvitieteelliset kokoelmat yhdistettiin 1850-luvulla, ja ovat nykyisen Luonnontieteellisen keskusmuseon kokoelmien alku. Vuodesta 1876 seuran säännöt kirjoitettiin sekä ruotsiksi että suomeksi, seurasta tuli kaksikielinen.

Toiminnan painopiste siirtyi jo varhain kokoelmien kartuttamisesta laajemmin kasvi- ja eläintieteelliseen tutkimukseen. Sata vuotta sitten Alvar Palmgren julisti puheessaan, että *Societaksen* tulisi olla seura isänmaan eläin- ja kasvitieteen tutkimukselle koko sen laajuudessa.

Nykyään seuran tärkeimpiä tehtäviä on tukea stipendein pro gradu-tutkielmien ja väitöskirjojen tekijöitä, *Memorandan* julkaiseminen sekä Nåtön biologisen aseman ylläpito yhdessä Ahvenanmaan lääninhallituksen kanssa. Lisäksi järjestetään kokouksia ja symposiumeja.

Nyt takaisin Palmgreniin 100 vuotta sitten! Näin hän päätti puheensa (lyhennettynä ja hieman nykyaikaistettuna): ”Tänään *Societas pro Fauna et Flora Fennica* kokoontuu osoittamaan kunnioitusta kuluneen sadan vuoden työlle. Te, jotka sata vuotta sitten kaukonäköisesti rakensitte perustan isänmaan eläintieteelliselle ja kasvitieteelliselle tutkimustyölle, ottakaa kunnianosoituksemme vastaan! Viimeisen sadan vuoden aikana luonnontiede on edennyt kuin siivin. Luonnontieteilijä seisoo hämmästyneenä pohtien, mitä uutta seuraavat sata vuotta tulevat kertomaan elämän historiasta. Tulevat sukupolvet *Societas pro Fauna et Flora Fennicassa*! Olkoon isänmaan kasvi- ja eläinmaailma tuolloin mahdollisimman täydellisesti kuvattu; ilmestyköön sen rakenne niiden lakien valossa, joita olemme vain etsineet! Te jotka sadan vuoden kuluttua muodostatte tämän seuran! Ottakaa tervehdyksemme vastaan meitä erottavan vuosisadan halki! Välittäkää se kaikille suomalaisen eläin- ja kasvitieteellisen tutkimuksen nimissä kokoontuneille!»

Olemme nyt 100 vuotta myöhemmin vastaanottaneet tervehdyksen. Kiitos Alvar Palmgren!

Kuten tiedämme, kehitys kaikilla biologian alueilla on ollut henkeäsalpaava Palmgrenin puheen jälkeen. Itse biologisen tutkimuksen kohteen eli luonnon tila ei kuitenkaan ole kehittynyt suotuisasti. Luonnon ja lajien kannalta asiat ovat menneet huonompaan suuntaan. Luonnon- ja lajiensuojelu oli ajankohtaista jo 100 vuotta sitten. Seuran julkaisuista voi esimerkiksi lukea, että metso katosi pesimälintuna Helsingin Lauttasaaresta vain muutamaa vuotta ennen satavuotisjuhlapäivää. Biologisen monimuotoisuuden vähenemisen laajuus on nykyään täysin eri suuruusluokkaa kuin silloin.

Tänään tiedämme paljon enemmän siitä, mitä tarvitaan ekosysteemien toimivuuden ja populaatioiden elinkelpoisuuden ylläpitämiseksi. Osaamme mallintaa ja tehdä ennusteita. Tilastotiede ja analyysimenetelmät ovat kehittyneet valtavasti. Nykyään maailma on enenevissä määrin köyhtynyt biotoopeista ja lajeista. Teoriassa tiedämme, mitä pitäisi tehdä lajiston monimuotoisuuden säilyttämiseksi. Nyt kuitenkin tarvitaan toimenpiteitä ja tekoja. Asiat, joita seura alkuaan edusti, ovat edelleen ajankohtaisia. Lajien, niiden levinneisyyden ja biologian tuntemus ovat avainasemassa elinvoimaisen luonnon säilymisen kannalta.

Meillä on siis täysi syy katsoa eteenpäin: voimme nyt tehdä kuten Palmgren teki sata vuotta sitten.

Te jotka sadan vuoden kuluttua vuonna 2121 muodostatte tämän seuran! Ottakaa tervehdyksemme vastaan meitä erottavan vuosisadan halki! Tulevaisuuden haaste on pystyä säilyttämään Suomen ja maapallon ekosysteemit toimivina, monipuolisina ja lajirikkaina. Välittäkää te puolestanne tervehdys eteenpäin kaikille niille, jotka tulevaisuudessa kokoontuvat Suomen eläintieteellisen ja kasvitieteellisen tutkimuksen nimissä!

200-vuotisjuhlan kunniaksi järjestettiin Luonnonperintösäätiön kanssa keräys suomalaisen vanhan metsän hankkimiseksi suojeltavaksi.

MESSAGE FROM THE PRESIDENT OF THE REPUBLIC OF FINLAND

This year Societas pro Fauna et Flora Fennica turns honorable 200 years. Societas pro Fauna et Flora Fennica, which was founded in 1821 in Turku and later moved to Helsinki, is Finland's oldest scientific society.

Since its founding, Societas pro Fauna et Flora Fennica has worked to improve the knowledge of the fauna and flora and to promote nature conservation in Finland. The society's collections of animals and plants, as well as symposia, excursions and publishing activities, have significantly contributed to an increased knowledge of the flora and fauna, and to botanical and zoological research in our country.

Today, Societas pro Fauna et Flora Fennica plays an important role, among other things, in awarding scholarships for scientific theses. At the society's symposia, current nature conservation issues have often been addressed from a scientific perspective. The society is also active in Åland, where the Nåtö Biological Station started its activities in 1964.

I would like to extend my warm congratulations to Societas pro Fauna et Flora Fennica on the occasion of its 200th anniversary, and thank the society for the work it has done for the Finnish fauna and flora. I wish all participants a successful anniversary symposium.

Sauli Niinistö
President of the Republic of Finland

REPUBLIKENS PRESIDENTS HÄLSNING

I år fyller Societas pro Fauna et Flora Fennica 200 år. Det är en hedersvärd ålder. Societas pro Fauna et Flora Fennica som grundades år 1821 i Åbo och som senare flyttade till Helsingfors, är Finlands äldsta vetenskapliga samfund.

Sedan grundandet har Societas pro Fauna et Flora Fennica arbetat för att förbättra kännedomen om djur- och växtvärlden och främja naturvården i Finland. Samfundets samlingar av djur och växter, symposier, exkursioner och publiceringsverksamhet har på ett markant sätt bidragit till en ökad kunskap om växt- och djurvärlden och till den växt- och djurvetenskapliga forskningen i vårt land.

I dag har Societas pro Fauna et Flora Fennica en viktig roll bland annat när det gäller att bevilja stipendier för vetenskapliga avhandlingar. På samfundets symposier har man ofta behandlat aktuella naturvårdsfrågor ur ett vetenskapligt perspektiv. Samfundet är också verksamt på Åland, där Nåtö biologiska station inledde sin verksamhet år 1964.

Jag vill rikta mina varma gratulationer till Societas pro Fauna et Flora Fennica med anledning av 200-årsjubileet och tacka samfundet för det arbete som det gjort för den finländska djur- och växtvärlden. Jag önskar alla deltagare ett lyckat jubileumssymposium.

Sauli Niinistö

Sauli Niinistö
Republikens president

TASAVALLAN PRESIDENTIN TERVEHDYS

Societas pro Fauna et Flora Fennica täyttää tänä vuonna kunnioitettavat 200 vuotta. Turussa vuonna 1821 perustettu ja sittemmin Helsinkiin muuttanut Societas pro Fauna et Flora Fennica on Suomen vanhin tieteellinen seura.

Perustamisvuodestaan lähtien Societas pro Fauna et Flora Fennica on työskennellyt eläin- ja kasvimaailman tuntemuksen sekä luonnonsuojelun edistämiseksi Suomessa. Seuran keräämät eläin- ja kasvimaailman kokoelmat, tapahtumat, retket ja julkaisutoiminta ovat edistäneet merkittävällä tavalla maamme eläin- ja kasvimaailman tuntemusta sekä eläin- ja kasvitieteellistä tutkimusta.

Nykyään Societas pro Fauna et Flora Fennicalla on tärkeä tehtävä muun muassa opinnäytetöiden rahoittajana. Seuran symposiumeissa on usein käsitelty ajankohtaisia luonnonsuojelukysymyksiä tieteellisestä näkökulmasta. Toimintaa on myös Ahvenanmaalla, jossa Nåtön biologinen asema on toiminut vuodesta 1964.

Onnittelen lämpimästi Societas pro Fauna et Flora Fennicaa 200-vuotisjuhlavuodesta ja kiitän työstänne suomalaisen eläin- ja kasvimaailman hyväksi. Toivotan kaikille symposiumiin osallistuville onnistunutta juhlatilaisuutta.

Sauli Niinistö
Tasavallan presidentti

Photographs on pages XIV–XL by Daniel Torsell / Epific

Roland Skytén, Magnus Lindström.

Jon Brommer, Marjo Saastamoinen, Aleksi Lehikoinen, Johanna Mappes.

Orvo Vitikainen, Pertti Uotila, Heikki Toivonen.

Henry Pihlström, Mikael von Numers, Tobias Tammelander, Patrik Karell, Heidi Björklund, Magnus Lindström.

Tomas Roslin, Jon Brommer, Mikael von Numers.

Tobias Tammelander, Aino Peltola, Wilma Lindberg, Magnus Lindström.

Jubilee Dinner Menu.

On the left: Henry Pihlström, Emma Vitikainen, Pertti Panula, Hanna Kokko, Kurt Fagerstedt. On the right Katja Rönkä, Stephen Venn, Johanna Mappes, Mats Gyllenberg, Marjatta Raudaskoski, Perttu Seppä.

On the left: Veikko Huhta, Hans Silfverberg, Orvo Vitikainen, Pertti Uotila, Terhi Ryttäri, Annina Kantelinen, Jaakko Kullberg, Liisa Simola. On the right: Ilpo Mannerkoski, Roland Skytén, Björn Federley, Torsten Stjernberg.

Tobias Tamelander, Aino Peltola

Marju Prass, Wille Fortelius, Sonja Still, Kai Lindström, Patrik Karell, Camilla Ekblad

Tomas Roslin, Marko Hyvärinen, Jouko Rikkinen, Mikael von Numers, Mikko Mönkkönen. Eeva Furman, Kristian Donner

Stephen Venn, Katja Rönkä.

Janne Heikkinen, Pertti Ranta

Heidi Björklund, Stella From, Janne Granroth, Eeva-Maria Tidenberg

Scandinavian rye and malt bread & butter.

Parsnip soup & roasted apple.

Pertti Panula, Hanna Kokko, Kurt Fagerstedt, Ulrika Candolin, Jarmo Saarikivi, Joni Ollonen.

Heikki Toivonen, Panu Kunttu, Anna Kärkönen, Jack Barkman

Marjatta Raudaskoski, Mats Gyllenberg, Johanna Mappes.

Pekka Niemelä, Martin Lodenius, Harri Saarinen, Toni Laaksonen.

On the left: Veikko Huhta. On the right: Laura Hiisivuori, Niko Johansson, Henry Väre, Torsten Stjernberg, Björn Federley, Roland Skytén, Ilpo Mannerkoski.

Pike-perch and Salmon Roll & White Wine Sauce, Hasselback Potatoes, Carrot Puree, Broccolini

Anna Kärkönen, Jack Barkman, Wilhelm Holmberg.

On the left Joni Ollonen, Kurt Fagerstedt, Henry Pihlström. On the right Marjatta Raudaskoski, Mats Gyllenberg, Johanna Mappes, Stephen Venn, Katja Rönkä.

Laura Hiisivuori, Niko Johansson, Henry Väre, Torsten Stjernberg.

Petteri Lehikoinen, Heidi Björklund, Stella From.

Mikael von Numers giving the Jubilee Dinner Talk.

Laura Hiisivuori, Jaakko Kullberg, Niko Johansson, Annina Kantelinen, Henry Väre.

Patrik Karell, Nina Hagner-Wahlsten, Kai Lindström, Sonja Still, Wille Fortelius, Tobias Tammelander, Marju Prass, Aino Peltola, Eeva-Maria Tidenberg, Wilma Lindberg, Janne Granroth, Magnus Lindström, Magnus Östman, Heidi Björklund, Kaisa Välimäki, Petteri Lehikoinen, Juho Paukkunen, Arja Kaasinen.

String Quartet Ainoa: Isa Halme (violin), Auroora Kiiski Touizrar (violin), Iisa Kostiainen (viola), Kristiina Hirvonen (cello).

The Finnish House of Nobility ballroom.

Panna Cotta with Red Currants.

Maria Hällfors, Mikko Mönkkönen, Eeva Furman, Kristian Donner

Annika Luther, Aleksi Lehikoinen, Marjo Saastamoinen, Leif Schulman, Lotta Sundström.

Gunilla Ståhls-Mäkelä, Magnus Östman, Kaisa Välimäki, Juho Paukkunen, Minna Pyykkö, Juhani Mänttäri.

Erkki Leppäkoski, Heta Rousi. Back turned: Camilla Ekblad.

Natur och Miljö's ("Nature and Environment") greeting to Societas pro Fauna et Flora Fennica by Magnus Östman.

Nordenskiöld samfundet's ("Nordenskiöld Society") greeting to Societas pro Fauna et Flora Fennica by Martin Lodenius.

The Finnish Association for Nature Conservation's greeting to Societas pro Fauna et Flora Fennica by Tapani Veistola.


Societas Biologica Fennica Vanamo's greeting to Societas pro Fauna et Flora Fennica by Annina Kantelinen.

Finska Läkaresällskapet's ("Finnish Medical Association") greeting to Societas pro Fauna et Flora Fennica by Pertti Panula.

Tvärminne Zoological Station's greeting to Societas pro Fauna et Flora Fennica by Magnus Lindström.

Marjo Saastamoinen, Leif Schulman, Lotta Sundström, Aino Juslén, Jon Brommer.


AVEC
Braastad Organic Finest VSOP
Baileys Original Irish Cream
Carlshamns Flaggpunsch Original
PROGRAM | OHJELMA
Middagstal | Illallispuhe
doc./dos. Mikael von Numers
Stråkkvartetten | Jousikvartetti Ainoa
Sibelius: Andante Festivo
Dvořák: Jousikvartetto F-duuri "Amerikkalainen",
osa I - Allegro ma non troppo
Haugen: Tjønneblomen

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More wood but less biodiversity in forests in Finland: a historical evaluation

Mikko Mönkkönen, Tuomas Aakala, Clemens Blattert, Daniel Burgas, Rémi Duflot, Kyle Eyvindson, Jari Kouki, Toni Laaksonen & Pekka Punttila

Photo: Video screenshot / RajuLive.fi

***Mönkkönen**, M., **Blattert**, C., **Burgas**, D. & **Duflot**, R., Department of Biological and Environmental Science & School of Resource Wisdom, University of Jyväskylä, FI-40014 Jyväskylä,* mikko.monkkonen @ jyu.fi, clemens.c.blattert @ jyu.fi, daniel.d.burgas @ jyu.fi, remi.r.duflot @ jyu.fi. ***Aakala**, T. & **Kouki**, J., School of Forest Sciences, University of Eastern Finland, FI-80101 Joensuu,* tuomas.aakala @ uef.fi, jari.kouki @ uef.fi; ***Eyvindson**, K., Norwegian University of Life Sciences, Faculty of Environmental Sciences and Natural Resource Management, NO-1432 Ås,* kyle.eyvindson @ nmbu.no. ***Laaksonen**, T., Department of Biology, University of Turku, FI-20500 Turku,* tokrla @ utu.fi. ***Punttila**, P., Finnish Environment Institute, FI-00790 Helsinki,* pekka.punttila @ syke.fi.

National forest inventories (NFI) in Finland provide empirical evidence for a marked increase in tree growth, total forest area, and total timber volume over the past century. Meanwhile, the assessments of threatened forest species and habitats indicate continuous degradation of biodiversity in Finnish forests. To shed light on this seeming paradox, we summarized the temporal patterns of forest characteristics (indicators) that have major influence on biodiversity, comparing the structure of current Finnish forests with natural and historical references. Using a variety of data sources, we estimated the proportion of area of old-growth forest and of deciduous-dominated forests, the density of large trees, and the amount of dead wood in Finnish forests under natural reference conditions, in the 1750s, 1920s (NFI1), and 2010s (NFI12). Our results show that levels of the forest structures essential to maintain ecologically diverse forests are below those that likely prevailed in Finland under natural reference conditions and in the 1750s. This scarcity is particularly pronounced for dead wood volumes and old forest area. The marked increase in the volume of living trees during the last century did not translate into improved biodiversity indicators and has not been effective for turning the tide of biodiversity loss in Finnish forests. We discuss actions that are necessary to safeguard forest biodiversity in Finland both in terms of protected areas and management in production forest.

Introduction

The hundred years of forest inventories in Nordic countries provide an exceptional time series on forest resources and their structure, allowing researchers to assess long-term changes over large spatial scales. These data from Finland show that during the past century forest growth has doubled, average per hectare growing stock (FAO 2020) has increased >50%, and drainage of millions of hectares of peatlands has provided more productive forest area. As a result, the current volume of growing stock is 1.7 times the growing stock 100 years ago (Korhonen et al. 2021). Simultaneously, three quarters of the forest habitat types are threatened (Kouki et al. 2018, 2019), there are more than 800 threatened species in Finnish forests, and forest-dwelling species is the largest group among all the threatened species (Hyvärinen et al. 2019). Moreover, the threat status of species has not improved between the two most recent assessments (2010 and 2019) and species are becoming more threatened in all habitats including forests (Hyvärinen et al. 2019). The paradox of having more wood but less biodiversity should be understood if we aim to sustainably manage forests.

Hundred years is still a short perspective to document forest history. To explore and understand this paradox, relevant time horizons are required that link natural forest successions to the impact of forest use. For example, human land use in the Nordic countries started many centuries ago, and therefore the changes we see in our forests over the past 100 years are contingent upon forest use during longer historical times.

To provide perspective regarding the changes in Finnish forests during the past 100 years, we compare their structure with those under natural reference conditions (no major human influence) and in 1750. The latter time point is used to assess threats and monitor the historical declines of ecosystems in the IUCN Red List of Ecosystems (IUCN 2015), and justified by the earliest onset of industrial-scale exploitation of ecosystems (Keith et al. 2013). In Finland, human population remained very low until the mid-18th century, after which population growth accelerated strongly. Simultaneously, slash-and-burn cultivation and human settlement expanded to more remote areas (Keto-Tokoi 2014a). Slash-and-burn cultivation, tar extraction, clearing forests for fields and meadows, and timber logging increased strongly, resulting in large-scale decline of primeval forests in the latter half of the 18th century and in the 19th century (Keto-Tokoi 2014a).

The early phases of intensive forest use were regionally highly variable. They had clear effects on forest characteristics, but these changes were most evident in southern Finland near the human population. Additionally, land clearing and slash-and-burn cultivation primarily affected the most fertile forest habitats first (Keto-Tokoi 2014a). Consequently, the forest landscapes in the late 1800s and early 1900s were quite heterogeneous and diverse, although the volumes of living trees were low in southern parts of the country. In fact, the historical analyses of forest use and timber supplies suggest that standing timber volumes were at a historical low in the early 1900s (Myllyntaus & Mattila 2002) when the Finnish national forest inventories (NFIs) began.

During the 1900s, intensive forest use expanded to even the most remote areas in northern Finland (Lihtonen 1949). Forest management and timber extraction occurred across all types of forests, regardless of their fertility or location (Kouki et al. 2001). This resulted in large-scale alteration of forest habitats. Forestry and management activities are the direct or indirect causes for changes in forest structure, threatening forest species (Hyvärinen et al. 2019) and habitats (Kouki et al. 2018). The major consequences of human use of forest resources are the decrease in old-growth forest area, number of large trees, amount of dead wood, and proportion of deciduous trees and deciduous-dominated forests, which are critical characteristics for biodiversity in boreal forests.

To understand the paradox of “more wood but less biodiversity”, we explored the temporal patterns of forest characteristics that have major influence on biodiversity, comparing the structure of current Finnish forests with their structure in the past. We entitle these forest characteristics as forest biodiversity indicators. We evaluated these changes using the data produced by the Red List evaluation of forest habitat types in Finland and Finnish NFIs. Provided the regional differences in forestry history, we made this assessment separately for southern Finland (including hemiboreal, southern, and middle boreal zones) and northern Finland (northern boreal zone) which represent 15.2 and 5 million ha of total productive forest land area, respectively (productive forest land refers to land where the annual tree growth is more than one cubic metre per hectare). Our study is closely related to the Red List assessment of forest habitats in Finland by Kouki et al. (2018, 2019). To that assessment, our current study adds a longer time perspective (the NFIs were only used for the period of 1960s onward in Kouki et al. (2018), i.e., for the last 50 years) and uses natural forests as a reference point to explore habitat changes (the farthest historical reference point in Kouki et al. was the year 1750). In addition, we are not aiming at a habitat type level analysis. Instead, we explore more thoroughly the overall country-level patterns from the natural state through 1750s to the 1920s, and finally, during the 100-year period that is covered by the NFIs, i.e., by comparing NFI1 (1920) and NFI12 (2014-2018).

Data and methods

Using a variety of data sources, we estimated the proportion of area of old-growth forest and deciduous-dominated forests, the density of large trees, and the amount of dead wood (Table 1). Site fertility and successional stage are strong drivers of the development of these forest features, of human use of forest resources, and of the historical distribution of natural forests. Therefore, the forest biodiversity indicators were estimated considering the observed or estimated proportion of various forest habitat types. We used the forest habitat classification from the Red List, which includes 15 heath forest habitat types (Kouki et al. 2018). The classification was based on site-fertility class (herb-rich heath, mesic, sub-xeric, xeric and barren heath forests), successional stage (young, mature and old), and partly on dominant tree species (conifer- vs. deciduous-dominated). We concentrated on the 12 major habitat types of heath forests, excluding the barren and considering deciduous-dominated heath as conifer-dominated forests. These exceptions cover only 3.2% of all heath forests in Finland according to NFI 11 (2009–2013, background data of Kouki et al. 2018).

Table 1. Overview of the different data sources used to compile the historic reference levels and the present situation as measured in the national forest inventory (NFI12). For the data, we concentrate on the 12 major heath forest habitat types (out of 15, Kouki et al. 2018).

Forest characteristics (biodiversity indicators)	Natural reference	1750s	NFI1 (1921–1924)	NFI12 (2014–2018)
Share of old-growth forest area (> 150 years)	Covering between 50% – 95% of the area; here, a conservative estimate of 50% was adopted (Berglund & Kuuluvainen 2021)	Estimates for southern and northern Finland (Kouki et al. 2018) based on historical maps of natural forests (Keto-Tokoi, 2014b) and on the age-class distribution suggested by the review of Berglund & Kuuluvainen (2021)	Percentage share of forests older than 160 years for NFI1 (due to coarser age class reporting for northern Finland) and 150 years for NFI12	
Share of deciduous-dominated forests	• In mesic & herb-rich heath forests all young forests and 50% of mature forests are deciduous-dominated and all old forests are conifer dominated • Forests on less fertile soils are conifer dominated irrespective of age (Berglund & Kuuluvainen 2021) • Relative share of site-fertility classes: NFI5 (1964–1970) (Kouki et al. 2018)	No estimates available	Values for whole Finland	
Number of large living trees	• Southern Finland: research data from natural forests (Kouki et al. 2018) • Northern Finland: research data from natural forests and data of NFI1 (1921–1924) (Kouki et al. 2018)	Estimates of Kouki et al. (2018); based on values for natural reference conditions, adjusted to reflect the distribution of natural forests and climatic conditions in 1750; 75% of natural reference in North, and 25% in South	Estimates of Henttonen et al. (2019); with threshold values of diameter at breast height >40 cm for South, and >30 cm for North	
Amount of dead wood	Research data from natural forests (Kouki et al. 2018)		Dead wood has been monitored from NFI9 (1996–2003) onwards; NFI9 data were used in place of NFI1	

Natural reference conditions

Berglund and Kuuluvainen (2021) estimated the natural reference conditions of boreal forests in northern Europe, indicating that old forests (at least 150 years old) were a prevalent or even dominant age-class, typically covering between 50% and 95% of the area. We adopted a conservative estimate of 50%. The remaining forest area was divided between young and mature forests following the age-class classification in Kouki et al. (2018): young forests (<40 years) covering 13% of the forest area, mature forests (40–150 years) covering 37%.

For the percentage share of deciduous-dominated forests we adopted the age distribution from Berglund and Kuuluvainen (2021) and assumed that in mesic and herb-rich heath forests all young forests and 50% of mature forests are deciduous-dominated, and that all old forests are conifer dominated. Forests on less fertile soils are assumed to be conifer-dominated irrespective of forest age. Eutrophication has changed the relative share of different site-fertility classes from 1960s onwards and thus, their shares under natural reference conditions were approximated using the data of the fifth NFI (1964–1970; see Kouki et al. 2018).

The densities of large living trees by each habitat types are based on empirical data from natural forests (Ilvessalo 1937, Rouvinen & Kouki 2002, Rouvinen & Kuuluvainen 2005, Aakala et al. 2009, Kreutz et al. 2015, Aakala et al. 2016, Punttila & Siitonen unpublished data), and, additionally, the data of the first NFI (1921–1924) in northern Finland as explained in Kouki et al. (2018). There is very little information on the densities of surviving large trees after wildfires in early successional stages. For this, it was assumed that the variation in the number of large trees depends on site fertility and, consequently, density of large trees in early successional forests decreases with increasing site fertility (see Kouki et al. 2018).

Similarly, the assessment of the amount of dead wood in the habitat types under natural reference conditions is based on data from natural forests (Siitonen 2001, Karjalainen & Kuuluvainen 2002, Rouvinen et al. 2002; Gibb et al. 2005; Rouvinen et al. 2005; Dahlström & Nilsson 2006; Ekbom et al. 2006; Ylläsjärvi & Kuuluvainen 2009; Aakala 2010; Josefsson et al. 2010; Ylisirniö et al. 2012) also considering site-fertility class and location (see Kouki et al. 2018). Estimates for the density of large trees and amount of dead wood were calculated as weighted mean values across age and site-fertility classes.

Forests and their structures in the 1750s

We used the share of old-growth forests in the 1750s estimated by Kouki et al. (2018). For that, they combined the historical distribution of natural forests from Keto-Tokoi (2014b) with site-fertility classes in different parts of Finland, and their varying likelihood of being used for slash-and-burn cultivation (Kouki et al. 2018). Information on tree species composition in Finnish forests is not available before NFIs started in 1920s, and thus we could not provide an estimate for the percentage share of deciduous-dominated forests in 1750s.

The densities of large trees and dead wood volumes were estimated by Kouki et al. (2018). Their estimation relied on corresponding values for forests under natural reference conditions for different site-fertility classes and successional stages (see above). Their approach makes the conservative assumption that dead wood and large trees were completely missing outside natural forests owing to human impact. Further, the expected amount of dead wood and large trees in natural forests was adjusted by a factor of 0.75 due to lower temperatures during the Little Ice Age (from ca. 15th to 19th century) (and hence slower tree growth) and more frequent fires (Kouki et al. 2018).

National forest inventory (NFI) data

For changes in forest characteristics important for biodiversity over the past 100 years, we used the first NFI (NFI1, 1921–24) and the most recent published NFI data (NFI12, 2014–2018) (Ilvessalo 1927, Korhonen et al. 2021). While for natural state and the 1750s the reporting for north and south strictly followed ecoregions, for NFIs we aggregated the county or municipality-level reporting to best fit the ecoregions. To obtain the share of old-growth forest, and due to reporting issues from the NFI (reported in 20-year age bins, except NFI1 for northern Finland that reports in 40-year bins), we made the conservative assumption that the area between age classes decreases linearly (e.g., we divided by half forest cover reported under 141–160 years to obtain estimate >150 years). We used Henttonen et al. (2019) to get NFI-derived estimates for the density of large trees. Dead wood has been only exhaustively monitored in NFI starting at NFI9 (1996–2003), therefore these data were used.

Results

Area of old and deciduous-dominated forests.

Under natural reference conditions, old forests (>150 years) covered at least 50% of the forest area. In southern Finland, their share had already shrunk by 50% by the 1750s (Table 2). Currently in southern Finland, old forest coverage is a small fraction compared with natural reference conditions (3%) and the 1750s (7%; Fig. 1) but slightly larger than in the 1920s (Table 2). In northern Finland, the decline in old forest coverage only started in the 20th century (Table 2), and their current cover is one-fifth of the forest area, and <40% of the coverage prior to the 1920s (Fig. 1).

Under natural reference conditions, deciduous-dominated forests covered >20% of forest area. There has been a 40–50% decline in their cover over the past century (Table 2) and current coverage is 35–50% from the natural reference condition (Fig. 1).

Large trees

Under natural reference conditions, the density of large trees has been several tens of stems per hectare (Table 2). By the 1750s in the south, the density had declined by 75% and continued declining till 1920s (NFI1) to a level that corresponds to <2% of natural density. NFI data shows marked recovery (>7-fold increase) in the density of large trees over the last 100 years, but still, current densities are only one sixth of the natural reference values and approximately 60% of the den-

Table 2. Values of forest characteristics important for biodiversity in Finland under natural reference conditions, in the 1750s, and according to national forest inventories in the 1920s (NFI1) and 2010s (NFI12). Relative change denotes the change between NFI1 and NFI12 except for dead wood volumes, for which it represents changes between NFI9 and NFI12. To facilitate comparison, two threshold level values of % old forests in NFI12 is given.

	Natural reference	1750s	NFI1 (1921–1924)	NFI12 (2014–2018)		Relative change (NFI1–NFI12)
% Old forests	>150 years	>150 years	>160 years	>150 years	>160 years	
North	50%	50%	39%	18.9%	17.1%	–56%*
South	50%	25%	0.7%	1.7%	1.1%	57%*
Whole of Finland	50%	32%	10%	5.9%	5%	–51%*
% Deciduous-dominated forests						
North	17.2%	NA	12.8%	6.3%		–51%
South	23.3%	NA	19.3%	11.1%		–42%
Whole of Finland	21.6%	NA	17.9%	10.0%		–45%
Large trees #/ha						
North	56	42	11.8	12.9		9%
South	36	9	0.6	5.1		743%
Whole of Finland	42	18	3.7	7.3		97%
Dead wood m^3/ha						
North	50	38	9.5**	7.5		–21%
South	110	27	2.8**	4.5		61%
Whole of Finland	94	30	5.8**	5.8		0%

* for forests >160 years. **NFI9 (1996-2003) estimate.

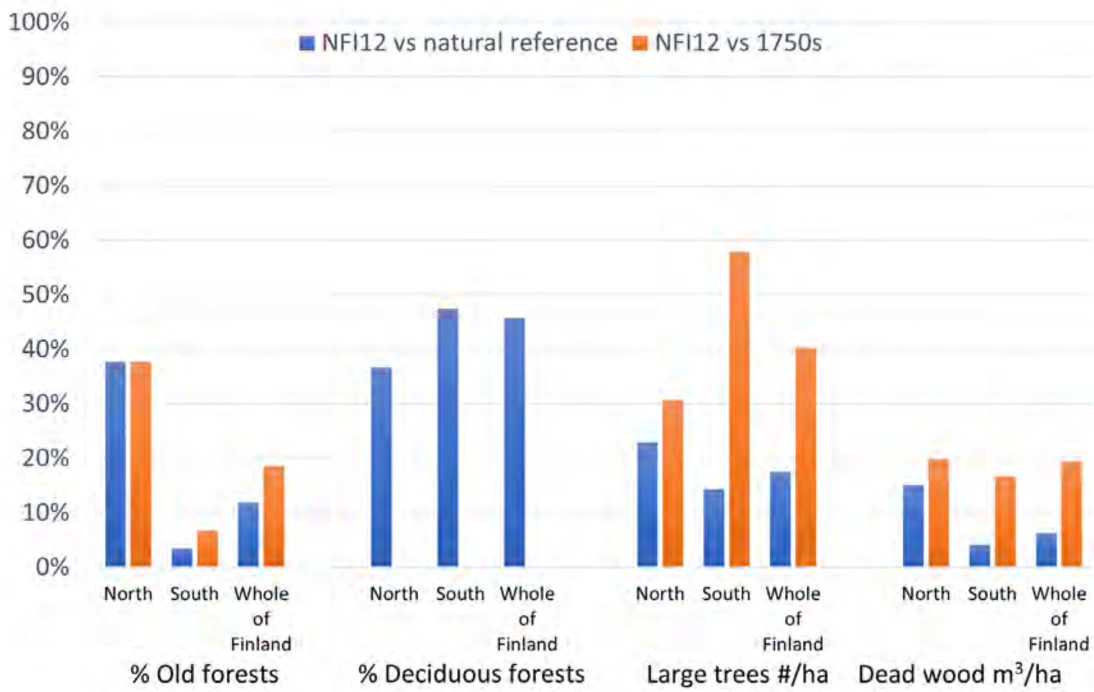

Figure 1. Percentage cover of old forests and deciduous forests, density of large trees and dead wood volumes in Finland according to NFI12 relative to values under natural reference conditions (blue bars) and in the 1750s (orange bars). The values are given for North (northern boreal forests), South (middle- & south- & hemiboreal forests), and for whole Finland.

sity in the 1750s (Fig. 1). In the north, the density of large trees markedly declined prior to the NFIs started in the 1920s and has ever since remained at a level that corresponds 25–30% of values under natural reference conditions and in the 1750s.

Amount of dead wood

Under natural reference conditions, dead wood volumes are >90 m^3/ha on average, with higher values in the south than in the north of Finland (Table 2). By the 1750s in southern Finland, dead wood volume had decreased considerably, and somewhat also declined in the north. Between NFI9 (1996–2003) and NFI12 (2014–2018) – the period for which NFI provides data of the amount of dead wood in Finnish forest – dead wood volume has increased in southern Finland but decreased in northern Finland, where it has yet remained higher than in the south. Considering the historical range, there has not been a remarkable change since NFI9 (Table 2). Current dead wood volume in the south is <5% of the natural reference value. In the north, the decline is more recent and effectively started in the 20th century, with current volume being 15% of the dead wood volume relative to the natural reference value, and about 20% relative to the 1750s value (Fig. 1).

Discussion

Current Finnish forests largely depart from natural state

Forest structures essential to maintain ecologically diverse biota are below those that likely prevailed in Finland under natural reference conditions and in the 1750s. This scarcity is particularly pronounced for dead wood volumes, and old forest area in southern Finland (Fig. 1). Korhonen et al. (2016) suggested that in the south, dead wood volume has been constantly low since 1920s and declining in the north until the 1980s. They concluded this from the NFI data concerning the volumes of hard dead wood (still usable as fuel wood) since the late 1930s (from NFI2 (1936–1938) to present).

Despite recent positive trends in the density of large trees and dead wood volumes particularly in the south, simultaneous negative trends in the threat status of forest species (Hyvärinen et al. 2019) and high numbers of threatened habitats (Kouki et al. 2018) indicate that these improvements have not been effective enough to turn the tide of biodiversity loss. Moreover, positive development in these structural indicators may be tempered by negative trends in the cover of old forests (at the whole country-level) and deciduous-dominated forests over the past 100 years. While the area of old forest in southern Finland started to increase after being only 0.7% in the 1920s (Table 2), it has declined both in the south and in the north over the past four decades (Korhonen et al. 2020). At the same time, the area of deciduous-dominated forests has increased in the south (Korhonen et al. 2020).

The current levels in the density of large trees and in dead wood volume remain clearly below natural reference conditions. It should be noted that large trees are not necessarily old, as current forest management regimes and timber pricing favor fast diameter growth. Also, climate change and the fertilizing effect of nitrogen deposition has accelerated tree growth in boreal forests (see Henttonen et al. 2017). Consequently, in southern Finland, only a small proportion (11%) of current large trees are old (>150 years), whereas in the north most (95%) large trees are old (Henttonen et al. 2019). Many species require trees that are both large and old (Pykälä 2019). Thus, as tree size is a poor proxy for its age in the present human-modified conditions, monitoring only the density of large trees does not sufficiently reveal changes in forest structures that are important for species.

Protected areas foster forest recovery

In southern Finland, the density of large trees and volumes of dead wood have been increasing since the late 1990s. For deadwood, this increase is largely due to positive development within protected areas, while the contribution of production forests is negligible (Korhonen et al. 2020). Dead wood volume in southern protected areas has doubled from 10 m^3/ha to about 20 m^3/ha, but in managed forests increased only slightly (from 2.7 to 3.9 m^3/ha) between NFI9 and NFI12 (Korhonen et al. 2020, 2021). In both managed and protected forests, the amount of dead wood still remains far below natural reference values, although it is above its historical lowest level. Despite the small cover (10%) of protected forests, 43% of large old trees are in forest reserves (Henttonen et al. 2019). These results indicate the ongoing but partial recovery of forest ecosystems from very intensive management in the past and emphasize the role of conservation areas in protecting biodiversity. As a large share of the protected forests area were previously managed and are gradually recovering, the density of large old trees and volumes of dead wood will continue to increase in forest reserves. In contrast, in managed forests the density of old trees may continue to decline following regeneration felling of the oldest age classes.

In terms of management strategy this means that first, more protected areas are necessary (Kouki et al. 2018, 2019). This is particularly important in southern Finland where only 2.7% of forest land is strictly protected (nature reserves and sites reserved for nature conservation and other statutory protected areas where no felling is allowed, stat.luke.fi/metsa), and where most forests are intensively managed for timber production. Second, the remaining biodiversity-rich natural or semi-natural unprotected forests should be prioritized when expanding the existing protected area network. As the recovery process of forests takes decades or centuries, the loss of these remnant forests is practically irreversible and hard to replace in the foreseeable future. As a complement, currently degraded or young forests could be spared so that they get a chance to recover their integrity in the future (Kotiaho & Mönkkönen 2017, Kouki et al. 2018).

The biodiversity value of managed forests can be increased

As managed forests cover nearly 90% of the country, they will inevitably have a major role in facilitating biodiversity recovery. However, their role critically depends on the management methods applied. Even though protection of biodiversity has been an important aim in managed forests in Finland since the 1990s, management for timber production in unprotected forests is still too intensive to allow the amount of dead wood to recover and trees to grow old. It is also noteworthy that although 6% of large, old trees are living retention trees in managed forests (Henttonen et al. 2019), most large, old trees are still subject to logging in ordinary production forests. Management practices can facilitate the recovery of essential structures to maintain ecologically diverse biota, such as increasing the numbers of – preferably large and old – retention trees left behind in logging operations and by emulating natural disturbances with prescribed post-harvest burnings (Heikkala et al. 2016, Suominen et al. 2019, Kouki & Salo 2020). This would primarily slow down the loss of important legacy trees from the landscape, and eventually facilitate the formation of large diameter dead wood in managed forests (Kouki et al. 2018).

The most cost-efficient means to maintain habitats for dead-wood dependent species in managed forests is to retain all the existing dead wood during logging operations by avoiding the destruction of snags and logs, and by refraining from harvesting dead trees for energy wood. The loss of existing dead wood may be very high, up to 80%, during logging and site preparation operations (Hautala et al. 2004). Refraining from all logging, including selective cutting, in valuable woodland key-habitats of managed forests will support maintaining valuable habitat features and their connectivity in managed landscapes (Laita et al. 2010). Finally, landowners have been shown to voluntarily conserve small forest patches occupied by charismatic species such as birds-of-prey (Santangeli et al. 2012), which will benefit also other species (Burgas et al. 2014). It has been suggested that this approach could be further developed to cover other types of biodiversity values and larger patches via compensation schemes (Santangeli & Laaksonen 2015).

Natural disturbances are opportunities for restoration

Our analyses are based on ecologically simplistic assumptions that forests and their features evolve gradually over decades and centuries. However, strong pulsed disturbances, such as wildfires, large storms or outbreaking insects may rapidly affect forest characteristics, including biodiversity indicators we have analyzed in this study. However, due to insufficient knowledge of the spatio-temporal distribution of disturbances, it is impossible to reveal their exact role in the past. Even more importantly, such disturbances are predicted to increase in the future, and their role may deviate and increase from their historical occurrence (Venäläinen et al. 2020). For the maintenance of biodiversity, large-scale and intensive disturbance provide opportunities to quickly restore some of the features lost from forests, or even restore fully functioning forest habitat types that are currently threatened. Further, disturbances create forest structures and habitats that are targeted in artificial restoration, often at a high cost (e.g., restoration burnings).

We strongly recommend developing strategic plans to take advantage of positive effects of natural disturbances to enhance ecological integrity inside production forests. Disturbances are spatially and temporally unpredictable, and, thus, it is crucial to have agreed forest policies on how to deal with them once the events occur (Thorn et al. 2020). This is of crucial importance for species that are dependent on dead, injured or charred wood. There is an obvious need to reconsider the Finnish Forest Damages Prevention Act, which obligates a forest owner to remove large-diameter conifers from forest stands if there are more than 10 m^3/ha of freshly damaged spruce trees or more than 20 m^3/ha of damaged pine trees. This Act effectively precludes rapid and cost-efficient accumulation of dead wood in unprotected forests, is detrimental to biodiversity and has unclear biological justification in preventing further damages particularly in pine forests (Martikainen et al. 2006, Komonen & Kouki 2008, Siitonen & Heliövaara 2013). Disturbances and their effects on tree mortality must not only be seen as economic losses but considered as highly potential and rapid investment opportunities in natural capital (sensu Dasgupta 2021) because of the positive biodiversity effects.

Conclusions

Forests in Finland have largely lost their ecosystem integrity and are faring poorly in a global comparison (Grantham et al. 2020). Our results show that this loss of ecological integrity in southern Finland is a result of a long process that spans over several centuries. Changes in forest habitats accelerated and were especially widespread and intensive during 1900s when currently applied intensive forestry expanded to the whole country and targeted all forest habitat types. Recent decades show slow recovery of degraded forest characteristics important for biodiversity. This recovery is an indication that forest management can be adjusted so that forest habitats and biodiversity are maintained better in the future. However, the future condition of Finnish boreal forests critically hinges on the management decisions we make today. The assessments of forest-dwelling species (Hyvärinen et al. 2019) and habitats (Kouki et al. 2018, 2019, this study) provide ecologically comprehensive and up-to-date background to improve ecological integrity in the Finnish forests.

Additionally, a recent analysis of alternative policy scenarios shows that forest policy can be tailored to meet the goal of biodiversity maintenance in Finland (Blattert et al. 2022). For example, the amount of dead wood and density of large trees can be increased but requires a policy that gives proper weight on both economic and ecological objectives and that has realistic tools to implement measures needed. Clearly, however, further coordinated efforts on how to maintain biodiversity in managed and protected forests will be required if the Finnish society wants to achieve genuinely sustainable forests and forestry (Kouki et al. 2018, Kuuluvainen et al. 2019, Korhonen et al. 2020).

The principles of sustainable forest management emphasize the value of ecosystem services and their value for people (Vanhanen et al. 2012). As the functioning of ecosystems is based on their structure and underlying biodiversity, there are opportunities to reconcile the maintenance of biodiversity with multiple benefits obtained by human communities from forest ecosystems (e.g., water quality or health and recreational value). A critical challenge in this context is how to balance biodiversity requirements with timber production and the flow of non-timber ecosystem services from forests over the long term.

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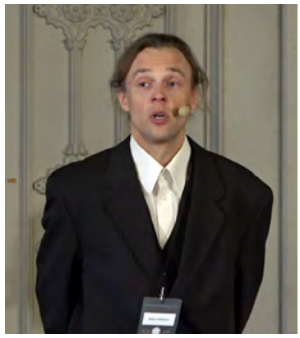

Photo: Video screenshot / RajuLive.fi

What do birds tell us about recent changes in the environment?

Aleksi Lehikoinen

Lehikoinen, A., Finnish Museum of Natural History, University of Helsinki. aleksi.lehikoinen @ helsinki.fi

The loss of biodiversity has become an increasingly important topic of societal discussions. However, measuring biodiversity loss is not easy compared to for instance documenting the other environmental crisis, the climate change. Therefore, different tools are needed to measure whether biodiversity has changed, and how it reflects known habitat changes and possible conservation actions. Birds have been used in many countries as indicators of environmental status. There are several reasons for this. There is a large number of bird enthusiasts around the world who collect data on species. This has led to the accumulation of a considerable amount of long-term data on birds, and the amount of data is increasing every year. Because birds are at the top of the food chain, which means that their numbers are likely to reflect changes at lower trophic levels. Birds are also ubiquitous in a variety of environments and every human knows something about birds, which greatly facilitates the popularisation of science and communication of the impacts of habitat change.

Climate change shifts distribution of birds

Birds have been used in numerous studies of environmental change, including climate change. The effects of climate change on animal species can be broadly divided into changes in species phenology, abundance and morphology. For example, long-term observation series on bird migration times in both Europe and North America show that spring migration begins earlier as springs warm up (Lehikoinen et al. 2019b). In contrast, the timing of autumn migration shows varying responses to climate change. Some species even advance their autumn migration as spring migration begins earlier (Lehikoinen et al. 2010). In some species, such as in waterfowl, migration is delayed, which may lead to a shift in wintering distributions of species (Lehikoinen & Jaatinen 2012, Lehikoinen et al. 2013).

The increase in wintering waterfowl abundance in coastal areas is one of the fastest phenomena caused by climate change in Finland (Lehikoinen et al. 2013, Fraixedas et al. 2015, Meller et al. 2016, Pavón-Jordán et al. 2019). Warming in early winter and decreasing ice cover have led to a tenfold increase in abundances of species such as common goldeneye *Bucephala clangula* and tufted duck *Aythya fuligula*. As recently as the 1980s, there were at most a few dozen wintering tufted ducks in the south-western archipelago, whereas now the numbers are already several tens of thousands (Lehikoinen et al. 2013). The increasing abundance of waterbirds in northern Europe is also reflected in declining abundances of some species at the southern edge of their range.

For example, wintering numbers of goldeneyes have declined significantly in Ireland, Switzerland and Germany (Lehikoinen et al. 2013).

In addition to waterbirds, abundances of landbirds have also shifted northwards as climatic conditions have shifted. Based on line transect counts of more than 100 species, the abundances have shifted northwards on average about 1.5 km per year in Finland since the 1970s (Virkkala & Lehikoinen 2014, Lehikoinen & Virkkala 2016). This means that southern species on average are becoming more abundant and spreading over an ever wider area in Finland. Northern species, on the other hand, are becoming scarcer and are moving further north. In general, however, the rate of species shifts is slower than the rate at which climatic conditions have changed and there is significant variation between species in their speed and direction of shifts. Some species are also moving south against climate predictions, such as the raven Corvus corax and the starling Sturnus vulgaris (Virkkala & Lehikoinen 2014, Lehikoinen & Virkkala 2016, Välimäki et al. 2016).

Changes in habitat quality

Climate change is not the only factor affecting bird populations. Human land use and changes to it, such as logging, also affect bird abundance. In Finland, the amount of logging has increased since the 1980s (Statistics from the Natural Resources Institute Finland 2022). This has led to a decrease in older forests and an increase in younger stands, which are becoming more dominant in the forest landscape. In southern Finland in particular, the proportion of forests aged 81–120 years has decreased, while the proportion of forests younger than 40 years has increased. In northern Finland, the proportion of forests over 120 years old has decreased and the proportion of forests between 41 and 80 years old has increased (Korhonen et al. 2020).

Recent population changes in forest birds are linked to species' habitat selection. The more the forest bird species preferred older forests, the more negative were their population trends in South Finland between 1984 and 2013 (Fraixedas et al. 2015a). Based on the population trends of species occurring in the same habitat, so-called habitat indicators can be developed. Such habitat-specific bird indicators have been implemented for a number of habitats, including forests, farmland, peatlands, wetlands and fells, and are presented on the luonnontila.fi website maintained by the Finnish Environment Institute (see Figs. 1–3).

For forest birds, both wintering and breeding bird indicators have been implemented. These show partly different trends. The breeding season indicator, which consists of the population trends of 25 bird species, has been largely stable since the 1980s. In contrast, the winter indicator for 12 species has declined significantly for decades (Fig. 1). For many species, the exact mechanisms of why changes in forest quality affect their populations are poorly understood, but the decline in wintering species in particular suggests that forest quality plays a greater role in winter survival. One better known mechanism has been demonstrated in the strongly declining, Endangered (EN) willow tit *Poecile montanus*. In this species, the more old-growth forest there is in the winter territory, the higher is the survival rate and the lower the stress levels of the individuals (Cirule et al. 2017). Winter bird counts have also estimated that winter bird densities are roughly eight times higher in forests compared to clearcuts and stands of saplings (Fraixedas et al. 2015b). Forest

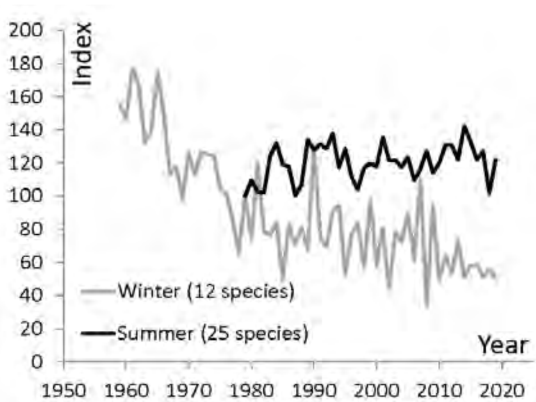

Figure 1. Finnish forest bird indicator for breeding (black) and wintering (grey, 12 species) birds. The breeding indicator is based on population trends of 25 species from line transect and point counts since 1979. The winter indicator is based on winter bird survey trends of 12 species since 1959. Both indicators have the value 100 in 1979.

quality is likely to have a greater impact on birds that are specifically wintering in forests than on many forest generalists during the breeding season (Virkkala et al. 2020). Climate change is also likely to partially compensate for the negative population effects of forest management, as many breeding forest bird indicator species are southern species, whose populations are expanding (Virkkala 2004).

The farmland bird indicator, which consists of the population trends of 14 species breeding in farmland habitats, has been declining for decades (Fig. 2), which is a pan-European phenomenon (Laaksonen & Lehikoinen 2013). However, not all such species show reduced numbers, and some species, such as jackdaw *Corvus monedula,* have increased in abundance in recent years. Among farmland species, those that breed in farmland edges or farmyards (7 species) are doing better than species which breed in the fields (7 species). There are however exceptions, such as barn swallow *Hirundo rustica* and house martin *Delichon urbicum*. These typical farmyard species have declined and are now classified as Threatened (Lehikoinen et al. 2019a).

In addition to farmland species, peatland bird species are also generally doing poorly in Finland. The combined population trends of 15 peatland bird species show a decline of almost 50% since the early 1980s (Fig. 3; Fraixedas et al. 2015). The situation of peatland species has been particularly affected by the drainage of peatlands in an attempt to increase forest growth for forestry purposes. Indeed, many peatland species have their highest densities in open, wet and undrained peatlands (Fraixedas et al. 2015). The status of the peatland bird population is significantly better in Estonia and the corresponding Estonian national bird indicator of nine peatland species is stable (Fraixedas et al. 2017). In Estonia, the majority of open peatlands are protected. In Finland only less than 15% of peatlands are protected and protection is heavily concentrated to northernmost Finland (Fraixeadas et al. 2017). Drainage of peatlands has been intense from southern Finland to southern Lapland, with a total length of about 1.4 million km of ditches.

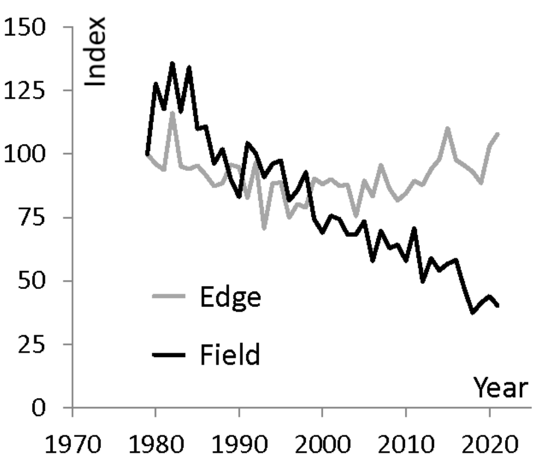

Figure 2. Finnish farmland bird for field (black) and edge (grey) species. Both indicators include 7 species and they are based on line transects and point counts situated in farmland habitats since 1979.

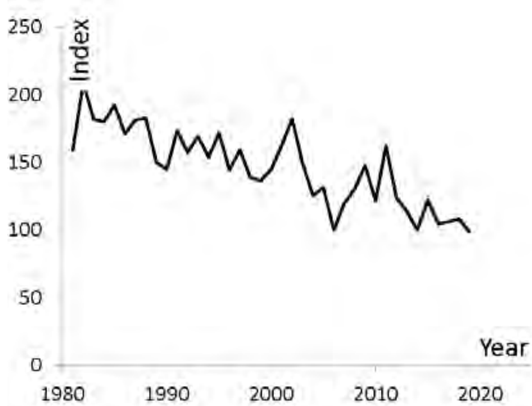

Figure 3. Finnish peatland bird indicator covers population trends of 15 species. The indicator is based on line transect and point count surveys in peatland habitats since 1979.

Not only does drainage affect the quality of peatlands, but ditches also transport nutrients and carbon to a wide area downstream of the catchment. Only recently has it become better understood that the emissions to water bodies from forest drainage are equivalent in magnitude to nutrient inputs from agriculture (Nieminen et al. 2017). The overall length of ditches around lakes can increase eutrophication, water browning and turbidity (Holopainen & Lehikoinen 2021). These changes in water chemistry affect the abundance and occurrence of many plants, invertebrates and fish. For example, submerged aquatic plants suffer from reduced water visibility, darkening water colour impairs aquatic invertebrates, and eutrophication increases the abundance of cyprinids (Moss et al. 2011, Arzel et al. 2020, Olin et al. 2002). All of these are linked to waterbird abundance, as submerged aquatic plants and benthic invertebrates are important food species for many waterbirds (Pöysä et al. 2013, Lehikoinen et al. 2016, Kareksela et al. 2021). Waterbirds may also suffer from food competition with cyprinids (Pöysä et al. 2013, Lehikoinen et al. 2016, Väänänen et al. 2012). According to national waterbird monitoring, waterbird populations have declined since the 1990s, especially in eutrophicated wetlands, while the situation is not as bad in oligotrophic water bodies (Lehikoinen et al. 2016). This suggests that changes in water quality in already eutrophicated waters have become unfavourable through hypertrophication, brownification and turbidity (Pöysä et al. 2013, Lehikoinen et al. 2016, Pavón-Jordán et al. 2017). Climate change will increase winter precipitation, which may also increase nutrient flow from the catchment area into water bodies in the future. Wetland species may also be more vulnerable to predation by two invasive predators, raccoon dog *Nyctereutes procyonoides* and American mink *Mustela vison*. It is currently unknown which of these two factors, water quality or predators, is more important in causing declines in wetland bird populations (Pöysä et al. 2013, Lehikoinen et al. 2016).

Future of the bird populations

Habitat-specific bird indicators summarise the population trends of species occurring in a similar environment, which can be used as a measure of environmental status. The decline of common species is worrying, as it indicates large-scale changes in nature. Habitat degradation is probably one of the main reasons for the decline of bird populations in Finland in a number of different habitats. Fortunately, in recent years, research has also accumulated information on different ways to restore habitats and thus improve the situation (e.g. Lehikoinen et al. 2017, Kareksela et al. 2021). Similarly, protected areas are now known to play an increasingly important role in mitigating the negative population impacts of climate change (Virkkala et al. 2014, Lehikoinen et al. 2019c, 2021). In the coming years, there should therefore be an increasing focus on identifying which restoration measures are most effective in different circumstances, and how to promote restoration and conservation on a broader scale to halt the biodiversity loss. Species monitoring will be key to assessing the impact of restoration measures, and there will be a greater need for habitat-specific indicators in the future. Species monitoring and indicators should therefore be further developed for other taxa than birds, thus improving our understanding of biodiversity trends.

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The impact of climate change on species in Finland


Photo: Video screenshot / RajuLive.fi

Maria Hällfors

Hällfors, M., Research Centre for Environmental Change, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, FI-00014 Helsinki. Finnish Environment Institute SYKE, Biodiversity Centre, FI-00790 Helsinki. maria.hallfors @ syke.fi

Climatic conditions constitute the very defining dimensions of abiotic conditions for biodiversity. Now these fundamental settings are changing at rapid pace, and this transformation is not only something looming around the corner, but the change is already here. In this summary I want to emphasize the responses through which species can adjust to a change in climate and I will describe some signatures of the effect of climate change on the fauna and flora in Finland.

Globally we have seen an increase in mean annual temperature of 1.3 ℃ since the pre-industrial baseline (berkleyearth.org/data; Rohde and Hausfather 2020). In Finland, however, a 2-fold temperature increase, 2.6 ℃, over the same time has occurred. By the end of the 21st century, we can expect an increase of more than 5 ℃ in Finland, i.e., in case we are globally able to halt the increase in emissions by 2050 and thereafter reduce them (SSP2-4.5; IPCC 2021). If we continue on our current path, however, and do not curtail greenhouse gas emissions (SSP3-7.0; IPCC 2021) Finns can expect to see a 6.8 ℃ degree increase by the end of the century. If we start cutting down emissions immediately and succeed in reaching net zero emissions globally by around 2080 (SSP1-2.6; IPCC 2021) Finland would not warm by more than a total of 3.5 ℃. A total increase ranging between 3–7 ℃ will, in any case, constitute a tremendous change for Finnish nature considering that the difference in mean annual temperature between Helsinki in the very south of the country and Sodankylä in mid-Lapland is on average 6 ℃ (Normal period 1991–2020; Finnish Meteorological Institute). What will a change of such magnitude imply for the species that make up our living environment? And should not this change be visible already, if we've already seen a 2.6 ℃ increase? The answer to the first question can be approached through the answer to the second. By quantifying and documenting the changes that we can see to date, we can, if not predict, at least approximate what nature might be up against during the coming decades. And nature is already changing, that is for certain.

In my research, I aim to understand how species are coping with climate change – which species are managing or even thriving under the new conditions, and which are suffering and might thus need focused conservation attention. One way of approaching this massive and burning question is by consider the alternatives that species have when confronted with environmental change. Over time, species have adjusted to specific environmental conditions under which they thrive and reproduce. Thus, if environmental conditions of a species should change, it must either (i) adjust in place to the new conditions through evolutionarily or plastic responses, or (ii) shift in space, i.e. disperse to areas where its requirements are better fulfilled. The speed of current climate change may outpace the ability of populations to respond through either pathway which means individuals will fail to replace themselves with offspring, populations will shrink and eventually the species will go extinct. In my research I have found examples of species fitting into each one of the above-mentioned categories: species that move, species that adjust, species that can do a bit of both, and species that are not responding. Let us begin with an example from the latter category, of a species that is possibly already heading towards the decline and extinction.

The Siberian primrose (*Primula nutans* subsp. finmarchicha) is a perennial plant that grows on seashore meadows. The variety *jokelae* (henceforth the southern variety) grows in Finland and Sweden by the Bothnian Bay and in Russia by the White Sea. The variety *finmarchica* (henceforth the northern variety) occurs on the shore of the Artic Sea in Norway and Russia (Fig. 1). We collected seeds from populations of both varieties and planted them in five botanic gardens: in their home environments in Svanvik, northern Norway, and in Oulu, northern Finland, as well as in Rauma and Helsinki further south in Finland and in Tartu, Estonia (Fig. 1; Hällfors et al. 2020a). We wanted to find out how strongly adapted the two varieties are to the local climatic conditions and how a warmer climate might affect them. We took measures on survival, size, and flowering over the next three years and expected that both varieties would thrive best within the range of the species (Oulu and Svanvik), potentially even showing higher fitness in their specific home locations if they are strongly locally adapted, and worse further towards the south.

Our results showed that both varieties, indeed, fared poorer in the southern gardens compared to Oulu and Svanvik, indicating that a warmer climate may be unfavorable for the species if it is incapable of adjusting or relocating. We were surprised, however, by our finding that the southern populations were more successful in northern Norway than in Oulu – even more successful than the northern variety there, in its home environment. When we compared our results to weather data from the study years and to historic average climate conditions, our findings started to make more sense. It turned out, that the experienced temperature conditions in Svanvik resembled the historic average temperatures in Oulu, while the experienced temperatures in Oulu resembled the historic average temperatures in the out-of-range gardens in Rauma, Helsinki, and Tartu. Within our experiment the northern variety did not experience conditions corresponding to historical temperature in its home site in any of the experimental sites, since even the coldest site, Svanvik, deviated from the historic mean annual temperature. This suggests that the climatic optima of both varieties have moved, at least partly, outside their current range and that the conditions that we aimed to mimic through our experimental design had in practice already shifted further north, which we did not consider initially when forming our hypotheses.

Based on our findings, we conclude that the Siberian primrose is already suffering from adaptational lag (McGraw et al. 2015) due to climate change, and that further warming may increase this maladaptation, especially for the northern variety. If it cannot adjust or move, the effects of global warming may contribute to the demise of this species. Dispersal is likely not a viable option, since suitable habitat lies hundreds of kilometers away with no effective dispersal corridors in between. One way to help species like this to survive current and future challenges would be to relocate them, by human hand, further north. In other words, species could be conserved though what is known as assisted migration (Hällfors et al. 2014). To investigate the potential for this species to adjust in place, we are currently conducting experiments utilizing quantitative genetics approaches to estimate the evolvability of the Siberian primrose. To increase the likelihood of adjustment, it would be important to ensure that species have sufficiently large high-quality habitats to preserve populations at a viable level. This would safeguard enough genetic variation within the populations, that is, different individuals that have a higher probability to possess characteristics that are suitable in the new conditions.

Let us next turn our focus towards the two adaptive alternatives and some studies identifying species able to capitalize on them. As a reminder, to avoid population decline and extinction when faced with environmental change like climate change, species can (i) adjust in place

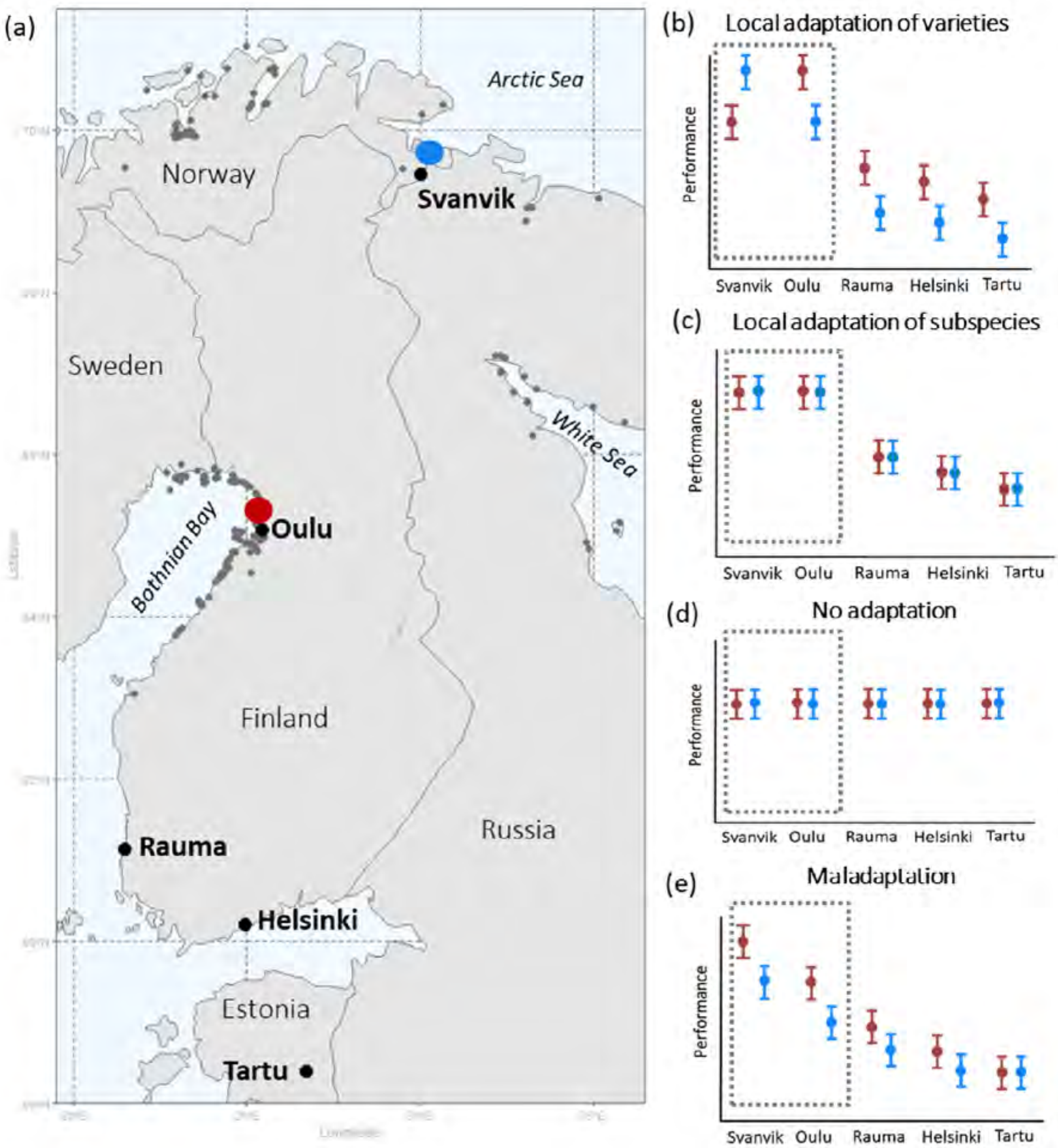


Figure 1. Geographical distribution of seed sampling sites and experimental gardens (a), and hypotheses of plant performance in experimental gardens (b–e) in the translocation trial on Siberian primrose (Hällfors et al. 2020a).
(a) shows the geographical distribution of seed sampling sites and experimental gardens with occurrences of *Primula nutans* ssp. *finmarchica* marked by dark grey points: Var. *finmarchica* occurs by the Arctic Sea in N-Norway and var. *jokelae* by the Bothnian bay in Finland and Sweden and the White Sea in Russia. Red, seed sampling sites of the southern variety (var. *jokelae*) in Finland; Blue, seed sampling sites of the northern variety (var. *finmarchica*) in Norway.
(b–e) show hypothesized overall performance of the tested varieties in all experimental gardens following opposing underlying scenarios of (b) local relative adaptation (sensu Brady et al. 2019) at the varietal and subspecies level, (c) relative adaptation of the subspecies to its current environment vs. areas outside it, (d) tolerance (through plasticity) towards all tested conditions (including those not currently present within the occurrence area of the subspecies), and (e) relative maladaptation caused by climate change (see text for hypotheses). Dashed area demarks within-range gardens, i.e., the reciprocal part of the experiment. Red, southern variety; blue, northern variety. Figure and caption reproduced from the original publication (Hällfors et al. 2020a) which is distributed under the Creative Commons Attribution-Non Commercial License 4.0 (CC BY-NC).

or (ii) shift in space. Let us start with thinking about how a species can adjust in place as temperatures increase. One such way could be, e.g., to simply develop a higher physiological temperature tolerance. We could also hypothesize that species like insects or plants should produce less pigmentation since the ambient temperature is higher and they do not need it for thermoregulation, or mammals and birds might reduce in size. However, one characteristic that lies close at hand and of which there exists large quantities of data for multiple species over a long time, is phenology. Phenology means the timing during the season when an individual expresses a certain central life-history stage, such as when birds migrate, when plants flower, or when adult butterflies fly and mate. Correctly timed phenology is critical for the overall success of an individual, since this timing determines whether the life history event is expressed during the time when the environment is most favorable for it, like their being plenty of insect larvae available for birds to feed their chicks with, or sunlight and lack of frost for new leaves to grow and start photosynthesizing. Several studies have shown that, under climate change, those species that advance their phenological timing in concert with advancing seasons tend to do better, and e.g., have more positive population trends (Møller et al 2008; Saino et al. 2011). Thus, concentrating on phenological change can be an informative lens through which we can understand how species are adjusting in place.

We know from previous studies that birds have advanced their spring migration and that some leave later in fall (Lehikoinen et al. 2019). Such changes would affect the time spent in breeding grounds and can, together with increased temperatures in the breeding sites, have affected both breeding timing and its duration. To study whether and how birds are changing their breeding phenology to altered seasons, we used a previously underutilized data set: the ringing data of bird chicks (Hällfors et al. 2020b). The banding or ringing time of bird chicks can be used as a proxy for breeding, since nestlings can be ringed when they are of a certain size. Thus, ringing time functions as an adequate surrogate for hatching time, and we can assume that if the hatching time has changed so too would the time of ringing have shifted. Every year, about 100 000 bird chicks are ringed in Finland by trained bird enthusiasts. For this specific study we used 800 000 ringing evens in unique nests for 73 species across four decades (data available in Hällfors et al. 2020c; Fig. 2). Because of the nature of these data, where bird chicks are continuously ringed throughout the occurrence of nestlings – we were able to define the beginning, the end, and the duration of breeding for each species (Fig. 2) within each of the four bioclimatic zones in Finland (Ahti et al. 1968).

The majority of the 73 bird species had advanced the timing of their breeding, both when it came to the beginning and the end of the breeding season. We saw an advance in the beginning of the breeding period by an average of 4.6 days. We also found that, for a third of the species, the duration of breeding had become shorter. Although only a minority of the species shortened the duration, this was enough to results in an average shortening of the breeding period across all species in the study: the average breeding period contracted by 1.7 days across all species. This contraction occurred since although the beginning of breeding had advanced, the end of breeding had advanced even more, by an average of 6.3 days. Because the timing of breeding was studied at a species level, in practice this means that, within a specific species, the latest individuals had advanced their breeding proportionally more than the early individuals. Among the species that shortened their breeding, almost all were resident or short distance migrants, which are the species that tend to breed earliest during the season. This suggests that residents and short-distance migrants may be better able to respond to increased temperatures in the spring and thus take better advantage of the earlier food and resource availability.

Our findings from this study using bird ringing data highlight the importance of quantifying phenological change across species and over the entire season to reveal shifts in the community-level distribution of bird reproduction. Our study also points out that evaluating changes throughout the season is crucial since changes may alter community-wide patterns of species co-occurrence and thereby trophic interactions: there might nowadays be more nestlings of the same species around at the same time, which would

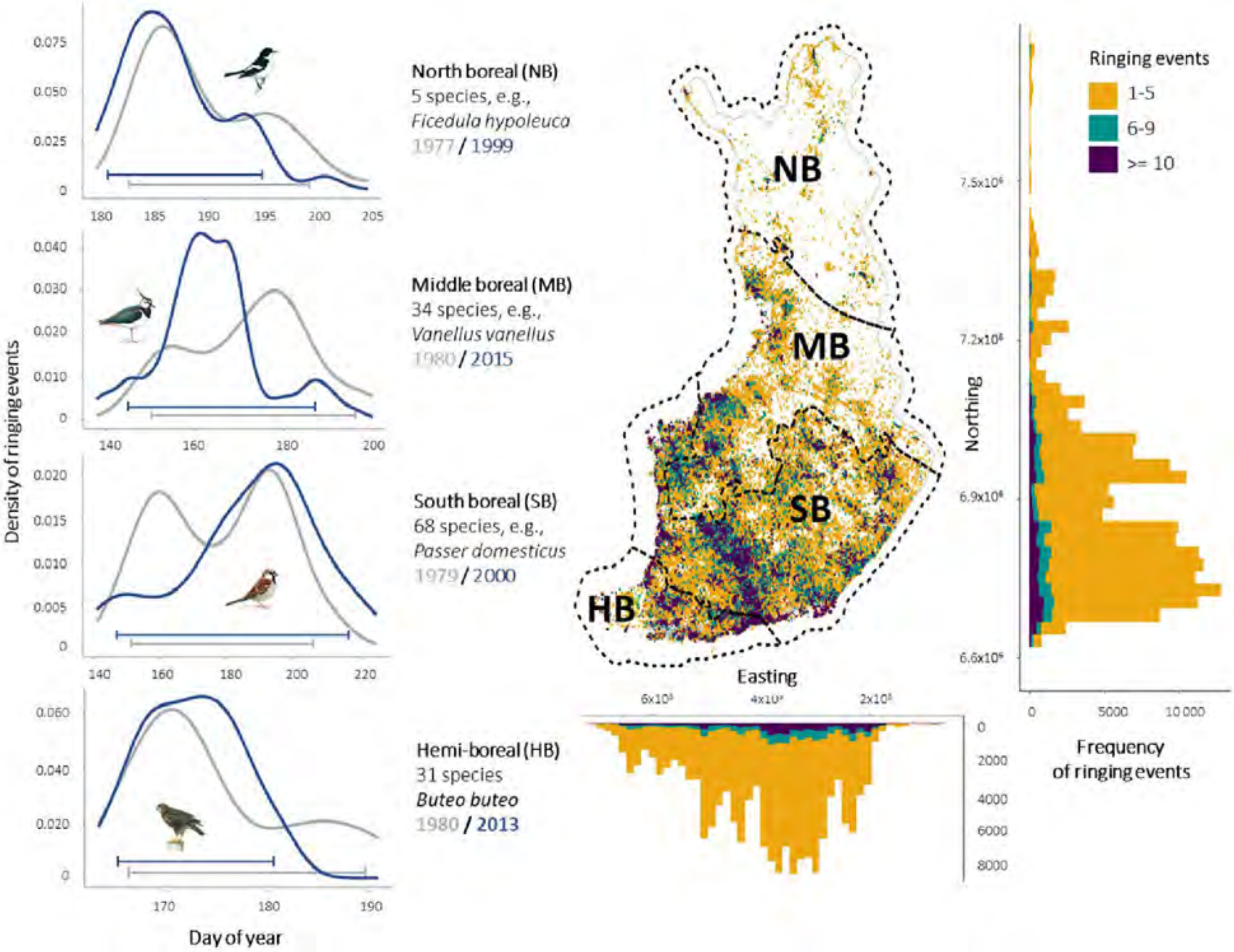
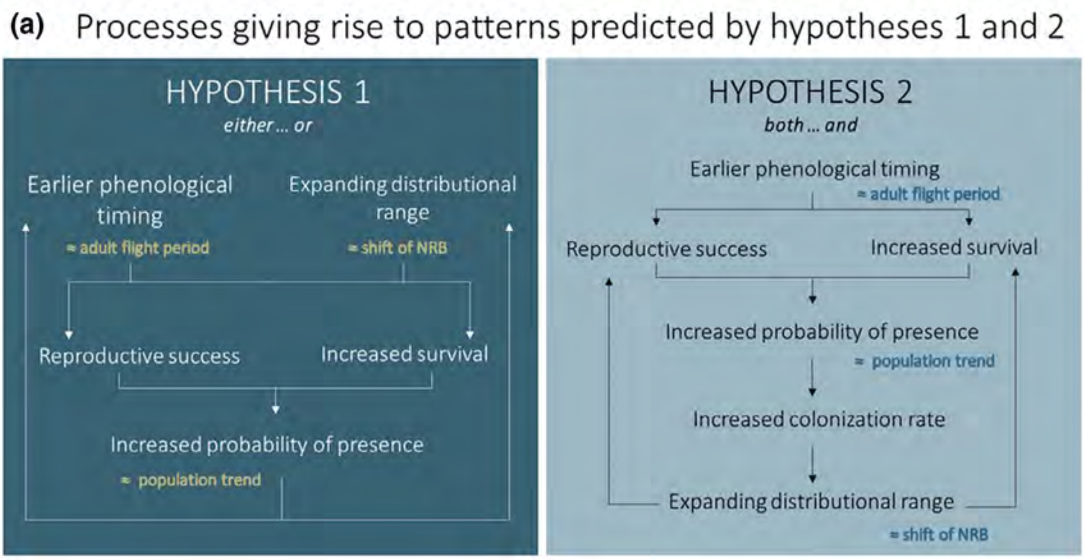


Figure 2. Spatial distribution of the nestling ringing data used in Hällfors et al. 2020b.
The map depicts the location of each ringing event across the four bioclimatic zones in Finland, and the marginal histograms show their distribution and sample size per spatial coordinate (European Terrestrial Reference System 1989 coordinate system).
The four side panels (Left) illustrate the distribution of ringing events over day of year for one selected species in each bioclimatic zone, showing two example years 20 to 25 y apart with different colors. Horizontal brackets indicate the phenological metrics calculated: beginning of breeding period (5th percentile), end of breeding period (95th percentile), and duration (difference between the end and the beginning). The number of species analyzed in each bioclimatic zone is shown beside each panel (73 species in total). There were 138 unique species-by-zone combinations as not all species were present in each of the four zones.
Bird illustrations are by Mike Langman (https://www.rspb-images.com).

mean that there are more chicks needing similar food at the same time. Whether these resources are also shifting over the season is now the key question. Insects, e.g., is a main food source for many bird species, but we know very little about how the temporal abundance of insects has changed. The potential loss of synchrony between interconnected species exemplifies one of the major uncertainties in the future functionality of ecosystems.

In another study we compared the pace of phenological shifts between different taxonomic groups. Here we used an enormous systematically collected dataset from long term monitored localities within eastern Europe and Russia (Ovaskainen et al. 2020). We show, like so many other studies (Parmesan & Yohe 2003; Thackerey 2010; Cohen et al. 2018), that there is huge variation in phenological shifts across taxa (Roslin et al. 2020). But among this variation, we do find some generalities. Spring events showed the strongest shift towards earlier dates, whereas autumn shifted strongly towards later dates. This was particularly evident for plants, which advanced early or delayed late events faster than other trophic levels. Fastest of all changed the abiotic events such as the melting of snow cover, or the breakup of ice, which had also been observed in this phenological study. This shows that overall, organisms are failing to keep pace with the variable climate, and that there is large variation both within and among taxonomic groups in the capacity to advance phenology. Just as with the birds in our study using ringing data, although the average response was to advance breeding, not all of the studies species shifted in time. Does this mean that species that are failing to adjust will eventually face the same faith as what we fear is occurring for the Siberian primrose? There is still the second lifeline available: shifting in space.

Figure 3 ▼► (on pages 22 and 23). Chart describing processes and predictions of the hypotheses in Hällfors et al. 2021. ▼Panel (a) describes the underlying processes that may give rise to the patterns predicted by the outlined hypotheses. Underpinning Hypothesis 1 (either phenology or range shift) is the assumption that species differ fundamentally in their abilities to adjust either in situ or via dispersal. Assuming that these strategies are adaptive, being able to use either strategy will lead to an increased probability of presence, which should be reflected in positive population trends. Positive feedback loops through larger population size further enhance the ability of both strategies to function. Underpinning Hypothesis 2 (both phenology and range shift), on the other hand, is the assumption that adaptive in situ responses in phenology increases the fitness of the individuals, leading to higher rates of survival and/or more offspring. This in turn increases the probability of presence (stronger population trends) and thus higher colonization rates which leads to the species being able to expand into habitats becoming suitable as climate changes (=shift in the northern range boundary [NRB]). A successful colonization of new available habitat further increases the probability of survival and reproductive success of individuals, which again has a positive effect on species abundance. In this study, the hypothesized underlying processes are investigated through proxies for range shift, phenology shift, and probability of presences as depicted by derived estimates in yellow versus blue font in the process charts: shift in NRB as a measure of species range shift; change in adult flight period as a proxy for phenology shift; and population trends as a proxy for probability of presence across the distribution.



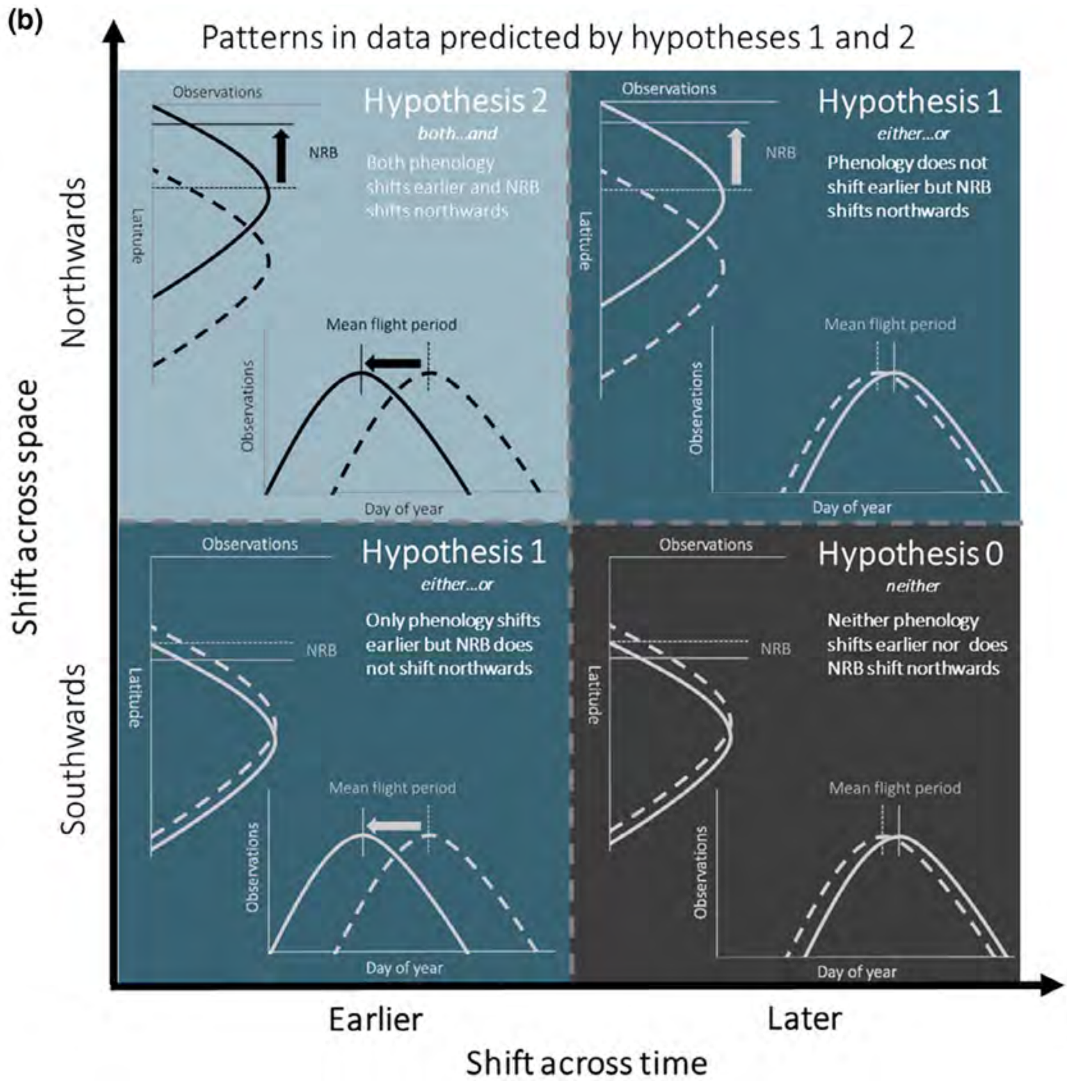


Fig. 3 cont.
▲ Panel (b) describes the expected patterns in the data, i.e., the combinations of responses, as regards NRB and phenology shift estimates, that would support Hypotheses 1 (either advanced phenology or northwards shifting NRB), 2 (both advanced phenology and northwards shifting NRB), and 0 (neither advanced phenology nor northwards shifting NRB). Although these proxies do not allow us to infer evidence for the underlying processes, they can inform us of the patterns across a wide sample of species. By combining them with information on population trends, we can infer how successful the strategies likely are on their own and in combination for species experiencing climate change, and what may be the consequences if species cannot utilize either of the strategies.
Figure and caption reproduced from the original publication (Hällfors et al. 2021) which is distributed under the Creative Commons Attribution License 4.0 (CC BY).

Palaeoecological evidence suggests that, during past changes in climate, most species have relocated rather than remained to face a new environment (Brook and Barnosky 2012). At the moment I am investigating range shifts of birds, moths, and butterflies in Finland. Finland is a good country to study range shifts within, since we have a long latitudinal extent and many species have their northern range boundaries in Finland. In this study under preparation, we want to find out how much the northern range edges have moved over the past decades and what characteristics describe species that are better able to utilize this response. Perhaps this propensity depends on their traits, like dispersal ability or overwintering stage. Or maybe their preadaptation to temperature conditions is the key: perhaps those more specialized to specific conditions are forced afoot while climatic generalist have more leverage to stay and adjust. In fact, as temperatures increase, both phenology shifts and range shifts can function to lower the experienced temperature (Socolar et al. 2017; Amano et al. 2014). Through phenology shifts populations can stay where they are but better match the new environment by, e.g., flowering or breeding earlier when the environmental window is favorable. The other options is to shift in space to other areas, often further north, and in that way keep the original phenological response in seasonal time. Could this explain why we do not see all species moving northwards or all species advancing their phenology – perhaps some use one strategy and some the other?

To find out, I tested the strategy choice of 237 moth species and 46 butterfly species by comparing temporal shifts in their flight period and spatial shifts in their northern range boundary (Hällfors et al. 2021a). For this study, I utilized data on Lepidoptera flight periods collected in two long-term monitoring projects coordinated by the Finnish Environment Institute (data available in Hällfors et al. 2021b). A dataset of citizen observations openly available through the Finnish Biodiversity Information Facility was utilized to calculate species range boundary shifts. The most straightforward hypothesis was that species would use one of the two strategies, as described above. But there is another possible scenario as well: responding adaptively by advancing one's phenology might actually induce a range shift response. As I already mentioned, species that advance their phenology tend to do better. We also know that stable or positive population trends, i.e., no change or increase in abundance, are often a prerequisite for species to expand their ranges, and that the dispersal rate from larger populations is higher and the probability of colonization increases with the summed contribution of individuals from neighboring source populations (Pärn et al. 2012; Hanski & Ovaskainen 2003). Thus, a competing hypothesis is, that species would combine both responses.

Like in so many other studies looking at range shifts or phenology shifts, we also found no overall direction in neither phenology nor range shifts: equally many species responded by advancing their phenology as did not, and equally many species shifted their range boundaries northwards as stayed put. We did see however, that species tended to shift their ranges northwards more often than they advanced their phenology. Overall, our results supported the idea that there is some complementary in the two responses, since roughly 45% of the species that we studied had either moved northward or advanced their flight period, but not done both. However, complementarity does not explain the lack of adaptive responses seen in studies concentrating on either range or phenological shifts, since as many as 40% of the species had still not responded in either way. On average, the populations of these poorly responding species had declined while the species responding in either way had positive population trends on average (Fig. 4). The largest increase in abundance was seen in the 15% of the species that both moved northward and advanced their flight, adding evidence to the notion that adaptive responses are connected with better thriving species.

A potential explanation for the infrequency of species responding optimally, that is, by both advancing their flight and moving northward or through either of the strategies could be a scarcity of suitable habitats. For organisms to be able to respond to climate change by shifting their ranges, enough suitable habitat of high-quality are needed. The amount of available habitat for many species has recently decreased (Kuussaari et al. 2007), resulting in many populations to decline. For example, many butterfly species have suffered from the decrease in meadows. Declining populations are usually not able to provide a sufficient basis for the species to spread to new areas. Small populations also contain less genetic diversity that could help the local populations adjust in place, e.g., by changing the timing of their flight.

Species have an amazing capacity to adjust, and nature is resilient and can buffer many disturbances and keep providing us with the ecosystem services that we depend on, but it cannot do this in a vacuum. With the rapid change we have brought about in the climatic environment, we cannot afford removing the very matrix that species need to respond appropriately: habitat. If we ensure sufficiently extensive and interconnected habitats

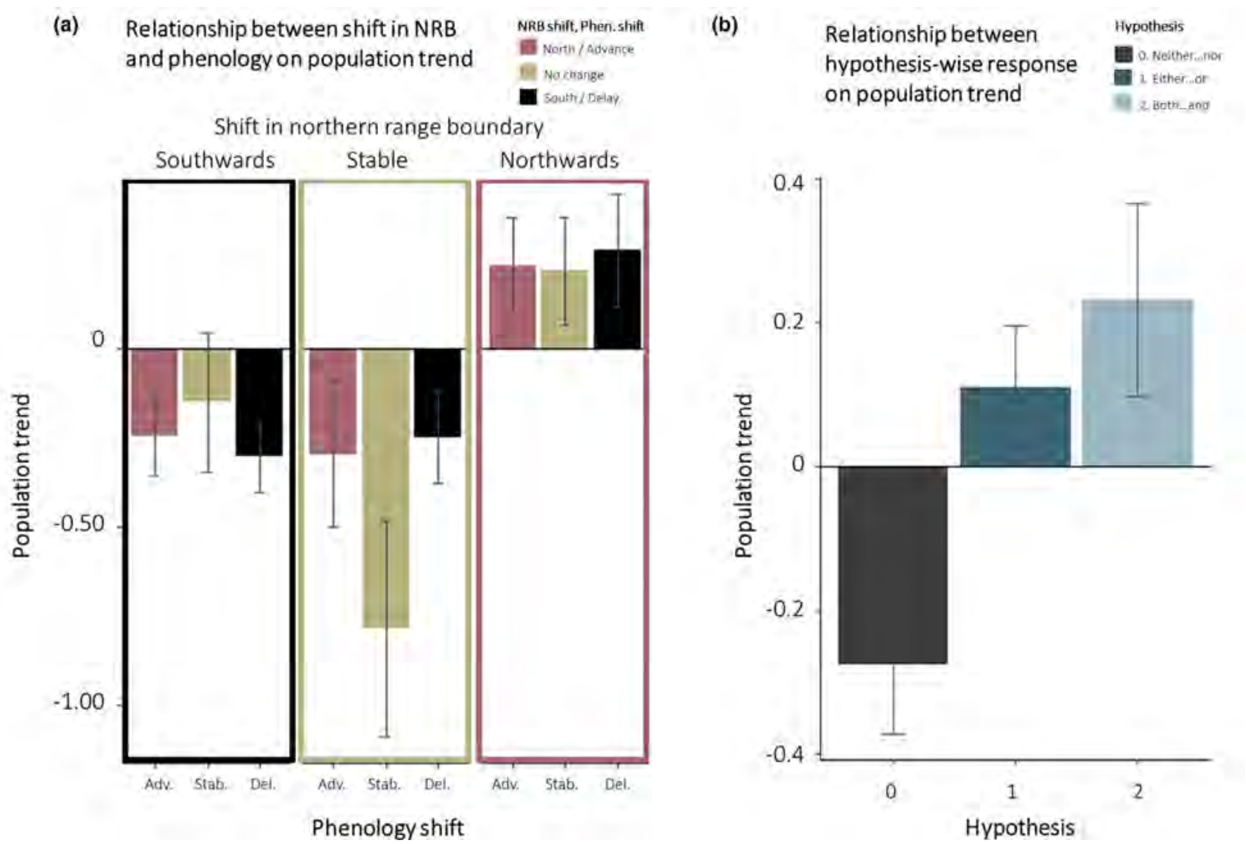


Figure 4. Relationship between responses and population trends found in Hällfors et al. 2021.
Panel (a) shows the mean population trend (±SEM) for species with different combinations of responses in phenology and NRB. The model (b) indicated that a shift in NRB had a significant positive effect on the population trend (Est. = 0.65; t = 3.36; $p < 0.001$).
Panel (b) shows the mean population trend (±SEM) for species with different hypothesis-wise responses (dark grey = Hypothesis 0 – the species neither shift NRB nor phenology; dark blue = Hypothesis 1 – the species shifts either NRB or phenology; light blue = Hypothesis 2 – the species shifts both NRB and phenology). Species that responded according to Hypothesis 1 showed stronger population trends (Est. 0.31; t = 2.51; $p < 0.05$), whereas species that responded according to Hypothesis 2 showed the strongest population trends (Est. = 0.52; t = 3.08; $p < 0.01$).
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of high-quality, species can more likely sustain sufficiently large and genetically variable populations which in turn can adjust in place when the environment changes. Safeguarding habitat will also allow species to move across space, dispersing through a habitat matrix and arriving in new habitat that they can colonize. Overall, to safeguard biodiversity as climate change intensifies, the best we can do is to allow nature room to make use of its resilience.

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What can the long-term ecological monitoring of the Åland islands meadow network tell us about changes in Finnish nature?

Photo: Video screenshot / RajuLive.fi

Marjo Saastamoinen

Saastamoinen, M., Life-history Evolution Research Group, Helsinki Institute of Life Science HiLIFE, FI-00014 University of Helsinki. marjo.saastamoinen @ helsinki.fi

Human induced changes in land use and in climate are having severe impact on natural populations and communities, as evidenced by recently reported declines in insects. Quantifying change and understanding the drivers underlying these changes requires long-term systematically monitored ecological data. The occurrence and abundance of the Glanville fritillary (*Melitaea cinxia*) butterfly in the Åland islands has been monitored across the 4 000 potential habitat patches continuously since 1993. This classic metapopulation has become an ecological model system in understanding how species persist in fragmented landscape. Due to the systematic long-term survey, we are now beginning to see also how on-going changes related to climate are affecting the ecology and population dynamics of the butterfly. As many other butterflies globally and in Finland, the Glanville fritillary butterfly also shows declining population trends in the Åland islands. In addition, the metapopulation fluctuations have become more synchronous in space with especially dry and warm summers having the most negative effect on the species overall.

Importance of long-term monitoring data in assessing change

When addressing questions related to responses of natural communities and populations to ongoing human-induced climate change and habitat loss long-term ecological monitoring data is of crucial importance (Brlík et al. 2021). Without such data it is very challenging to quantify how ecological systems have changed over time, to identify drivers of these changes or to forecast future trends. With data from monitoring schemes at varying spatial and temporal scale on different taxa in both terrestrial and marine systems researchers have, for example, demonstrated shifts in geographical ranges and in phenology in response to climate change (Parmesan et al. 1999, Bellard et al. 2012, Lenoir & Svenning 2015). During the last few years terrestrial insect declines have also been reported, especially in North America and in some European regions (Van Klink et al. 2020). Especially worrisome are indications of declines of previously abundant and wide range species. Habitat loss and degradation and chemical pollution have been suggested as the main drivers of the population declines of European butterflies (e.g. Wagner 2020, Warren et al. 2021) but the underlying mechanism and connection to on-going climate change still remain relatively unknown. Long-term monitoring data of insects populations are thus crucial in filling this knowledge-gap.

A more detailed information on a group of well-studied taxa can provide us insights that will help to understand and identify causal mechanisms underlying insect declines worldwide. Butterflies are highly sensitive to changes in their environment (Dennis et al. 2003), their ecology is often well understood, and many countries have long history of monitoring their spatial occurrence and even abundance via voluntary monitoring schemes. Butterflies are thus good candidates to act as an early warning indicators to assess risk of biodiversity loss resulting from climate change (Warren et al. 2021). Many butterflies in Europe and also in Finland are shifting their ranges and phenology in response to climate change, yet many are also experiencing declining population trends (Hällfors et al. 2021, Warren et al. 2021). Understanding changes in population trends require more detailed across population level assessments.

In Finland, the systematically and continuously collected annual survey of the Åland islands' meadow network provides a dataset of unique spatial and temporal resolution (Opedal et al. 2020). This dataset includes monitoring of the Glanville fritillary butterfly Melitaea cinxia, its specialist parasitoid wasp *Cotesia melitaearum*, and the specialist fungal pathogen *Podosphaera plantaginis* infecting *Plantago lanceolata*, one of the two host plants of the butterfly. Below, I describe the monitoring data collected from the Åland islands and briefly highlight some key aspects of the research carried out in this study system over the past 30 years (for a more thorough review on the butterfly research see Niitepold & Saastamoinen 2017, Ovaskainen & Saastamoinen 2018). My focus here is on the research on the Glanville fritillary butterfly. In the end I review some of the more recent work assessing the potential impact of on-going climate change on the ecology of the butterfly in the Åland islands.

History and main fields of research

In the early 90's the late professor Ilkka Hanski was looking for an empirical model system that he could use as a natural laboratory to test the theories he had developed in relation to metapopulation biology (reviewed in Ovaskainen & Saastamoinen 2018). He settled on the Glanville fritillary butterfly that in Finland only occurs in the Åland islands archipelago. In Åland the occurrence of the butterfly is restricted to the natural meadows and pastures in which one or both of the larval host–plants, the ribwort plantain (*Plantago lanceolata*) and the spiked speedwell (*Veronica spicata*) are present. Female butterflies lay their eggs on these plants, which the larvae then feed on during their development in the summer and after breaking diapause in the following spring. In 1993, Hanski and colleagues initiated the survey, that would become one of the best known ecological model systems in studying spatial and metapopulation ecology. During the fall survey the potential habitats of the Glanville fritillary butterflies are monitored for the presence and abundance of the butterfly based on their conspicuous overwintering larval nests found at the base of the host plants (for detail see (Ojanen et al. 2013) (Fig. 1). During the following years the fall monitoring of, currently around 4 000 mead-

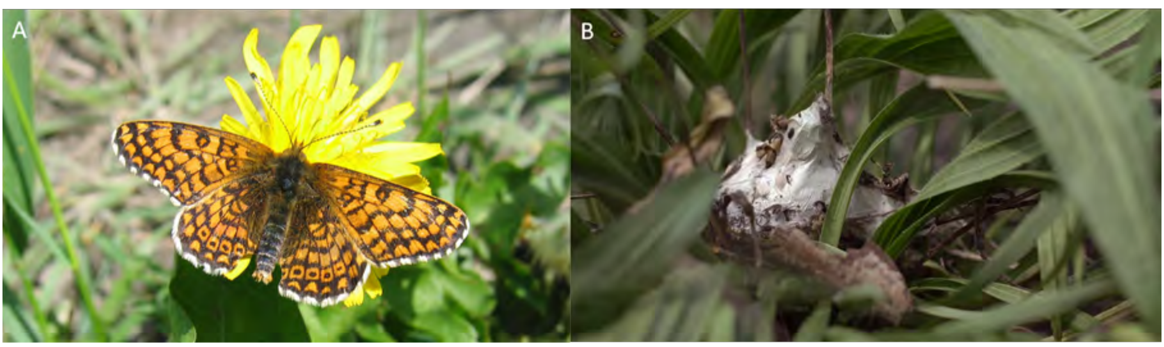

Figure 1. Adult Glanville fritillary butterfly (*Melitaea cinxia;* photo by Marjo Saastamoinen) and the larval over wintering nest (photo by Cano J. M. Arias).

ows, pastures, and even road margins, within the entire study region (50 × 70 km), became more systematic, coordinated and carried out by the students of the University of Helsinki hired as research assistants for a two week period. During the spring, the occupied habitats are revisited to assess overwintering survival of the butterfly families found during fall survey. The survey focusing on the Glanville fritillary butterfly and its host plants was soon expanded to include more community level assessment of interacting species: the occurrence of a specialized plant pathogen powdery mildew, *P. plantaginis*, of *P. lanceolata*, and presence/absence data of a specialist Hymenoptera parasitoid of *M. cinxia*, *C. melitaearum* (spring survey). The research on the plant pathogens has been seminal in assessing ecological and evolutionary questions related to disease dynamics in natural plant populations and communities (Laine et al. 2019, Numminen & Laine 2020, Susi & Laine 2020). The studies focusing on the parasitoids have demonstrated, for example, how dispersal and host range define and interact with habitat fragmentation for interacting species (reviewed in van Nouhuys 2005) and how bottlenecks influence parasitoid genetic structure and associated symbionts (Duplouy et al. 2021).

The habitat network in the Åland islands is highly fragmented and the Glanville fritillary butterfly has a classic metapopulation structure, defined by a high rate of local population turnover (local extinctions and recolonizations; Hanski 1999). The metapopulation size fluctuates greatly among years (Fig. 2). Consequently, much of the early work focused on assessing different aspects of metapopulation biology, such as impacts of spatial structure, namely patch area and connectivity (or isolation) of the habitat patches on colonization-extinction dynamics (Hanski et al. 1994), and their extensions to model more dynamic landscapes (Hanski 1999). These work provided practical tools also for conservation biology, for example assessing minimum amounts of suitable habitat requirements, extinction thresholds and viable population size (Hanski et al. 1996), metapopulation capacity (Hanski & Ovaskainen 2000), extinction debts (Hanski & Ovaskainen 2002), and so forth. The butterfly system has also been used to study how landscape structure and population processes jointly influence spatial genetic patterns (Orsini et al. 2008, Fountain et al. 2016, Fountain et al. 2018) and variation in a key life history traits, namely dispersal (Heino & Hanski 2001, Haag et al. 2005). It has also been pioneering in showing the role of inbreeding in influencing population extinction probability (Saccheri et al. 1998) and how allelic variation in candidate gene related to dispersal feed-backs to influence ecological dynamics (Hanski et al. 2017, DiLeo et al. 2018).

The land use and agricultural practices in the Åland islands are still quite traditional in comparison to the mainland Finland and most of Europe. This has most likely protected many butterflies

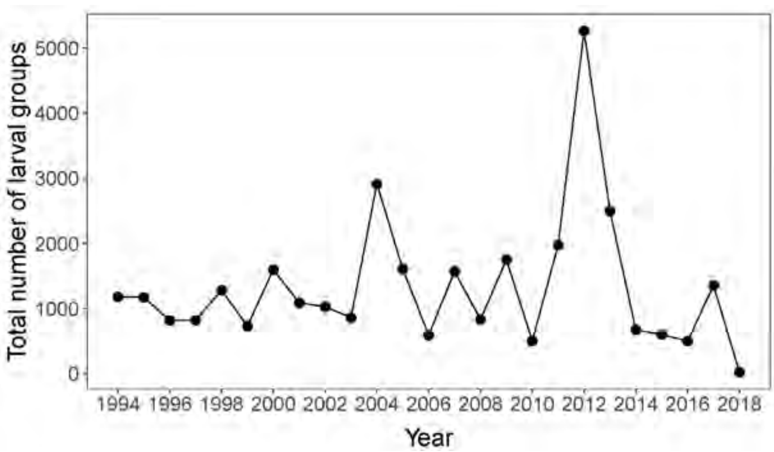

Figure 2. Changes in number of larval groups found during the fall survey 1993-2018. To correct for the minor changes in data collection among the years, data presented comes from patches that have been continuously surveyed (i.e. no missing data) since 1993.

and insects, including the Glanville fritillary butterfly, from the most common threats identified as drivers of decline, namely increased use of pesticides and loss of habitat such as traditional biotopes. Due to the absence of these more common threats, it is possible to use the system to study the impacts of climate change.

Can we see ecological changes in the Glanville fritillary butterfly over the 30-year study period due to climate change?

Changes in climatic conditions can have tremendous impacts on ectotherms directly via climate warming and changes in precipitation but also indirectly via changes in resource availability (Wagner 2020, Warren et al. 2021). In the Glanville fritillary butterfly, there is increasing evidence showing that changes in precipitation have more profound impacts than shifts in temperature, most likely due to the impact precipitation has on host plant abundance.

Based on theory, the long-term viability of a metapopulation is dependent on independent fluctuations and dynamics of its local populations (Hanski 1999). Such asynchronous dynamics alleviate fluctuations at the metapopulation level as a whole, as declining populations in some areas can be rescued from other areas with more positive population growth rates. The long term metapopulation viability can thus be compromised if spatial synchrony in population growth rates increases, for example due to changes in dispersal, predation or climate, which may all influence local population dynamics. Tack et al. (2015) used 21 years of the monitoring data from the Åland islands meadow network to analyse spatio-temporal dynamics of the butterfly. They showed two striking patterns. First, the amplitude of year-to-year fluctuations in the size of the metapopulation as a whole seemed to have increased over time. Second, they demonstrated an overall increase in the level of spatial synchrony in the population dynamics (Tack et al. 2015). In a related study, Kahilainen et al. (2018) combined longer time series of monitoring data of the butterfly with climate data for the same time period to assess whether the increased spatial synchrony in the butterfly population dynamics could be explained by an increase in synchrony of weather conditions. Results firstly highlighted that precipitation rather than thermal conditions from spring to late summer are key environmental drivers of the population dynamics, and hence associated with population growth rate of the butterfly. Furthermore, it was evident that the increase in metapopulation synchrony was paralleled by an increase in the synchrony of key weather parameters (Kahilainen et al. 2018). The study further showed that there has been no change in dispersal propensity or strength of trophic interactions with a specialist parasitoid, *C. melitaearum*, over the study period, both of which could have been alternative explanations for increased metapopulation synchrony.

It has been suggested that preferences for warm microhabitats may become maladaptive under climate change (Benton et al. 2003). The Glanville fritillary butterfly in the Åland islands lives at its northern range margin, and as an adaptation show a preference to utilize microclimatic conditions in which also higher proportion of host plants show signs of drought exposure, especially in warm and dry summers (Schulz et al. 2019, Salgado et al. 2020). Both warmer microclimatic conditions, but also feeding on mildly drought exposed host plants ensure more successful development during relatively short time window in the summer (Rosa et al. 2019, Verspagen et al. 2020, Kahilainen et al. 2022), before thermal conditions cool down in autumn and diapause is initiated. Increased larval development is beneficial because over-wintering survival seems to be higher for larger larvae (Rytteri et al. in prep), although larvae have some flexibility in when to enter diapause (i.e. 4th or 5th instar; Kahilainen et al. 2022). Salgado et al. (2020) further showed, by combining field experiments with 10 years of larval nest location and precipitation data, that the preferred drought-exposed microhabitats maximize larval nests survival in most summers. Unfortunately, female butterflies do not seem to shift habitat preference even under extreme climatic conditions such as heatwaves (Salgado et al. 2020). This mother’s choice of warmest microhabitats for oviposition that is adaptive under predominant conditions, indeed resulted in high larval mortality in the dry summer of

2018 when the plants at these sites dried out entirely. The preference for warmest microhabitats has maladaptive consequences also for the post diapause larvae under warm spring conditions, as demonstrated by Rytteri et al. (2021): Exceptionally warm weather early in the spring can cause a phenological asynchrony between butterfly larvae and their host plants. An exceptionally early and warm spring lead to larvae breaking the diapause earlier without equally advancing host plant growth, which resulted in high larval starvation. This work on the Glanville fritillary highlighted the important role of microclimatic variability within and among populations in buffering the negative impacts of warm spring conditions (Rytteri et al. 2021).

In summer 2018, Northern Europe was struck by an extreme heatwave (Bastos et al. 2020). Due to this event, we also got direct information on how such extreme conditions may impact the Glanville fritillary butterfly in the Åland islands. We combined the ecological monitoring data with climatic and satellite data to demonstrate that year 2018 indeed was an anomaly with extremely low climatic water balance values and extremely low vegetation productivity indices across the Åland islands meadow network (van Bergen et al. 2020). The population growth rates of the butterfly were strongly associated with the climatic conditions, and consequently we observed a drastic demographic decline of the butterfly, with an all-time low of only 91 larval nests being recorded during the autumn survey (van Bergen et al. 2020). Similarly, the number of occupied patches was an order of magnitude lower than in any average year (van Bergen et al. 2020). Even though based on our ecological understanding of the system, we could predict a decline in abundance, the observed decline was even more severe than anticipated by our predictions. Thus, responses of natural populations to extreme climatic events are difficult to predict even in a well-studied system. The Glanville fritillary has recovered in most parts of the Åland islands since this historical crash evidenced in 2018 (Saastamoinen, personal communication), most likely due to good enough habitat connectivity. Oliver et al. (2015) used long-term monitoring data of the British butterflies together with predictive modelling to demonstrate how the recovery of the drought-sensitive butterflies followed by a drastic decline due to extreme drought in 1995 dependent on the amount of semi-natural habitat within the landscape. However, it is becoming evident that similarly to many insects, the Glanville fritillary butterfly is also showing slight negative population trend in patch occupancy over time in the Åland islands (Opedal et al. 2020). The drivers of this negative population trend is unknown, but it is likely a combination of the changes in the climatic conditions as well as variation in host plant abundances, which fluctuate in response to climate, land use and other environmental factors (Opedal et al. 2020).

Concluding remarks

The Glanville fritillary metapopulation in the Åland islands is an ecological model system in studying spatially structured populations. The long-term monitoring data provides evidence that climate change is profoundly impacting the ecology and evolution of the butterfly by altering its dynamics and previous adaptations. In particular, the seeming lack of behavioural flexibility in habitat and oviposition site choice may result in drastic consequences if dry and warm summers and early warm springs become more frequent with climate change, which both are predicted climate change scenarios based on the recent IPCC report (IPCC 2022). Furthermore, the increased synchrony across the metapopulation may potentially increase the extinction risk of the metapopulation over time. Importantly, however, the system harbours high levels of genetic variation, increasing adaptive potential. In addition, the traditional agricultural practices in the Åland islands, at least at the moment, support good quality habitat and well-connected network, which will hopefully allow persistence of the butterfly in long-term future.

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Rethinking research: the role of tradition in the study of marine invertebrates

Erik Bonsdorff

Bonsdorff, E., Environmental and marine biology, Åbo Akademi University, FI-20500 Turku/Åbo. ebonsdorff @ gmail.com

Scientific tradition is a key-element behind innovation and novelty in science. Relying on tradition provides a sense of security for the individual researcher but may also hamper scientific progress. By rethinking and reformulating previously stated research-topics and questions, science can profit from already existing data and knowledge. For this, however, a conceptual framework for critical thinking must exist for exchange of scientific ideas and findings. Tradition and critical thinking supply the framework for understanding data collected today in relation to previously accumulated information and scientific knowledge. This paper reflects upon these processes from the perspective of marine biological studies on soft-sediment invertebrates in Finland during the past 100 years exemplified by the works of Sven G. Segerstråle, with his education rooted in the old and traditional, and yet daring to think and work in innovative pathways.

Introduction

Scientific tradition is often thought of as a key-element driving innovation and novelty in society at large and within science more specifically. Relying on tradition provides a sense of security for the individual researcher but may also hamper scientific progress. By rethinking and reformulating earlier research-topics and questions, and by reformulating scientific hypotheses, science can profit from already existing data and knowledge. To do so, there must, however, exist a general framework for critical thinking and for exchange of scientific ideas and findings. One such arena is provided by scientific and learned societies and academies, which contribute to upholding the needed basic platform. *Societas pro Fauna et Flora Fennica* (SFFF), founded in November 1821 and thus being the oldest learned society in Finland, plays an important role in both collecting and conserving ideas and knowledge about the terrestrial and aquatic fauna and flora of Finland and its nearby regions (Wallgren 1996).

From originally striving to describe and record the biota found in Finland, SFFF today is one of several scientific organizations in Finland offering academic guidance as well as economic and logistic support both to young early-career scientists and to established researchers in their efforts to uphold the traditions of natural history as a foundation for the plethora of advanced and high-level research groups within biosciences and ecology in Finland at universities and museums as well as at various institutes. How, then, can the modern and often effectivity-driven science ('science for benefit') of today draw from the descriptive or strictly curiosity-driven science of previous times? Are not modern efforts elements of a completely different set of scientific academic traditions? My tentative answer is 'no they are not'. In this paper I exemplify this from the narrow perspective of specific marine biological studies on soft-sediment invertebrates in Finland during the past 100 years.

Knowledge beyond a static image of nature

The natural science of the past 200 years indeed forms the foundation upon which current analytical and predictive curiosity-driven and applicable research is based. In a way one can say that the natural sciences are built in part on a strong Humboldtian tradition – see for instance the biography on Alexander von Humboldt (1769–1859) by Wulff (2015) – and in part on the famed quote of Johann Wolfgang von Goethe (1749–1832) stating that '*All intelligent thoughts have already been thought; what is necessary is only to try to think them again*'. The need to observe, interpret and understand nature became increasingly strong during the utilitarian era of the 18th century (more prominent in Finland during the first decades of the 19th century) as well as a result of the era of enlightenment with scientists and thinkers such as Isaac Newton (1642–1727) and Voltaire (or Francois-Marie Arouet, 1694–1778) as prominent spearheads, which lead to the need for a systematization of what was observed. Hence the Linnéan (Carl von Linné 1707–1778) approach to classify the living nature became defining for much of our natural end environmental science even today, paving the way for in-depth analysis reaching beyond systematics during the 19th century, with Charles Darwin (1809–1882) being the founding father of modern evolutionary biology and ecology, in turn basing parts of his thoughts on the fathers of modern palaeontology and geology, namely Georges Cuvier (1769–1832) and Charles Lyell (1797–1875), who had set out the pathway of thinking beyond the concepts of creation and a static image of nature.

Accepting change, succession and evolution is fundamental to our current intra-disciplinary understanding of nature. *Societas pro Fauna et Flora Fennica* became the founder of museal collections and taxonomic compilations in Finland (Wallgren 1996). The work largely built on traditions inherited from Sweden (Linné and his disciples, and the Royal Swedish Academy of Sciences, founded already in 1739) as well as from Europe in a wider perspective with natural history museums being founded in countries and cities with strong universities at the time. During the 19th century, several leading natural scientists in Finland made their mark for these collections. Among them Evert Julius Bonsdorff (1810–1898) who's collections including skeletons of now extinct mammals are still part of the Natural History Museum in Helsinki (see Wikgren 1996 for an overview of the history of biology in Finland).

The Baltic Sea and its benthic invertebrates exemplify tradition in research

One hundred years after its foundation, in 1921 as *Societas pro Fauna et Flora Fennica* celebrated its first centenary, marine science was a young and fumbling branch of academic study and research in Finland. Some physical and oceanographic features of the sea had been monitored for a few decades, such as mareographs measuring variations of sea level, and other basic features of our coastal waters (Poutanen & Leppänen 2021). These data now provide valuable references for our current interpretation of climate change-related aspects of the Baltic Sea and the entire Baltic Sea region ranging from the sea itself to the terrestrial and atmospheric systems surrounding it (Meier et al. 2022, Viitasalo & Bonsdorff 2022).

Descriptive biological studies had begun during the last decades of the 19th century (Wikgren 1996, Pokki 2009), and as fishing and fisheries were socially and commercially important, the organisms that provide food for fish were collected and recorded, and so the first inventories of the zoobenthic fauna of our coastal and offshore waters had begun (Haahtela 1996, Poutanen & Leppänen 2021). The continued need for mapping and description of the fauna and flora of the Finnish coastal waters today is perhaps best documented in a recent book including an Atlas based on the national habitat-mapping and biodiversity inventory project VELMU (Viitasalo et al. 2021).

One specific field of descriptive zooecology in Finland is the study of aquatic (both limnic and marine) zoobenthos, displaying a great taxonomic and functional variability along the environmental Baltic Sea gradient (Bonsdorff 2006, Ojaveer et al. 2010, Gogina et al. 2016, Viitasalo et al. 2021). This stems from the fact that the benthic invertebrates constitute an important and reliable food source for benthic-feeding fish. To understand the dynamics of commercial fish-stocks as well as non-commercial fish populations in general, benthic surveys in the Baltic Sea were started already in the early 1900s, with the first systematic study partially covering Finnish offshore waters was a large survey by Hessle (1924). This study became a foundation for later monitoring-surveys up until today (Villnäs & Norkko 2011).

It is justified to ask why this field of zoology and ecology is of general interest, and the answer lies in the above-mentioned role of the benthic fauna as food for fish, but also in several overarching facts: the sediment-water interface in the oceans is the largest ecological interface on Earth, and the diversity at Phylum-level is highest in this ecological realm. The benthic invertebrates play key-roles in ventilating the sediments, thus contributing to the remineralization of nutrients and recycling of other important elements on a global scale. From a local or regional perspective, the relatively long-lived and stationary organisms have a high value as indicators of ecosystem-health (Janas et al. 2017, Thrush et al. 2021). Although the analytical methods have improved immensely during the last decades, and environmental mapping has become more precise, environmental monitoring as well as scientific interpretation of long-term changes in the Baltic Sea rely on basically asking and reformulating the same scientific questions over and over in true Goethean manner. The precision has improved, but the conceptual framework has remained surprisingly similar over time (Hessle 1924, Sjöblom 1955, Andersin et al. 1977, Laine 2003, Villnäs & Norkko 2011 illustrate a chain of examples encompassing Finnish coastal and offshore waters).

Haahtela (1996) in his presentation and paper for the 175-year anniversary seminar of *Societas pro Fauna et Flora Fennica*, presented an inventory and a literature-overview of the basic faunistics of invertebrates of both marine and inland waters of Finland. He provided a thorough taxonomic overview, including a large bibliography regarding all key taxa, with 295 adequate references. Haahtela (1996) is still an important and valuable reference for the faunistics of the Finnish marine and brackish-water invertebrates. There is, however, one sector within the taxonomy of Baltic Sea invertebrates which has changed significantly since the 1990s, namely the so called non-native and invasive species, several of which have established viable populations during the last 20–30 years. These newcomers have not yet changed the rationale of the research, be it documentation or experimentation in the field or in aquaria. The methods have, however, diversified (such as molecular analysis for taxonomy, and numerical tools for validating findings in statistical terms), and open databases facilitate our efforts to stay updated on the distributions of species, but the basic questions as to what species are found under which conditions and why remain surprisingly similar over time. For the non-native invasive ones, the database AquaNIS (www.corpi.ku.lt/databases/index.php/aquanis/) provides an accurate and up-to-date source of basic information, and the ecological implications of them are summarized in Ojaveer et al. (2021).

Scientific tradition, Sven G. Segerstråle and the importance of curiosity-driven research

Scientific tradition is, as illustrated above, oftentimes linked to certain individual scientists who have dared challenge the knowledge and scientific 'truth' of their respective times. When it comes to the marine invertebrates, Finland clearly has had one outstanding forerunner at the national and international levels, namely Professor Sven G. Segerstråle (1899–1994), who according to WorldCat (worldcat.org) published 173 publications in three languages (among them 73 papers in English, 43 in German, and several in Swedish). The two most widely cited ones are Segerstråle 1957a (a comprehensive book chapter on the Baltic Sea as a system) and Segerstråle 1973 (the *Macoma-Pontoporeia* theory). Both these works can be classified as 'citation classics' for the invertebrate fauna of the Baltic Sea. A word-cloud based on the titles of his works shows that he covered a wide range of topics between the late 1920s and the early 1980s, and he published scientific papers during no less than 7 decades. The most impressive aspect of the word-cloud is that any benthic ecologist of today would be proud to have such a wide array of topics, species and environments covered during their careers. The top-tier of words is: Baltic Sea, Gulf of Finland, Gulf of Bothnia, Atlantic Ocean, Marine animals, Marine biology, Glacial lakes, Salinity, Amphipoda, Isopoda, Mysidae, Gammaridae, *Pontoporeia*, *Macoma* to name just a few.

What, then, were the main topics of his research, and how have these in turn affected others later and in parallel to him, what is his legacy for Finnish marine invertebrate zoology and ecology, apart from being the first one to pick up on the international trends of studying organisms that few people even know are there? Apart from having an extraordinary career in his field, Segerstråle played a key-role in the foundation of the Nordic Council for Marine Biology, which between 1956 and 1994 provided opportunities for several thousand Nordic students of marine biology to learn from all aspects of the field in just about every corner of the Nordic marine network of field stations (Wikgren 1996, Pokki 2009, Poutanen & Leppänen 2021). Wikgren (1996) specifically points out the importance of Segerstråle in the formulating and testing of specific hypotheses (which was not common in the early half of the 20th century) and following up on his thinking through extensive field work leading to experimental testing of both intra-and interspecific interactions of the zoobenthos (an approach largely neglected until the 1980s and 1990s). Through his examples in both research and education, he gave the younger generations a chance to realise the importance of knowing the scientific heritage and past thinking in order to understand and comprehend the present, and even be able to predict future responses to environmental change (as an example, Segerstråle 1957a mentioned non-native invasive species before they were discussed at all for our coastal waters, perhaps because general zoogeography and the distribution of glacial relict-species as well as paleofossil remains of bivalve shells were among his themes – see Segerstråle 1957b). To name just a few, Segerstråle as a person and through his publications significantly and positively influenced the thinking and work of Finnish benthic ecologists such as V. Sjöblom, P. Bagge, P. Tulkki, E. Leppäkoski, J. Lassig, A.-B. Andersin, H. Sandler, R. Varmo, E. Bonsdorff and A. Norkko. Through them there is now an active and gender-balanced generation of researchers at universities and research institutes (M. C. Nordström, H. Nygård, A. Törnroos-Remes, A. Villnäs and others).

Based on observations in the field, Segerstråle (1927) reformed the understanding of possible migratory behaviour of bivalves. *Tellina – Macoma - Limecola baltica* (*balthica*) seemed to move towards deeper waters along the surface of the sediment. His reasoning was almost 70 years later supported by Bonsdorff et al. (1995). Thus, already from the onset of his scientific career, Segerstråle dared ask questions for the sake of advancing science and inspiring novel research. Segerstråle's main field studies were on the benthic infauna along the southern Finnish coast, specifically in the archipelagos of Pellinge and Tvärminne. Finding similar patterns of species assemblages, and in population dynamics, he was able to reconstruct and interpret settling of juveniles, and both positive and negative correlations between species as well as population dynamics for the bivalve *Macoma* (*Limecola*) *balthica* and the amphipod *Pontoporeia* (*Monoporeia*) *affinis*, as well as between communities and their environmental drivers, notably salinity, temperature, and depth (Segerstråle 1933, 1962). A key-factor for his understanding of the animal-sediment interactions was the fact that ground-breaking work on sediment-chemistry was being conducted simultaneously at the Finnish institute of marine research, where Segerstråle was employed (Gripenberg 1934, Poutanen & Leppänen 2021). In addition, Segerstråle (1933, 1962) initiated and inspired the long-term studies of coastal and archipelago benthic infauna that later became the foundation for modern area-specific monitoring and interpretations of mechanisms driving population- and community change for coastal zoobenthos used as indicators of ecosystem health (Bonsdorff et al. 2003, Rousi et al 2013, Hewitt et al. 2016, Forsblom et al. 2021).

Studying distributional patterns within and between the local benthic invertebrate assemblages on the coast of the Gulf of Finland (most notably around Tvärminne zoological station, where accompanying environmental parameters were continuously recorded), Segerstråle (1957a) was able to draw general conclusions comparable to the global ones made by Gunnar Thorson in Denmark (1957). His zoogeographical interests expanded to encompass the concept of glacial relicts (Segerstråle 1957b), with special focus on marine, limnic and brackish water crustaceans (isopods, amphipods, and mysids), thus setting the stage for later genetical studies concerning speciation driven by gradual geographical isolation (for example Väinölä et al. 1994).

Biological interactions such as competition, predation, and physical disturbance are hard to analyse in the field. Yet Segerstråle in his seminal papers (1969, 1973) put forward the famous *Macoma-Pontoporeia* theory, in which he postulated that the negative correlation found in the field between newly settled individuals of the bivalves and high abundances of the amphipod is due to predation by the amphipod. *Pontoporeia* was generally considered to be deposit-feeding on sediment-particles and organic matter rather than showing predatory behaviour, and colleagues elsewhere doubted and contested his theory (notably Ankar 1976). Segerstråle (1978) defended his findings and his theory, but it took another 20 years before he was proven right (Ejdung & Elmgren 1998), after experiments first confirming that the *Macoma*-spat was indeed a favourable food-item for other invertebrate predators and omnivores (Ejdung & Bonsdorff 1992, Aarnio et al. 1998). The *Macoma-Pontoporeia* theory in many ways became a classic and a starting-point for modern-day food web studies of the Baltic Sea (Kortsch et al. 2021).

Conclusive remarks

As can be seen from the above, it is possible for individual scientists to become forerunners within their fields of science, and even shape the pathways their entire research subject (in this case marine benthic ecology) takes for decades. Simultaneously it is evident and important to acknowledge the role of tradition and history within science irrespective of field or topic. Without the inspiration of insightful thinkers such as von Linné, Humboldt, Darwin and others, there would perhaps not have developed a need for collecting specimen for museum-purposes, and without such collections the concepts of studying organisms in their environment and the interactions between them, be they natural or anthropogenically modified. Sven G. Segerstråle was one of perhaps a handful of such marine scientists in Finland. Through his biological and ecological curiosity-driven interests and works, strong generations of scientists were fostered, and today we see how such broad and long-term knowledge allows us to contribute to the scientific debate on a basin-wide and even on a global scale (Reusch et al. 2018). It is safe to say that for scientific progress we need both an understanding of and respect for scientific tradition, and an open innovative and curiosity-driven research agenda.

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The changing fauna and flora of Finland – discovering the bigger picture through long-term data

Photo: Video screenshot / RajuLive.fi

Tomas Roslin & Anna-Liisa Laine

***Roslin**, T., Spatial Foodweb Ecology Group, Department of Agricultural Sciences, Faculty of Agriculture and Forestry & Research Centre for Ecological Change, Research Programme in Organismal and Evolutionary Biology, Faculty of Environmental and Biological Sciences, University of Helsinki, Finland,* tomas.roslin @ helsinki.fi*. Department of Ecology, Faculty of Natural Resources and Agricultural Science, Swedish University of Agricultural Sciences (SLU), Sweden,* tomas.roslin @ slu.se. ***Laine**, A.-L., Research Centre for Ecological Change, Research Programme in Organismal and Evolutionary Biology, Faculty of Environmental and Biological Sciences, University of Helsinki, Finland. Department of Evolutionary Biology & Environmental Sciences, University of Zürich, Switzerland.*

To discern changes in nature during the current era of unprecedented biodiversity change, there is no alternative to systematic long-term data collection efforts. Finland holds a globally unique treasure trove of long-term ecological data series, each springing from its own origins, purposes and approaches. If sensibly used, these data provide a unique baseline for what was before, insight into current directions of change, and a scientifically sound foundation for informed policies. To leverage the mobilisation of these data, we conduct a basic SWOT analysis of the Strengths, Weaknesses, Opportunities, and Threats associated with our national data treasure. As Strengths, we identify the globally unique extent, depth and coverage of data. As Weaknesses, we identify the fragmented nature of data storage, access, and taxonomic coverage. As Opportunities, we show how new syntheses spanning across decades and taxa may reveal both the extent of and mechanisms behind biodiversity change. As Threats, we point to the alarming lack of long-term funding, legislation and coordination of these time series. We conclude that these data provide a unique potential for informing relevant policies – and that this potential can only be secured, tapped and maintained by transformative changes in national monitoring strategies, funding and legislation.

Introduction

The Finns take pride in their nature. Think of the Finnish passport. Where other passports feature statesmen or -women, a statue or a historical site, the Finnish passport show lakes, trees buried in deep snow, a narrow trail dwindling away over a mire, or a boat crossing lake Kilpisjärvi – with iconic Fjeld Saana in the background (Fig. 1A,B). The same iconography applies to our currency. The Finnish markka came with swans and spruces. Now these very themes feature in the euro age: Finnish coins feature water lilies, capercaillies and roan (Fig. 1C). It seems it was always clear to the nation where its identity came from – and from where it derived its wealth.

The modern iconography builds on a long tradition of appreciating national living resources.

Finnish Government, PD via Wikimedia Commons

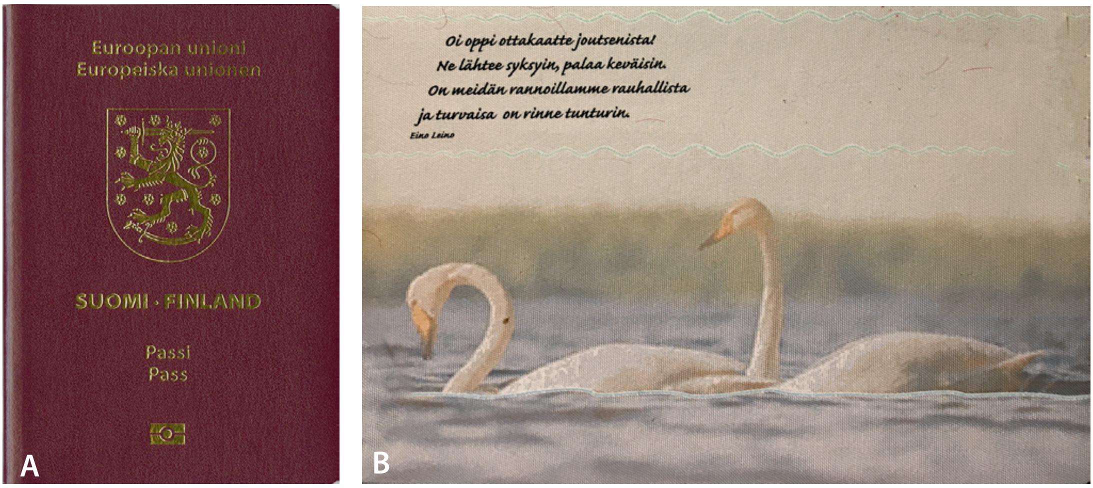

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Figure 1. National Finnish iconography featuring nature and wildlife, here illustrated by the Finnish passport (A), its contents (B: individual spread) and national currency (C; including examples from both the era of the Finnish markka and the current euro).

During the current era of unprecedented biodiversity change, our ability to understand and predict what is changing and why is still astonishingly limited. This makes extant data both irreplaceable and infinitely valuable from a both national and international perspective. In our brief essay, we will examine how Finland has systematically surveyed its living nature over time, and how this effort has developed into a national treasure of long-term data. To augment the mobilisation of these data, we will conduct a basic SWOT analysis of the Strengths, Weaknesses, Opportunities, and Threats associated with our national data treasure. But to understand the status quo, we should start by considering how these data came into being.

A brief history of Finnish time series

To discern long-term changes in nature, there is no alternative to observations spread over time. What is more, historical data cannot be generated in hindsight, making any extant records priceless. Finland holds a globally unique treasure trove of long-term data recorded in the past. Today's data are the outcome of a long chain of events.

In the 18th century, when Finland was Sweden, the national economy was in tatters. This misfortune had been brought upon the nation by its wars. For Sweden, the 17th and 18th century were marked by a long series of wars, with the national coffer being emptied by attempts to conquer all Europe. Once Charles XII had eventually been wiped out by a Norwegian bullet, the nation had to be rebuilt. Mapping its living resources was part of this process (Broberg 2019).

The travels of Carl von Linné (Fig. 2) were driven by this utilitarian need. His journeys across Sweden (including Finland) were aimed at mapping its living resources; his task was to explore how nature was and could be used to the benefit of the population and the Crown. Since sensible agricultural practices should be matched with nature's calendar, Linné started mapping when plants and animals awaken in different parts of the reign. For this purpose, Linné and his later successors (including 19th-century professor Hugo Hildebrand Hildebrandsson) recruited the intelligentia of their time, providing eyes and observations across the kingdom. Thus came about the earliest time series: that of phenology – as still continued today (Fig. 3).

Over the centuries, war has continued to be a driver of natural inventories. After the independence of Finland, the new nation needed an inventory of its forest resources. This need spawned the first National Forest Inventory in 1921–1924 (Fig. 4), which was rerun during the harsh economic years of 1936–1938 (Haapanen 2014). The same need grew stronger after the second World War, when the Soviet Union demanded compensation for Finland allegedly causing the war. Since much of the payment was based on forest products, national forest resources were surveyed again in 1951–1953 – now already adding to an established series of snapshots of our forests and their state, later repeated more or less every decade.

Importantly, what was recorded would naturally reflect what was perceived as important. The National Forest Inventory was designed to reflect forest extent and productivity, whereas biodiversity was so far a concept not even minted. Only in later were aspects of diversity added, such as dead wood and surveys of the understory vegetation added to the effort (Anonymous 2016).

Further examples of direct needs to map natural resources are the game triangles initiated by Game and Fisheries Research Institute (currently Luke). To know how much game one can hunt, one needs to know the stock to be hunted. Initially, bag statistics were used to describe changes in stocks. In 1945, a so-called game survey

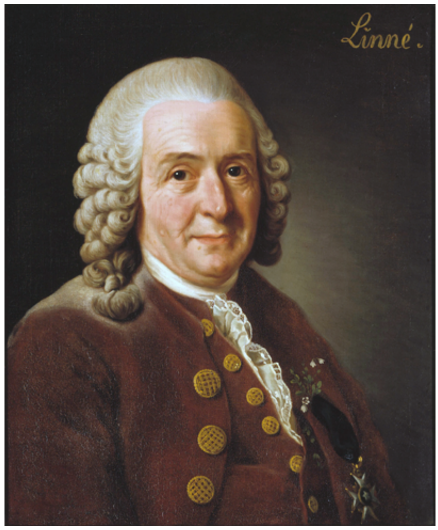

Figure 2. The travels of Carl von Linné were across Sweden and its eastern parts (now Finland).

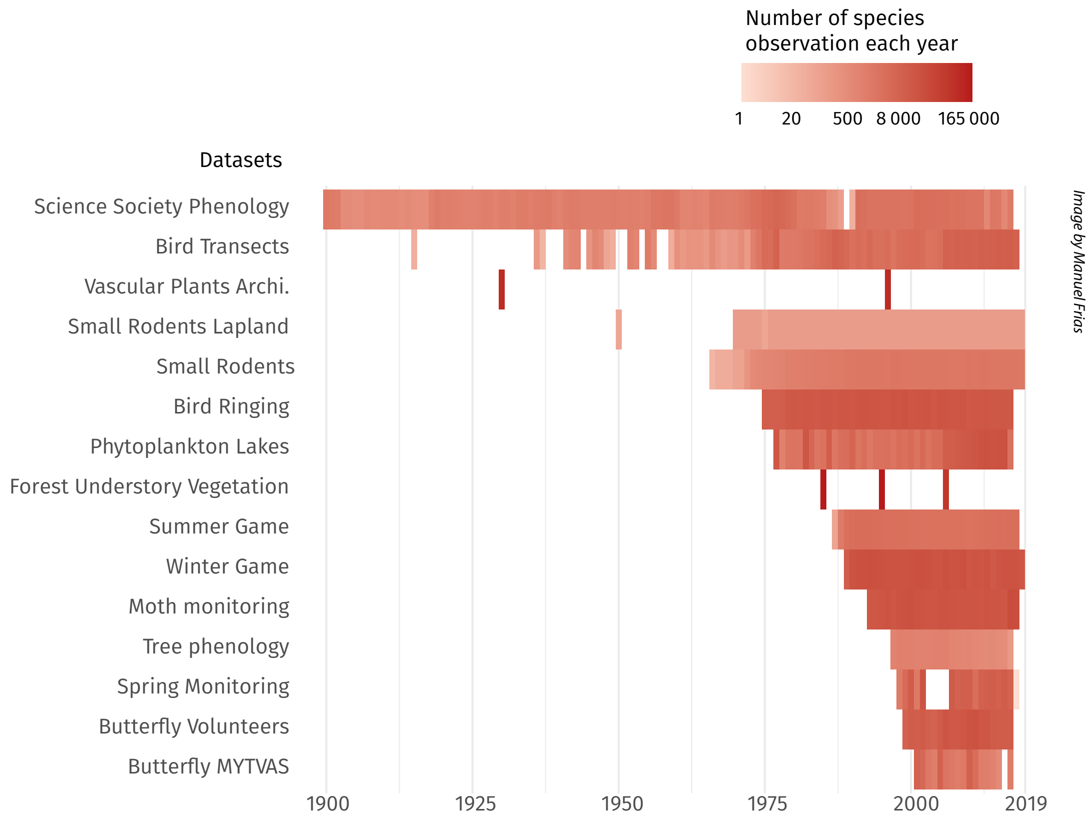

Figure 3. The temporal coverage of Finnish long-term data series. The graph shows both the time span (length of the bar, with decades along the abscissa) and the number of species observations per year (depicted by the colour, with a visual legend at the top right). The density of observations is highest during the last few decades, but some observations go far back in time. Note that the longest time-series was initiated by Carl von Linné (Fig. 2) through the Science Society Phenology, and now spans nearly 270 years. The Forest Understory Vegetation data were collected at 10–11 year intervals until 2006, while other datasets have, in general, been collected on an annual basis. The exception is the data set on Vascular Plants from the South-western Archipelago, which is based on an original survey in the 40s with resurveys in the 2000s (Fig. 4).

was started, in which about 500 observers from all over Finland described the relative abundance of the most common game species in their camping area and the change in the abundance of the stock compared to the previous year. In the monitoring of forest fowl and mammals, transect counts began in the early 1960s. However, the abundance and variability of common game species (and mammals in particular) was poorly understood until the late 1980s. In the 1980s, efforts were made to find a method that would provide information on as many game species as possible through a single census. Late-summer counts were initiated to count broods of game fowl, whereas winter counts were focused on snow tracks – a method long used in Russia. This programme has then been sustained ever since, as implemented by hunters' associations (Lindén et al. 1996; Helle et al. 2016).

Utilitarian inventories springing from the needs of production and usage (above) are but one end of the spectrum. The other extreme are time series springing from the interest and enthusiasm of individual researchers. Ole Eklund (Fig. 5A) was a botanist born in Korpo, an island in the Southwestern archipelago on Finland, in 1899. In 1910, he began compiling a flora over his home municipality. The study area was gradually enlarged and eventually included most of the Archipelago Sea, with thoroughly compiled species lists of the vascular plants from about 1 500 sites (usually individual islets). The most intensive

Luke / photographic collection of Yrjö Ilvessalo

Figure 4. Field inventory during the first National Forest Inventory in 1921–1924.

work occurred in the 1920s and 1930s, whereas in 1946 Ole Eklund tragically died, at an age of only 47 years. His work was later continued by Mikael von Numers (Fig. 5B), who – likewise, out of own interest – has revisited and resurveyed a massive number of sites in the 21st century, and found massive changes in the occurrence of plants across islands (von Numers & Korvenpää 2007, von Numers 2015). These types of visit-revisit designs provide enormous opportunities for observing large-scale change and their drivers (Opedal et al. 2020).

Somewhere in between the utilitarian and the purely "curiosity-driven" initiatives, we see curiosity-driven initiatives found useful for production, and thus later adopted for utilitarian purposes. A prime example here is the pioneering work of professor Olavi Kalela (Fig. 6A) in exploring population densities of small rodents in Lapland. His enthusiasm was transmitted to his young student Heikki Henttonen (Fig. 6B), who – later a professor himself – has personally generated a more than 50 year-long time series on the population densities of small mammals (voles) in Lapland. The former Forestry Research Institute (now Luke), hired another vole aficionado – Asko Kaikusalo – for recording vole densities across Finland. Given the economic implications of vole damages on silviculture, these originally curiosity-driven time series have since formed the basis for predicting seedling damage, and for understanding the population-dynamic drivers of forest damages by voles (for a classic summary of Nordic time series, see Hanski and Henttonen 2002).

Most recently, we see initiatives being fruitfully adopted in the opposite direction: from utilitarian premises to curiosity-driven science. With Finland's entry into EU, the EU-level ban on national economic subsidies (as biasing competitive constellations) was combined with some EU-

Photo: Memoranda Societatis pro Fauna et Flora Fennica 1947

Photo: Mikael von Numers 2014

Figure 5. The two *primi motori* behind the extensive dataset on vascular plants from the Southwestern Archipelago: Ole Eklund (A; 1899–1946) and Mikael von Numers (B; current chair of Societas pro Fauna et Flora Fennica).

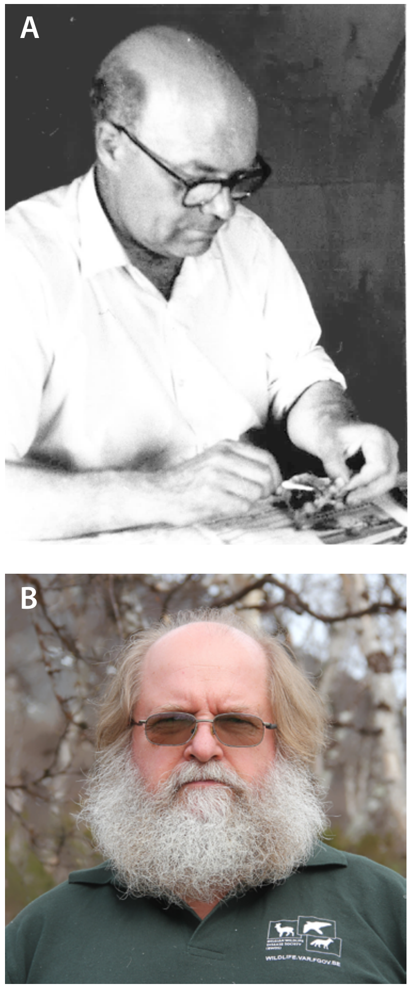

Photo: University of Helsinki

Photo: Heikki Henttonen 2011

Figure 6. The pioneers behind the long-term data on small rodents in Finnish Lapland: professors Olavi Kalela (A) and Heikki Henttonen (B).

support for environmentally-friendly actions. As a result, there was a need to critically evaluate whether environmental subsidies really gave the desired effects. This yielded a series of follow-up studies of the impacts of agri-environment measures (MYTVAS). Here, the potential for using the follow-up studies for some wider scoring of the state of the environment was quickly realised by researchers, yielding both some acrid reports on the true nature of the subsidies (Kleijn & Sutherland 2003; Schulman et al. 2006; Kuussaari et al. 2008; Aakkula et al. 2012) and many insights into basic ecology (e.g. Ekroos et al. 2010; Jonason et al. 2017; Toivonen et al. 2017; Mäkeläinen et al. 2019).

As a result of these semi-independent and internally uncoordinated initiatives, the Finnish state is now the proud owner of millions of records (Fig. 3). Springing from the different origins, purposes and approaches described above, these long-term data now cover our nation as a deep information blanket (Fig. 7).

In terms of their information contents, the long-term data series of Finland form a globally unique treasure trove. These data have been collected systematically using clearly defined methodology, resulting in a unified data format that allows comparative analyses through space and time. As such, these data fulfil the criteria required of any official national statistics. If sensibly used, they provide a unique baseline for what was before, insights into current directions of change, and a scientifically sound foundation for informed policies. Nonetheless, without retracing the roots of each data series, its origins and focus, there is clearly no way we can understand the motley nature of today's data. And without compiling all data in a standardised, accessible format, it is impossible to compare them to each other. Hosted by the University of Helsinki, the Research Centre for Ecological Change (Fig. 8) has been the first research consortium to do so, and to thus gain an overview of the status quo. It is against this background that we will next set out to examine the Strengths, Weaknesses, Opportunities, and Threats associated with our national data treasure.

SWOT – Strengths, Weaknesses, Opportunities, and Threats

Strengths

Long-term data hold a special place in both science and policy. Due to the credibility of such data, both researchers and policy-makers tend to invest particularly high trust in evidence backed by time series (Hughes et al. 2017). From a scientific perspective, we can only discern change by comparing a new state with a previous one. Time series allow us to detect the extent of change, by

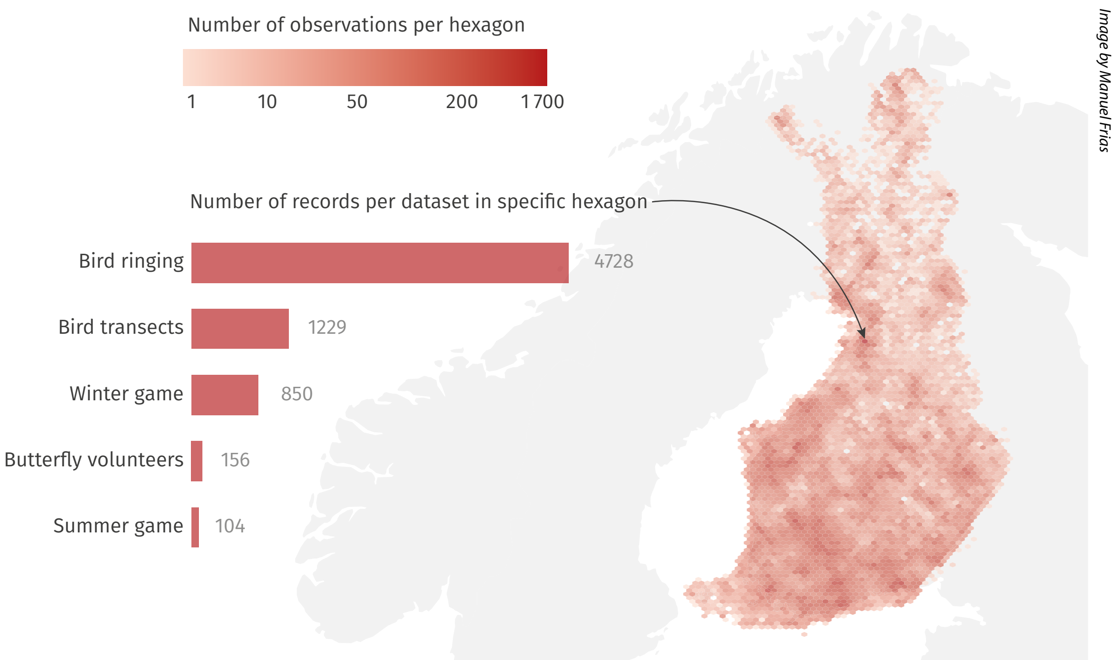

Figure 7. The spatial coverage of Finnish long-term data series. In this map, the area of Finland has been divided into hexagons with a diameter of 10 km. The colour hues shows the total number of records compiled for each hexagon (with a visual legend at the top left). The bar chart inset shows exact figures for records in individual data sets (cf. Fig. 1) for a single, well-studied hexagon.

Figure 8. Members of the Research Centre for Ecological Change, gathered for the World Biodiversity Forum in Davos 2020. From left to right: Laura Antão, Tomas Roslin, Pauliina Hyttinen, Jarno Vanhatalo, Maria Hällfors, Giovanni Strona. Benjamin Weigel, Marjo Saastamoinen, Elina Kaarlejärvi, Anna-Liisa Laine (Director of the Centre) and Manuel Frias.

revealing both what changes and what does not change. If wide and long enough, they will also reveal the spatiotemporal extent, i.e. where and when the change has occurred.

Many Finnish time series are indeed wide and long enough to reveal both past and ongoing change (Fig. 3,7). Consequently, these data are also exceptionally well suited for generating model-based predictions on how nature responds to human driven environmental change – a key requisite when designing policies that account for biodiversity. From a global perspective, national Finnish data series are uniquely rich, deep and long. From a taxonomic perspective, they are diverse – albeit far from comprehensive (see below) – by spanning organisms such as plankton, birds, mammals and moths (Fig. 9). The prime strengths of Finnish long-term data are thus in their socio-political credence, in their globally unique extent, in their depth and in their coverage (Table 1).

Weaknesses

What long-term data hold in credibility (see Strengths, above), they lack in causality. Just like any other observational data, they are correlative in nature. By revealing what features change in unison, they may thus point to associations between tentative cause and effect – but they cannot logically prove them without added experiments. Yet, given the practical challenges involved in experimentally manipulating proposed drivers at a relevant scale, correlations will oftentimes be all we can hope for and work with as a basis for policy. The statistical tools for analysing these types of data have improved considerably over time, allowing to quantify also unmeasured variation over space and time, resulting in more robust estimates of the drivers of change (e.g. Cameletti et al. 2012; Norberg et al. 2019).

Weaknesses in causation are certainly shared by any observational data. More specific to the Finnish long-term data is the fragmented nature of data storage, the restrictions on open access, and the gaps in taxonomic coverage (Table 1). At present, both the collection and storage of long-term data are split between Luke (e.g. rodents, other mammals, game species, forest vegetation), SYKE (e.g. plankton, moths, butterflies), the Natural History Museum Luomus (e.g. data on birds from transect counts and ringing, etc) and Åbo Akademi university (vascular plants of the Turku

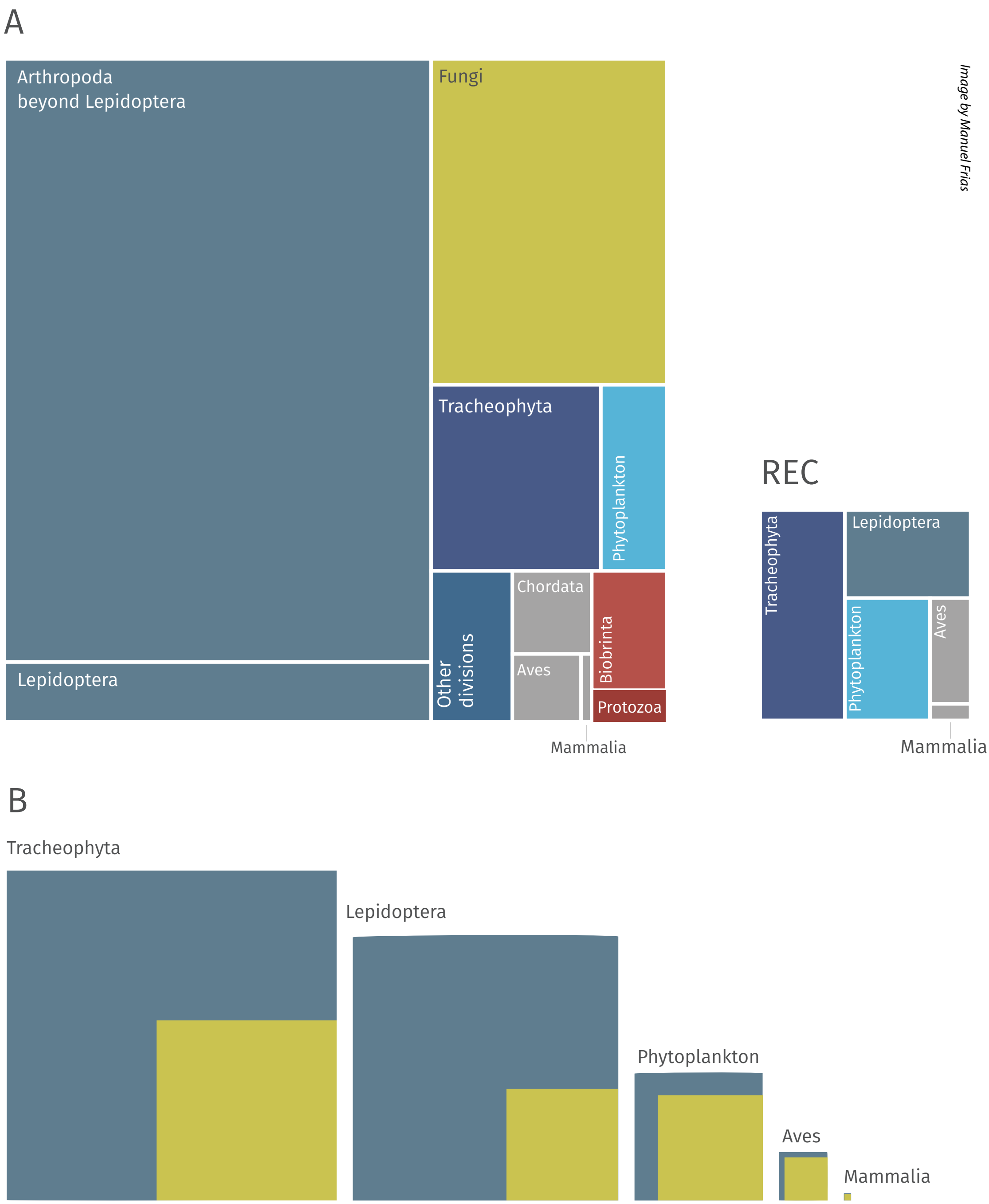

Figure 9. The taxonomic coverage of Finnish long-term data series. Shown in A is the composition of taxa across the full Finnish fauna and flora (left-hand quadrat; figures based on the taxonomic checklist of FinBIF (2022)) versus taxa included in the long-term records compiled by the Research Centre for Ecological Change or REC (right-hand quadrat; data sets summarized in Fig. 3). Shown in B is the group-specific fraction of taxa included in the REC data base, with the dark-blue square showing the total number of taxa listed in Finland and the light-green square showing the taxa included in the data base compiled by REC. For both (A) and (B), the area of each square is proportional to the total number of taxa. Importantly, we note that the taxonomic checklist of FinBIF (2022) is incomplete, as omitting multiple taxa due to gaps in knowledge and current taxonomic expertise. Figures for phytoplankton by courtesy of Benjamin Weigel (REC) and Kristiina Vuorio (SYKE).

Archipelago). There is little or no coordination among these initiatives, and no central data hub through which all data may be accessed (nor anyone responsible for curating them or linking them to the adequate metadata). Making sense of the current data sprawl is no easy task, as individual data sets are currently held by different institutions, collected by different means, and their synthesis has never been planned in any coordinated manner.

At present, the utilisation of the Finnish data treasure is seriously compromised by conservative policies for data sharing. As all long-term data series were initiated before the paradigm shift to open science, access to several long-term data series is still restricted and their curation into easily accessible data with associated metadata has not always been completed. This results in a peculiar jungle of study-specific permits and legal agreements – despite the striking fact that most of these data were generated by public funds, and officially for the use of society.

As a final weakness, the depth and extent of taxon-specific data stand in no proportion to the species richness or perceived ecological importance of the respective taxa (Fig. 9). Some of our least diverse taxa (birds and mammals) account for the lion's share of all records, whereas some of the most diverse and ecologically important taxa (such as fungi; Clemmensen et al. 2013; Tedersoo et al. 2014, 2020) remain outside of all systematic monitoring efforts (save some habitat- and species-specific re-surveys). This status quo was brought into broad daylight by the global interest in insect decline, as breaking in 2017 (e.g. Hallmann et al. 2017, Sánchez-Bayo & Wyckhuys 2019). With a sudden interest in insect abundances and population trends, Finland proved as poorly prepared as the rest of the world to report on the status and trends of the nation's presumably most diverse organism group. To the credit of the nation, Finland did hold long-term records of both moths and butterflies (order Lepidoptera), as for both of these groups, monitoring programmes had been initiated during the last half-century (Fig. 3; Heliölä et al. 2010, Leinonen et al. 2016). In response to this knowledge gap, a national pollinator survey is currently being developed (Heliölä et al. 2021).

Opportunities

Until 2018, no single research team or institution or research team had compiled Finnish long-term records across taxa (see Fig. 3). The opportunities inherent of such a compilation are clearly immense (Table 1). By comparing long-term trends among taxa and regions, one may reveal both the extent of biodiversity change in Finnish nature, and point to its underlying drivers. A compilation of data at hand will also suggest knowledge gaps, and form the basis of any strategic planning of the future monitoring of Finnish nature.

In illustration of the extensive opportunities at hand, Antão et al. (2022) recently combined four decades of climatic data with distributional data for 1,478 species of birds, mammals, butterflies, moths, plants and phytoplankton across Finland. They found that climate change has been rapid during the study period, with stronger increases in temperature and precipitation in northernmost Finland compared to the mid- and southern zones, and a drastic decrease in the duration of snow cover across the country (Fig. 10). These changes have not been reflected in any drastic turnover of species among decades, but instead in prevalent shifts in the relative position of species within their climatic niche (Fig. 11). At higher latitudes, where climatic changes have been stronger, a greater proportion of species have responded to climatic change.

The patterns resolved by Antão et al. (2022) are as drastic as they are transformative. They reveal how climatic imprints are restructuring Finnish biomes, with different species respond in different ways. For a nation which has sired the classification of both species (Linnæus 1753, 1758) and communities (Hult 1881), and the classification of forest types as based on species combinations (Cajander 1949), these findings run deep, by challenging the view that communities come as pre-set types, or can be managed as stable entities.

Importantly, none of these insights had been possible by focusing on a taxon-specific time series on its own – the pattern can only be extracted by comparing taxa and latitudes to each other, and by combining long-term data on climate with long-term data on living nature. The example above highlights the untapped opportunities of Finnish long-term data.

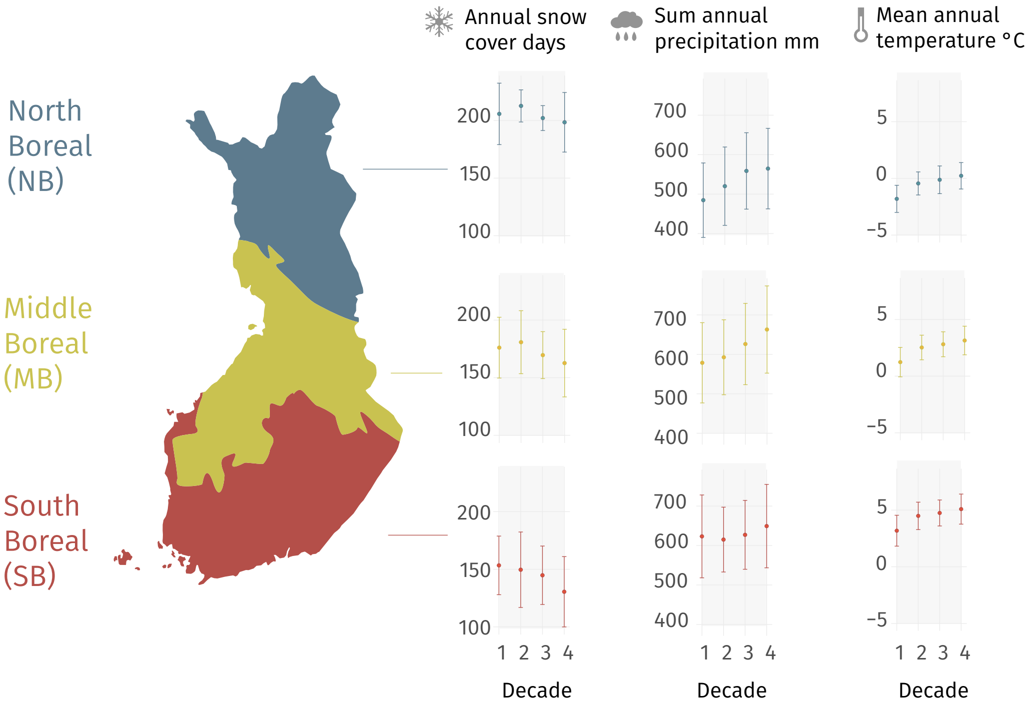

Figure 10. Climate change during the past four decades in different parts of Finland. Shown are means and standard deviations for annual mean temperature, sum precipitation and snow cover days in each of the biogeographical zones depicted on the left and analysed by Antão et al. (2022), with the decades corresponding to 1: 1978–1987, 2: 1988–1997, 3: 1998–2007 and 4: 2008–2017. Image courtesy of Laura Antão, Benjamin Weigel and Manuel Frias, data from Antão et al. (2022).

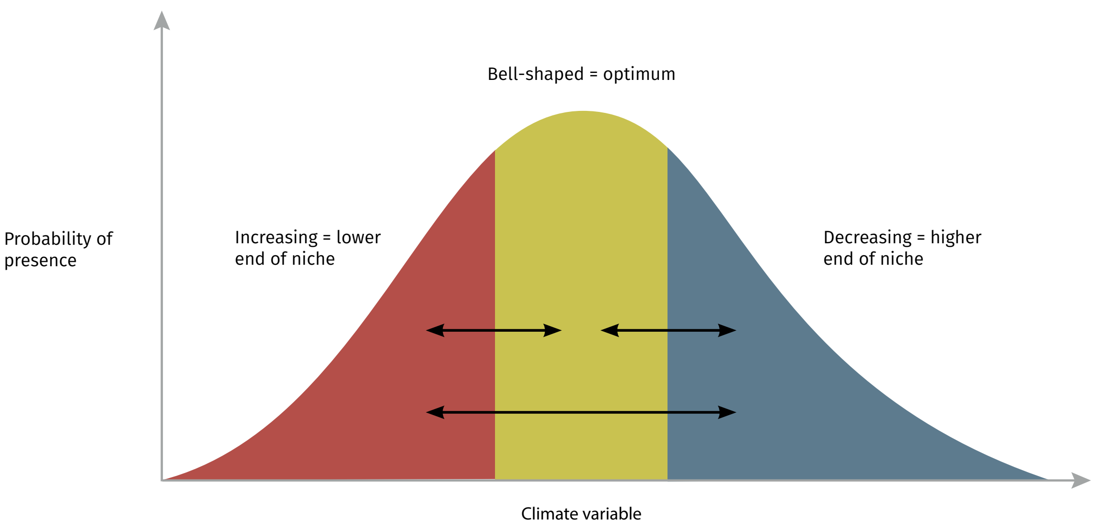

Figure 11. Conceptual illustration of the main type of changes observed among Finnish plants and animals with progressing climate change. The climatic shifts summarised in Fig. 10 have resulted in prevalent shifts in the relative position of species within their climatic niche. With a warming climate, the relative position of species within their niche has shifted substantially over time. Among decades, a large proportion of species shifted position between the lower end of niche space (where an increase in the climatic covariate has a positive impact on species occurrence), the niche optimum (i.e. the bell-shaped area of the curve) or the upper end (where an increase in the climatic covariate has a negative impact on species occurrence).

Threats

As unique (see Strengths) and scientifically significant (see Opportunities) as the Finnish time series are, their very existence is balanced on a knife's edge. A time-series can only shed new light on changes in the environment if it is maintained intact. Nonetheless, some of the longest running time series have been discontinued (Helama et al. 2020), and there are no guarantees for the continuation of the other ones. The forest understorey vegetation survey was halted for over 15 years despite the fact that forests represent the largest ecosystem in Finland. Finally, in 2021 a new nation-wide forest vegetation survey was launched again. This is commendable, but the data gap of 15 years that coincides with a period of extensive change in both climate and forestry practices considerably limits our ability to understand the drives of change in these plant communities. As key threats, we thus point to the alarming lack of long-term funding, legislation and coordination of these time series (Table 1).

At present, there is no legal obligation for authorities to sustain a single time-series. This basic consideration makes all time-series prone to short-sighted policies and budget cuts. Data not collected in a given year can never be collected again. Current monitoring programmes are typically run on a shoestring, and their coordinators are forced to spend much more time on fighting for their survival than on data curation, let alone on strategic planning for the future. What imperils the future of Finnish time series is thus their spread across institutions, their lack of coordination and their exposure to short-sighted policies.

Recommendations

Our survey of the current state of affairs points to globally unique opportunities – but also to a vast potential so far left untapped. Finland has a long tradition of treasuring its natural riches and of inventorying their state. The resulting data provide a globally unique potential for informing relevant policies, but this potential can only be secured, tapped and maintained by transformative changes in national monitoring strategies, funding and legislation. To overcome the weaknesses and to confront the major threats here identified, we point to four needs: legislation, open access, coordination and strategic planning.

In terms of legislation, only a legally binding framework can secure the future of Finnish programmes. These resources are much too valuable to leave to the vagaries of short-sighted policies. Just as the nation has decided to safeguard key statistics on economics and population structure by legislation on national statistics, so should we lay down the relevant legislation around the collection and maintenance of hard numbers on our joint natural capital.

Table 1. Strengths, Weaknesses, Opportunities, and Threats associated with our national treasure of long-term data series.

Strengths	Weaknesses
• Socio-political credence	• Correlative nature
• Globally unique extent	• Fragmented data generation and storage
• Depth (i.e. numbers of records)	• Restrictions on open access
• Spatiotemporal coverage	• Gaps in taxonomic coverage
Opportunities	**Threats**
• Evidence for extent of change in Finnish nature	• Lack of long-term funding
• Syntheses across taxa and regions	• Lack of legal framework
• Pointers to underlying drivers	• Lack of coordination
• Identification of knowledge gaps	
• Basis for strategic planning of future monitoring	

In terms of open access, we should see to it that current data are really accessible to all. No authority, institution or researcher can claim to be collecting and managing data to the benefit of society unless these data are openly shared. The current shadow of a protectionist past presents a major hurdle to the efficient use of national data.

In terms of coordination, we have pointed to a state where no party had ever compiled extant data for a comprehensive overview. The study by Antão et al. (2022) reveals the massive scientific opportunities inherent in any such exercise, whereas allowing the current state to continue represents a major loss to us all – not least to society. Only by joining forces may we tap the potential of investments already made.

Finally, in terms of strategic planning, the current syntheses of data point to major challenges. As stressed by Antão et al. (2022), recent compilations of extant data point to one major take-home message: different species and species groups in Finnish nature react differently to ongoing change. Thus, there is no simple, overall trend to record. Rather, different taxa and different metrics change in different directions, and overall change can only be characterised by this very multitude of trends.

The pattern resolved is an inconvenient truth. Yet, the beginning of all wisdom is the acknowledgement of facts. Any sensible use of resources calls for knowing what those resources are and how they change in time. If the fact is that change is complex, well then we need to arm ourselves for recording its relevant dimensions.

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Biodiversity loss, consumption and telecoupling – Why do we need to look beyond our borders?

Photo: Video screenshot / RajuLive.fi

Ilari E. Sääksjärvi, Misteli Tuominen & Juulia Räikkönen

***Sääksjärvi**, I. E.,* ileesa @ utu.fi *, **Tuominen**, M., **Räikkönen**, J.,* juuraikko @ utu.fi*, Biodiversity Unit, 20014 University of Turku, Finland.*

Biodiversity loss is advancing rapidly, and the previous international goals for halting biodiversity loss have not been met. Besides protecting biodiversity within, e.g. Finland, it is essential to understand that our current way of life is causing global biodiversity loss through, for example, overconsumption. The current paper aims to increase understanding of the complex multi-level human impacts beyond our borders, resulting in significant global challenges. We discuss biodiversity loss and consumption with telecoupling, a phenomenon related to the geographical separation of consumption and production of goods and services that accelerates climate change and biodiversity loss in distant locations through international trade.

Introduction

The critical global challenges, climate change and biodiversity loss have been identified as the top two most severe risks to the future of humankind over the next ten years (World Economic Forum 2022). Moreover, it is clear that limiting climate change and halting biodiversity loss are mutually supporting goals (Pörtner et al. 2021). In this paper, the main focus is on biodiversity loss, yet climate change is also addressed since it has been a hot topic in academia and society for years. In contrast, biodiversity loss and its critical implications have, so far, received less attention.

It has become evident that biodiversity loss is advancing rapidly due to changing sea and land use (resulting in habitat loss, degradation and fragmentation), unsustainable exploitation of species, climate change, pollution and invasive non-native species (IPBES 2019). Unfortunately, the previous international goals for halting biodiversity loss have not been met and according to recent estimates, up to one million species risk vanishing within the next few decades (IPBES 2019). The biodiversity loss is also advancing in Finland; for example, 11.9% of the Finnish species evaluated in the last assessment of threatened species were classified as threatened, and 312 were assigned regionally extinct (Hyvärinen et al. 2019).

The current paper addresses the topical question of why it is essential to examine biodiversity loss beyond the borders of nation-states. The impacts of human activity are visible everywhere on Earth. Humans and the human-created systems in different places have become increasingly connected through flows of international trade, migration and ecosystem services. At the same time, other species and their habitats have been intentionally or unintentionally involved in this interaction. Here, we discuss telecoupling, a framework that aims to comprehend the complex multi-level human impacts beyond our borders, resulting in significant global challenges, e.g., climate change, biodiversity loss, and declining food and energy security (Liu et al. 2013).

Consumption and biodiversity loss

The global population has doubled since 1970, and consumption has increased dramatically in total and per capita spending (Liu 2022). Global consumption patterns significantly impact both climate change and global biodiversity loss, but previous research has mainly addressed climate change. Globally, household consumption emissions account for circa 70% of global greenhouse gas emissions (Dubois et al. 2019, Hertwich & Peters 2009, Ivanova et al. 2016).

Even though it is increasingly recognised that consumption patterns also lead to biodiversity loss, the effects are still more challenging to measure. While Lenzen et al. (2012) estimated that international trade accounted for 30% of threats to species globally, Wilting et al. (2017) were among the first to systematically quantify these losses in relation to land use and greenhouse gas emissions associated with the production and consumption of goods and services. Their analysis revealed that food consumption was the most important driver of biodiversity loss in most countries. The biodiversity loss per citizen varied between countries, but higher values were associated with increasing per-capita income. Similarly, the share of biodiversity losses due to greenhouse gas emissions in the biodiversity footprint increased with income (Wilting et al. 2017).

IPBES (2019) and Diaz et al. (2019) identified human activity and overconsumption as significant factors affecting the main drivers of biodiversity loss. They called for a transformative change, i.e., a fundamental, system-wide reorganisation across technological, economic, and social factors, including paradigms, goals, and values. The transformative change, in turn, requires leadership and management interventions, including concrete incentives for environmental responsibility, increased cross-sectoral cooperation, pre-emptive actions in institutions and businesses to stop nature's deterioration, more effective decision-making and stronger environmental laws (IPBES 2019).

According to IPBES (2019; see also Diaz et al. 2019), implementing such interventions targets eight specific keys to transformative change: biodiversity education and knowledge-sharing, inclusive and fair biodiversity conservation, and technological and social innovations and investments that facilitate the transformation. The remaining five keys are directly linked to consumption: decreasing total consumption and waste, enabling a good life not based on ever-increasing material consumption, letting go of outdated values while adopting new social norms for sustainability, and reducing inequalities that undermine individuals' abilities for sustainability. From the perspective of global responsibility, the last key is the most relevant: "internalise externalities and telecouplings", which will be discussed in more detail.

Telecoupling

The concept of telecoupling is increasingly used as a framework to understand globally distant interactions and their sustainability implications (Liu et al. 2013, Newig et al. 2019). It is an umbrella concept referring to socio-economic and environmental interactions over distances and a logical extension of research on coupled human and natural systems in which interactions occur within particular geographic locations (Liu et al. 2013). For example, the consumption of biofuels in Western countries can have significant environmental and socio-economic impacts in distant locations through land use change and other drivers of biodiversity loss (Liu et al. 2013).

Thus, telecoupling can be viewed as a transdisciplinary and multi-level solution to overcome the complexity caused by globalisation and the tendency to focus on single places and to remain entrenched within individual disciplinary silos (Liu et al. 2013, Hull & Liu 2018). The concept was first introduced by Liu et al. (2013) in an article titled "Framing sustainability in a telecoupled world". To better understand and integrate various distant interactions, they proposed a framework containing five major interrelated components: agents, causes, effects, flows, and coupled human and natural systems (Liu et al. 2013).

Agents include autonomous decision-making entities that directly or indirectly facilitate or hinder telecouplings. Causes are factors that influence its emergence and dynamics. Effects refer to socio-economic and environmental consequences or impacts of telecoupling. Flows are movements of material, energy, or information (e.g., manufactured goods, food, natural resources, organisms, knowledge, trade agreements, or financial data) between the systems that are transferred as a result of actions taken by agents. Finally, systems are coupled human and natural systems or integrated systems in which humans and nature interact. Each system is in a geographic location, has specific contexts, and consists of many human and natural elements and processes (e.g., climatic and soil conditions, habitats, accessibility, topographic features, economic and political institutions and policies).

For each telecoupling, systems can act as sending, receiving or spillover systems. Sending systems refer to origins, sources, or donors of material, energy, or information flows, such as exporting countries. Receiving systems, in turn, refer to destinations or recipients obtaining flows from the sending systems, such as importing countries. Finally, spillover systems affect or are affected by the interactions between sending and receiving systems, such as a third party in a trade agreement (Liu et al. 2013). According to Kapsar et al. (2019), the spillover system integrates unintended consequences into the telecoupling process to be recognised as a part of a much larger system. This contextualisation lays a foundation for systematically and consistently predicting the potential impacts of different policy actions and promoting the sustainable development of complex systems.

Consumption effects beyond our borders

Indeed, telecoupling is related to the phenomenon in which the consumption and production of goods and services have become geographically separated. Through international trade, consumption causes greenhouse gas emissions and biodiversity loss in distant locations, creating a geographical displacement between cause and effect (Irwin et al. 2022, Liu 2022).

For example, Nissinen and Savolainen (2021) estimated that Finland's consumption-related emissions are up to one-third higher than the officially reported emissions, as they include only emissions produced in a given country. Instead, according to Salo et al. (2021), the advantage of the consumption-based approach is that it also considers embedded emissions of imported goods (Peters & Hertwich 2008) and the overseas relocation of polluting industries, i.e., carbon leakage (Kanemoto et al. 2014). Even though Finland has a clear objective to be carbon neutral by 2035, climate strategies have given little weight to the consumption-based approach or set clear targets that acknowledge the emissions we produce beyond our borders (Sitra 2021).

The connections between final consumption and human activities that directly impact biodiversity loss are embodied in complex global supply chains that harness, manipulate, and transform nature's outputs into products and services, generating economic activity at each process stage (Irwin et al. 2022). Notably, according to Wilting et al. (2017), more than 50% of the biodiversity loss associated with consumption in developed economies occurs outside their territorial boundaries.

Irwin et al. (2022) used the ”extinction-risk footprint” to measure country-level contribution to species' extinction risk. The method quantified each country's role as both a steward of the biodiversity within its borders (territorial extinction-risk footprint) and a consumer of products whose supply chains extend beyond its borders (consumption extinction-risk footprint). The interplay between these generates a domestic footprint (the impact of a country's consumption on extinction risk within the country), an exported footprint (the impact of other countries' consumption on extinction risk within the country), and an imported footprint (the impact of a country's consumption on extinction risk outside of the country) for each country. The analysis of 188 countries revealed that 76 countries were net importers of extinction-risk footprint and 16 were net exporters of extinction-risk footprint. In 96 countries, domestic consumption was the largest contributor to the extinction-risk footprint.

Regarding policy interventions, the net importers of extinction-risk footprint (e.g., France, Germany, Japan, the UK, and the USA) must focus on ameliorating the impacts of their consumption by providing sufficient support to conservation and sustainable production in extinction-risk exporting countries. Furthermore, variations between the characteristics of each country's extinction-risk footprint highlight the need to tailor national policy interventions cognizant of the locations of both direct impact and consumption (Irwin et al. 2022).

Conclusions and discussion

Addressing and solving global challenges, such as biodiversity loss and climate change, requires a new approach that considers the complexity of networks and interactions and the extent of the impact of human activities. In addition, global actors at different levels need to bear responsibility for these challenges to achieve a more sustainable future.

Universities and scientists must also react to this need and create innovative and transdisciplinary approaches to tackle ecological crises. While telecoupling offers a possible framework for interdisciplinary research contexts, other frameworks or methods can also facilitate a profound understanding of the global effects of complex networks of human activities. For example, global responsibility (e.g., Silvola et al. 2021) provides another multi-level approach, while lifecycle assessment (e.g., Asselin et al. 2020) can be used as a more concrete tool in quantifying these global effects on biodiversity loss.

The authors of the present paper are involved in a transdisciplinary SRC-funded research project on Biodiversity-respectful leadership (BIODIFUL), which builds the perspective of leadership. Amid the plethora of leadership research, a multi-level appreciation of sustainable leadership connected to the natural environment is needed. To this end, BIODIFUL's scientific objective is to examine how individual (consumer-level), organisational (business-level), and societal (institutional-level) leadership can facilitate the transformation towards biodiversity-respectful activities. As BIODIFUL focuses on two systems, food and nature-based tourism and recreation, the telecoupling literature offers fruitful discussions on the agriculture and food industry, tourism, and also governance, which is closely related to leadership research (Duan et al. 2022, Eakin, Rueda & Mahanti 2017, Ibarrola-Rivas et al. 2020, Laroche et al. 2020, Newig et al. 2019, Newman et al. 2022). Moreover, it is an example of a framework that can enhance transdisciplinary research. Various scientific disciplines, such as ecology, economics, environmental science, geography, and political science, have already used telecoupling to study sustainability in multiple contexts and industries (Kapsar et al. 2019).

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Societas pro Fauna et Flora Fennica – 200 years
A survey of the activities 1997–2021

Carl-Adam Hæggström


Photo: Carl-Adam Hæggström

When Societas pro Fauna et Flora Fennica celebrated its 175 years jubilee, Professor Henrik Wallgren wrote an outline about the Society´s activity since the foundation of the Society in 1821 (Wallgren 1996).

When I became a member of the Society in 1963, the focus of the activities was on monthly meetings, usually with one lecture and thereafter short scientific messages and reports on publishing and library activities. Further activities of the Society were statements on topics regarding nature conservancy, granting of scholarships, mainly for students and young scientists, and the operation of the Nåtö Biological Station (NBS) in the Åland Islands, beginning in 1964. Field trips now and then were also included.

The Society published six different publications in botany and zoology. Five of these, with the exception of Memoranda Societatis pro Fauna et Flora Fennica, ceased in 1978. The publications were spread via an exchange system throughout the World to over 800 scientific societies, libraries, etc. The library of the Society was transferred to the Viikki Campus Library in 1980. Thus, the number of different of exchange organisations receiving Memoranda was cut to 330.

This report will concentrate on the activities of the Society during the last 25 years. Annual reports in Finnish and Swedish on the Society's activities and in Swedish on the activities taking place at the Nåtö Biological Station have been published every year in Memoranda Societatis pro Fauna et Flora Fennica (https://journal.fi/msff).

The focus of the Society has changed during the years. Three main fields of activity have continued over the years, namely the arrangement of one main conference about a specific topic per year, supporting students and young scientists with scholarships and the scientific work performed at the Nåtö Biological Station in the Åland Islands.

Meetings

The monthly meeting activity slowed down during the years and the interest in meetings with traditional lectures is reflected by the number of participants in the meetings:
1996–1997: 11–49 participants, mean number 23
2009–2010: 5–21 participants, mean number 11
2015–2016: 5–8 participants, mean number 7.

Due to the Covid-19 pandemic, two distance meetings were arranged in 2019–2020.

Symposia

During the last 25 years, a symposium was arranged almost every year. The Society organised the symposia between 1996 and 2010, thereafter the Society was a co-organiser together with Aronia at the University of Applied Sciences Novia, the Finnish Society of Sciences and Letters, the national IUBS committee, Societas Biologica Fennica Vanamo, Åbo Akademi University and the nature conservancy authorities of the Government of Åland. During the last few years, the organiser was either the Finnish or the Nordic Society Oikos.

The symposia were held chiefly in Helsinki, but quite a few were arranged in Åbo (Turku). One was arranged in Esbo (Espoo), one Mariehamn in the Åland Islands, one in Jyväskylä, one in Oulu and one in Trondheim, Norway.

Seven to eleven lectures were given at the symposia. The number of participants was between 40 and 100.

The topics of the symposia were diversified, for instance:
– fauna, flora and biodiversity
– different aspects on nature conservation
– hydrobiology
– current cooperation in biology between Finland and China
– Carl von Linné – scientist and physician
– evolution 150 years after Darwin

Since 2012, the focus has been on ecology and evolutionary biology.

Excursions

The Society arranged excursions during the period 1997–2013. The number of participants was between 5 and 24. Some of the excursions were domestic, e.g., field excursions in the archipelago areas of SW Finland, including one spring field excursion in the Åland Islands. One field excursion was arranged by the Society in cooperation with the society Turun Eläin- ja Kasvitieteellinen Seura (TYKS) to the Swedish island of Öland. Another one was arranged by TYKS to the Swedish island of Gotland. Further, the members of the Society were invited to participate in an excursion to Russian Karelia, arranged by the Nordenskiöld Society of Finland. Several places on the western shore of Lake Ladoga, including the monastery island of Valamo (Valaam), as well as the Karelian Isthmus, were visited.

Scholarships

The Society has granted scholarships to students and scientists in botany, ecology, hydrobiology, population biology and zoology. Due to a favourable development of the funds, the granted sum has significantly increased and more and more re-

▼ Figure 1. A small but brave crowd in Sibbo Storskog in Hindsby. PhD Anders Albrecht guides. Photo: C.-A. Hæggström, May 4, 2013.

searchers have been able to receive scholarships. A few figures may show the positive development:

– 1997, 10 scholarships, total sum 12 000 €
– 2001, 34 scholarships, total sum 47 000 €
– 2006, 36 scholarships, total sum 66 300 €
– 2011, 63 scholarships, total sum 112 000 €
– 2018, 42 scholarships, total sum 216 850 €
– 2019, 37 scholarships, total sum 155 130 €
– 2020, 33 scholarships, total sum 194 590 €

Members

The number of the Society's members has increased during the years, but it is difficult to keep track of the members as the Society does not have a membership fee. The number included two honorary members, 37 corresponding members and 910 ordinary members in 1997. By 2020, the figures are 9 corresponding members and 1 148 ordinary members.

Nåtö Biological Station

The activity began in June 1964. Eight scientists were working at the Station in that year. During the years, the number of scientists visiting the Station increased and the research work was both diversified and consolidated. The Station can offer accommodation and a modest laboratory space for researchers. As a maximum, about 8–10 persons can work at the Station at the same time.

Professor Henrik Wallgren retired as Prefect for the Station at the end of the year 2000. Then a new regulation for the Station was adopted as a cooperation between the Society and the Alandian Government in 2001. The previous regulation was adopted in 1968. In accordance with the new regulation, a management group was appointed from 2002 onwards. This group consists of four members of the Society and two members of the Alandian Government. Later, the Government appointed two alternate members. The term of office for the members is three years.

MSc Eeva Hæggström (1944–2017) retired as the Assistant (called Amanuensis) of the Station at the end of 2002. After that the following persons have been Assistants:

– student Thomas Kuusela, 2003–2008
– MA Tomas Lehecka, 2009–2015

▼ Figure 2. A view of Nåtö Biological Station (NBS) seen from the southwest. From left to right: the small house, the windmill, built in 1886, and the main building. Photo: Eeva Hæggström, October 9, 2009.

► **Figure 3. Work in progress in the laboratory of NBS. Photo: Eeva Hæggström,September 18, 2011.**

► **Figure 4. The Station's management group during a meeting. The persons from left to right: PhD Inkeri Ahonen, PhD Ralf Carlsson, MSc Mikael Wennström, PhD Gunilla Ståhls, the amanuensis, MSc Tomas Lehecka, PhD Torsten Stjernberg and nature conservation curator Jörgen Eriksson. Photo: Eeva Hæggström, October 9, 2009.**

– MSc Laura Kauppi, 2016–2017
– MSc David Abrahamsson, 2018 – 2020
– MSc Hanna Wiklund, January – July 2021
– MSc Laura Mattila, August – October 2021

Research work at the Station

The Station has been the base for several different projects performed in the Nåtö area or in other parts of the Åland Islands. Many projects have focussed on collecting a specific taxon (animal, plant, fungus, etc.) for master's, licentiate or doctoral dissertations and other scientific work. Several of the researchers have returned year after year to collect data for their research.

A milestone in the research activities was when the *cinxia* project began in 1992. The project was initiated and led by Professor Ilkka Hanski (1963–2016).

The initial effort comprised studies of the occurrence of the Glanville fritillary (*Melitaea cinxia*) and the two food plants of its larvae, name-

▲ **Figure 5. Professor Ilkka Hanski and his children are studying a specimen of *Oryctes nasicornis*. at NBS. Photo: Eeva Hæggström, June 1996.**

► **Figure 6. The research worker Guang-Chun Lei with cages containing larvae of *Melitaea cinxia* outside NBS. Photo: Eeva Hæggström, July 1994.**

ly *Plantago lanceolata* and *Veronica spicata*. Meadow patches all over the main Island of Åland were search for the butterfly, its larvae and meadow patches with the food plants. After a few years, studies of the parasitoids of *Melitaea cinxia* and the hyperparasitoids of the parasitoids were conducted by Dr. Saskya van Nouhuys and her co-workers. (Hanski & Ovaskainen 2000, van Nouhuys & Hanski 2000, 2002, 2005, Erlich & Hanski 2004, van Nouhuys & Lei 2004, Harvey et al. 2005,van Nouhuys 2005, Hanski et al. 2006, van Nouhuys et Kaartinen 2008, Saastamoinen & Hanski 2008, Reudler Talsma, Biere et al. 2008, Reudler Talsma, Torri & van Nouhuys 2008, Shaw et al. 2009, Castelo et al. 2010, Hanski 2011, Reudler et al. 2011, Kraft & van Nouhuys 2013, Pinto-Zevallos et al. 2013, Saastamoinen et

Figure 7. Three of the reserchers in the *cinxia* project in the laboratory of NBS. From left: Guang-Chun Lei, Ilik Saccheri and Mikko Kuussaari. Photo: Eeva Hæggström, June 1996.

al. 2013, Ahola et al. 2014, Montovan et al. 2015, Nair et al. 2016, van Bergen et al. 2020, Dallas et al. 2020, Opedal et al. 2020.)

Melitaea cinxia's host plant *Plantago lanceolata* is parasitised by the mildew *Podosphaera plantaginis*. The interaction between the host plant and the pathogen, and the epidemiology were studied by prof. Anna-Liisa Laine and her research team (van Nouhuys & Laine 2008, Jousimo et al. 2014; Laine et al. 2019; Halliday et al. 2020, Numminen & Laine 2020).

Further research included studies on factors influencing the colonisation of arbuscular mycorrhiza and plant viruses in populations of *Plantago lanceolata*. (Susi et al. 2019; Sallinen et al. 2020; Susi & Laine 2021.)

The *cinxia* project and its extensions are the internationally most important of all research work done at Nåtö Biological Station. During the years, the *cinxia* project grew and diversified in the MRG (Metapopulation Research Group) and the MRC (Metapopulation Research Centre) at the University of Helsinki. Today, the metapopulation of *Melitaea cinxia* is the best known metapopulation in the world.

Between 14 and 28 persons were working in the *cinxia* project at Nåtö Biological Station during the years 1997–2005. About 50 persons participated in the mapping of larval nests of *Melitaea cinxia* every autumn and about ten persons were then using Nåtö as their base.

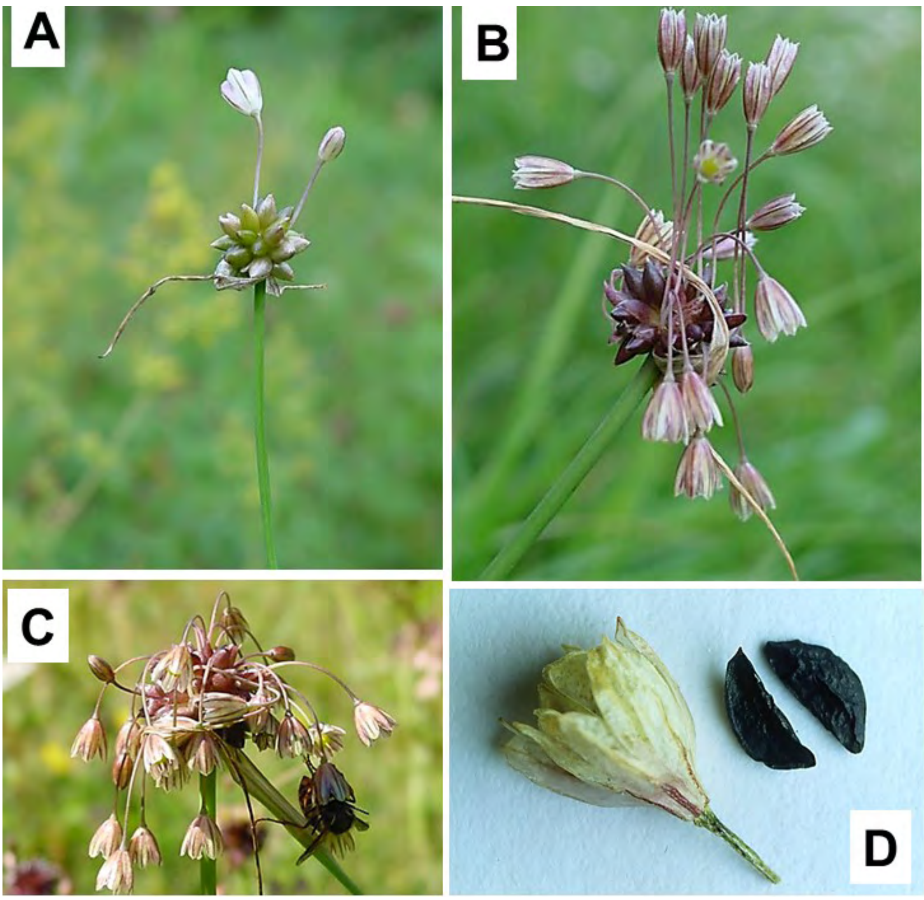
From 2006 onwards, the research activities of the MRG and MRC were mainly located at the agricultural centre of Åland Islands in Jomalaby, but minor parts of the research work have also been performed at Nåtö since then.

A second milestone was when the book ”Ålands flora” (The Flora of Åland) by Carl-Adam and Eeva Hæggström was published in December 2008 (Hæggström & Hæggström 2008). This is the first landscape flora regarding vascular plants published in Finland. A second corrected and enlarged edition was published two years later (Hæggström & Hæggström 2010).

A third milestone was when the Society applied for funding of a project from Åland's Penningautomatförening PAF (the Alandian ATM association) in 2015. The proposed project should be accomplished with the Station as a base. Money was received for 2016. Since then, new applications have been submitted to PAF every year

▼ Figure 8. Two of the projects carried out at NBS. To the left: The bat fauna of Åland, 2018. There is a bat identification device in the box above the ladder. To the right: Inventory of amphibians in mainland Åland, 2020.

◄ **Figure 9. Two more projects carried out at NBS. To the left: The Osprey (*Pandion haliaetus*) in the Åland Islands, 2019. To the right: The Little Ringed Plover (*Charadrius dubius*) and the Sand Martin (*Riparia riparia*) in the Åland Islands, 2020.**



▼ **Figure 10. The field garlic (*Allium oleraceum*) at Nåtö.**
A. Top end of a shoot with small greenish bulblets and a few whitish flowers of a tetraploid (2n = 32) specimen. August 13, 2003.
B. Top end of a shoot with large violet bulblets and many lilac flowers of a pentaploid (2n = 40) specimen. August 13, 2003.
C. A colony wasp (*Vespula* or *Dolichovespula* species) visiting a flower of a pentaploid specimen. July 26, 2002.
D. A ripe fruit (capsule and two seeds. September 17, 2003.
All photos: C.-A. Hæggström.

and one or more projects have been implemented. A written report on each project was sent to the Environmental Authorities of the Alandian Government in Mariehamn. The projects were:

- Inventory of the flora and vegetation of the sandy islands of Åland, Linda Sundström and Robin Sjöblom, 2016.
- Inventory of the flora and vegetation of 12 wooded meadow and grazed nature areas on mainland Åland, Robin Sjöblom, 2017.
- The bat fauna of Åland, Nina Hagner-Wahlsten and Simon Granholm, 2018.
- The Osprey (*Pandion haliaetus*) in the Åland Islands, Joona Koskinen, David Abrahamsson, Torsten Stjernberg and co-workers, 2019–2021.
- The White-tailed Eagle (*Haliaeetus albicilla*) in the Åland Islands, Torsten Stjernberg and co-workers, 2020 and 2021.
- The Little Ringed Plover (*Charadrius dubius*) and the Sand Martin (*Riparia riparia*) in the Åland Islands, Joona Koskinen, 2020.
- Inventory of Amphibia in mainland Åland, Tom Hoogesteger, 2020.
- Inventory of Amphibia in the archipelagos of Åland, Tom Hoogesteger, 2021.
- The Caspian Tern (*Hydroprogne caspia*) in the Åland Islands, Patrik Byholm, 2021.

Numerous other research projects were either performed at the Station, or had the Station as a base. Here a few examples:

- The White-tailed Eagle (*Haliaeetus albicilla*) in the Åland Islands, Torsten Stjernberg and co-workers. These studies were funded in previous years by, e.g., WWW Finland, the authorities of Åland and private funds.
- The population biology, including generative reproduction of the field garlic (*Allium oleraceum*), C.-A. Hæggström, Helena Åström and Eeva Hæggström, 1997–2003.
- Fish disease, cadmium and other heavy metals in the coastal waters, sea bottom sediments and flounders, as well as the sea water quality, Heinz-Rudolf Voigt, 1997–2014.
- Endangered Lepidoptera in the Åland Islands, Erkki M. Laasonen and Leena Laasonen, 1998–2021.

Figure 11. Participants in the field excursion of the Botanical Society of Lund, Sweden, walking in the old spruce wood Västerskog in the western part of Nåtö Island. Photo: C.-A. Hæggström, June 11, 2014.

– Coleoptera in the Åland Islands, Tom Clayhills and co-workers, 2002–2018.
– The bat fauna of Åland, Nina Hagner-Wahlsten, 2008–2013.
– Spider studies, Niclas Fritzén, 2008–2014.
– Studies on slime moulds (Myxomycetes, Mycetozoa or Mycogastria), Panu Kunttu and co-workers, 2012–2014.
– The Lepidoptera of Nåtö Island, 2014–2021, Janne Liikanen, Simo Korpela, Asko Oksanen & Olli Virtanen.

Symposia

In connection with the Station's 35th anniversary, a symposium was organised on June 28, 1999 with the theme ”The wooded meadows of Åland – a mosaic of life”. This symposium was a joint effort together with several corporations in Åland: the Nature Conservancy Department of the Alandian Government, The Nature Management Institute of Åland, The Museum of Åland, the association Åland's Nature and Environment, and the Agenda 21 office in Mariehamn. The symposium

Figure 12. Two researchers of the Botanical Society of Lund taking photographs of the rare grass *Melica picta* at Lemböte Granholm, north of Nåtö. The grass has not been found in Scandinavia. Photo: C.-A. Hæggström, June 11, 2014.

Figure 13. Botanists from Denmark, Norway and Sweden studying the flora at the so-called *Sesleria* meadow in Nåtö Island. The ashes are dead because of the fungus disease ash dieback *Hymenoscyphus fraxineus*. Photo: C.-A. Hæggström, June 11, 2019.

Figure 14. Botanists from Denmark, Norway and Sweden on the road through Nåtö Västerskog. The storm called Alfrida, which hit Åland during the night between 1 and 2 January 2019, felled practically all the trees in the central part of the spruce forest to the right. Photo: C.-A. Hæggström, June 11, 2019.

was held at the Nature Management Institute of Åland in Jomalaby. Nine lectures were held and about 50 persons participated in the symposium.

The 50th anniversary of Nåtö Biological Station was celebrated in 2014. This was highlighted through the symposium ”Biological diversity – a race for life and death” on 16 May. The symposium was organised in consultation with the Åland University of Applied Sciences. A number of recent research projects were presented. More than 50 persons participated in the symposium. The anniversary received justified attention both in the Åland press, the radio and the TV news. Three field excursions were also arranged in conjunction with the anniversary symposium.

Courses and excursions

Over the years, various courses and excursions have been held at the Station. Some examples:

- Field courses in knowledge of vascular plants, 1997–1998. These courses were included in the programme of the summer university activity in Åland.
- The spring flora, field course for students from the Unit for Swedish-language teaching at the Department of Life Sciences, University of Helsinki, 1997–2019, 7 to 12 students and two teachers.
- Swedish University of Agricultural Sciences' autumn excursion, 2004, wooded meadow field excursion for 30 students.
- The joint course ”Landscape planning”, arranged by Novia University of Applied Sciences and Hanko Summer University, 2008, field excursion in the wooded meadow area and the old spruce wood of Västerskog in Nåtö, 24 persons.
- The Swedish Species Information Centre at the Swedish University of Agricultural

Sciences, Uppsala, staff excursion, 2010, 45 persons were guided along the Nåtö nature trail.
- Excursion for Finnish botanists, 2011, 56 persons were guided along the Nåtö nature trail, on Harskatan promontory and in the old spruce wood of Västerskog.
- The Dendrological Society of Finland, field excursion in Nåtö, 2012, 15 persons.
- Consultation days for agricultural environmental protection, 2013, 29 participants from the Ministry of the Environment and the Centres for Economic Development, Transport and the Environment, field excursion along the Nåtö nature trail.
- Cultural landscape course arranged by Novia University of Applied Sciences, 2013, wooded meadow excursion in Nåtö, 11 students.
- Maj and Tor Nessling Foundation, 2014, 16 persons were guided along the Nåtö nature trail.
- Lund Botanical Society, field excursion in the Åland Islands 2014, 15 persons.
- A three-day course including excursions on ”the life of insects”, arranged by the University of Oulu, 2017–2019, 10 students and two teachers.
- The upper secondary school Lärkan’s field course in Åland, 2019, 12 students and two teachers.

Other activities of the Society

The society has given statements in nature conservation and environmental protection matters to various authorities, e.g., the Landscape Government of Åland.

The Society supported ”The wildflower day”, a day when short excursions with information about plants encountered along the way is arranged for the general public. This event takes place on the third Sunday in June. It was initiated by the Danish Botanical Society in 1988. The national botanical associations of Norway and Sweden joined the activity in 2002, followed by several organisations in Finland in 2003. Iceland joined the activity in 2004.

The following organisations are arranging and / or financing the ”The wildflower day”:

- Biology and Geography Teachers’ Association
- The Botany Unit of the Finnish Museum of Natural History
- Metsähallitus, Parks and Wildlife Finland
- Societas pro Fauna et Flora Fennica
- Societas Biologica Fennica Vanamo
- Finnish Association for Nature Conservation
- Finnish Environment Institute

The Finnish Association for Nature Conservation has been the main organiser of ”The wildflower Day”. During the day, an average of 80–90 guided trips from Åland to Lapland have been organised and there have more than one thousand participants, one year even more than two thousand.

The future – new challenges?

Societas pro Fauna et Flora Fennica has been successfully active for 200 years. But which is the Society’s role in the future? It is difficult to say what is to come. The Society’s operations have changed over the years and will probably change in the future. However, some key areas of activity can be assumed to remain in the foreseeable future:

- Cooperation with other organisations in the field of science.
- Scholarships for students and scientists in botany, ecology, hydrobiology, populations biology, zoology and associated branches of natural sciences.
- Continuation in the activities at Nåtö biological station.

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Musical session was provided by String Quartet Ainoa. Above: Auroora Kiiski Touizrar (violin), Iisa Kostiainen (viola).
Below; Isa Halme (violin), Kristiina Hirvonen (cello). Photographs by Daniel Torsell / Epific.


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