Alien plants, animals, fungi and algae in Norway: an inventory of neobiota

Hanno Sandvik · Dag Dolmen · Reidar Elven · Tone Falkenhaug · Elisabet Forsgren · Haakon Hansen · Kristian Hassel · Vivian Husa · Gaute Kjærstad · Frode Ødegaard · Hans Christian Pedersen · Halvor Solheim · Bård Gunnar Stokke · Per Arvid Åsen · Sandra Åström · Tor-Erik Brandrud · Hallvard Elven · Anders Endrestøl · Anders Finstad · Stein Fredriksen · Øivind Gammelmo · Jan Ove Gjershaug · Bjørn Gulliksen · Inger Hamnes · Bjørn Arild Hatteland · Hanne Hegre · Trygve Hesthagen · Anders Jelmert · Thomas C. Jensen · Stein Ivar Johnsen · Egil Karlsbakk · Christer Magnusson · Kjell Nedreaas · Björn Nordén · Eivind Oug · Oddvar Pedersen · Per Anker Pedersen · Kjersti Sjøtun · Jon Kristian Skei · Heidi Solstad · Leif Sundheim · Jon E. Swenson · Per Ole Syvertsen · Venche Talgø · Vigdis Vandvik · Kristine B. Westergaard · Rupert Wienerroither · Bjørnar Ytrehus · Olga Hilmo · Snorre Henriksen · Lisbeth Gederaas

H. Sandvik (☒) · E. Forsgren · F. Ødegaard · H. C. Pedersen · B. G. Stokke · S. Åström · T.-E. Brandrud · A. Endrestøl · J. O. Gjershaug · T. Hesthagen · T. C. Jensen · S. I. Johnsen · B. Nordén · J. E. Swenson · K. B. Westergaard · B. Ytrehus Norwegian Institute for Nature Research (NINA), 7485 Trondheim, Norway E-mail: hanno@evol.no ORCID: 0000-0002-5889-1606

H. Sandvik · O. Hilmo · S. Henriksen · L. Gederaas Norwegian Biodiversity Information Centre, 7446 Trondheim, Norway

D. Dolmen · K. Hassel · G. Kjærstad · F. Ødegaard · A. Finstad NTNU University Museum, Norwegian University of Science and Technology, 7491 Trondheim, Norway

R. Elven · H. Elven · O. Pedersen · H. Solstad Natural History Museum, University of Oslo, 0318 Oslo, Norway

T. Falkenhaug \cdot V. Husa \cdot A. Jelmert \cdot E. Karlsbakk \cdot K. Nedreaas \cdot R. Wienerroither Institute of Marine Research, 5817 Bergen, Norway

H. Hansen · I. Hamnes Norwegian Veterinary Institute, 0106 Oslo, Norway

© Springer Nature 2019

This is a post-peer-review, pre-copyedit version of an article published in <u>Biological Invasions</u>. The final authenticated version is available online at: http://dx.doi.org/10.1007/s10530-019-02058-x.

H. Solheim · B. A. Hatteland · C. Magnusson · L. Sundheim · V. Talgø Norwegian Institute of Bioeconomy Research (NIBIO), 1431 Ås, Norway

P. A. Åsen

Natural History Museum and Botanical Garden, University of Agder, 4604 Kristiansand, Norway

S. Fredriksen

Department of Biosciences, University of Oslo, 0316 Oslo, Norway

Ø. Gammelmo

BioFokus, 0349 Oslo, Norway

B. Gulliksen

Department of Arctic and Marine Biology, Arctic University of Norway (UiT), 9037 Tromsø, Norway

B. A. Hatteland · E. Karlsbakk · K. Sjøtun · V. Vandvik

Department of Biological Sciences, University of Bergen, 5020 Bergen, Norway

H. Hegre

FlowerPower, 0358 Oslo, Norway

E. Oug

Norwegian Institute for Water Research (NIVA), 4879 Grimstad, Norway

P. A. Pedersen · J. E. Swenson

Norwegian University of Life Sciences (NMBU), 1432 Ås, Norway

I K Skei

Department of Biology, Norwegian University of Science and Technology (NTNU), 7491 Trondheim, Norway

P. O. Syvertsen

Natural History Department, Helgeland Museum, 8624 Mo i Rana, Norway

Abstract We present the results of an inventory and status assessment of alien species in Norway. The inventory covered all known multicellular neobiota, 2496 in total, 1039 of which were classified as naturalised. The latter constitute c. 3% of all species known to be stably reproducing in Norway. These figures are higher than expected from Norway's latitude, which may be due a combination of climatic and historical factors, as well as sampling effort. Most of the naturalised neobiota were plants (71%), followed by animals (21%) and fungi (8%). The main habitat types colonised were open lowlands (79%), urban environments (52%) and woodlands (42%). The main areas of origin were Europe (67%), North America (15%) and Asia (13%). For most taxa, the rate of novel introductions seems to have been increasing during recent decades. Within Norway, the number of alien species recorded per county was negatively correlated with latitude and positively correlated with human population density. In the high-Arctic territories under Norwegian sovereignty, i.e. Svalbard and Jan Mayen, 104 alien species were recorded, of which 5 were naturalised.

Keywords

Alien species, casual species, naturalised species, neomycetes, neophytes, neozoa

Introduction

Inventories of alien species are necessary for maintaining updated national faunas, floras and fungas. In addition, they are the basis for impact or risk assessments of alien species (e.g. Essl et al. 2011; Blackburn et al. 2014; D'hont et al. 2015; Sandvik et al. 2019). Finally, inventories play an important role in macroecological studies addressing the mechanisms, patterns, drivers and consequences of biological invasions (Pyšek et al. 2017, 2018). National inventories are available for a number of countries, including e.g. Austria (Essl and Rabitsch 2002; Rabitsch and Essl 2006), Czech Republic (Pyšek et al. 2002, 2012), Germany (Nehring et al. 2013, 2015; Rabitsch and Nehring 2017), Liechtenstein (Staub 2006), Luxembourg (Ries et al. 2013, 2014), Portugal (de Almeida 2012), Russia (Vinogradova et al. 2018), Slovakia (Medvecká et al. 2012) and Switzerland (Wittenberg et al. 2006). The delimitations of these inventories differ among studies, i.e. they vary in their taxonomic, historical or ecological coverage (e.g. only vascular plants, only neobiota, only aquatic species, only invasive species) or other criteria.

In Norway, the first and incomplete inventory of alien species was compiled in 2007 (Gederaas et al. 2007). In 2012, the results of a complete revision and extension were published online in a searchable database (Artsdatabanken 2012, available in Norwegian only) and summarised in a printed report (Gederaas et al. 2013). As part of the national strategy "to prevent the import, release and spread of alien organisms that have or may have adverse impacts on biological or landscape diversity" (KLD 2015b: §1), the Norwegian Biodiversity Information Centre (NBIC, *Artsdatabanken* in Norwegian) is responsible for updating and revising this inventory (KLD 2015a). The inventories of alien species in Norway are used as input for impact assessments, which identify alien species that have adverse effects on native biota or ecosystems (Artsdatabanken 2018; Sandvik et al. unpubl.).

Here, we present the results of the third inventory of alien species occurring in Norway, which was completed in 2018. The inventory covered all multicellular neobiota. The delimitations are detailed in the next section. The resulting list is given in Online Resource 1. Our focus is here on descriptive statistics of the inventory, including the taxonomic, ecological, biogeographic and temporal patterns related to naturalised alien species in Norway.

Methods

Definitions and delimitations

Following IUCN (2000:4–5), we define as *alien species* any "species, subspecies, or lower taxon occurring outside of its natural range (past or present) and dispersal potential (i.e. outside the range it occupies naturally or could not occupy without direct or indirect introduction or care by humans)[,] includ[ing] any part, gametes or propagule of such species that might survive and subsequently reproduce". This is consistent with other commonly used definitions of alien species (Richardson et al. 2000, Pyšek et al. 2004). Because this definition is rather broad, the set of alien species included in the inventory was narrowed down using four delimitations:

- (1) *Historical delimitation.* An alien species is included only if it was introduced to Norway after 1500, i.e. if it is a neophyte, neozoan, neomycete etc. (see e.g. Preston et al. 2004), which are here collectively referred to as neobiota. (This delimitation excludes archaeobiota. For some species, the status had to be decided by expert judgement, because very few written sources are available regarding the state of Norwegian nature before the middle of the 18th century, making it difficult to infer whether a given species had been introduced before or after 1500.)
- (2) Geographical delimitation. An alien species is included only if it crossed national borders or the boundaries of the Norwegian Economic Zone during its introduction. (This delimitation excludes "regionally alien species", i.e. species that have been introduced to certain parts of Norway, while being native to other parts of the country. It entails that each species has the same status either alien or native throughout mainland Norway, whereas Svalbard and Jan Mayen are assessed separately, see Geographic region below.)
- (3) *Ecological delimitation*. An alien species is included only if it has been documented to occur in the wild in Norway, or if it occurs in Norway and has the potential to reproduce in the wild. (This delimitation excludes species that are alien to and occur in Norway, albeit exclusively indoors or in cultivation and without the potential to reproduce upon escape.)
- (4) *Taxonomic delimitation*. Alien taxa are included if they are ranked as species, while alien taxa below the species level are included if their ecology or life history is sufficiently distinct. Unicellular and genetically modified organisms are not included. (This delimitation excludes most subspecific alien taxa, for which an exhaustive list would be impossible.)

The status of alien species is described using the categories introduced by Blackburn et al. (2011). Table 1 explains these categories and how they have been implemented for the present inventory. Alien species in the categories C0–C2 are commonly referred to as *casual*, species in the categories C3–E as *naturalised* alien species (Richardson et al. 2000; Pyšek et al. 2004; Blackburn et al. 2011).

Geographic region

The assessment area comprised the Norwegian territories in the northern hemisphere, i.e. mainland Norway (including coastal islands), the Arctic archipelago of Svalbard (Spitsbergen and surrounding islands, including Hopen and Bjørnøya [Bear Island]), the actively volcanic island of Jan Mayen, and the maritime waters surrounding these three areas (i.e. territorial waters plus the Norwegian Economic Zone around mainland Norway, the Fisheries Protection Zone around Svalbard, and the Fisheries Zone around Jan Mayen). Svalbard and Jan Mayen are treated as separate assessment areas from mainland Norway, i.e. a species native to mainland Norway but introduced to Svalbard or Jan Mayen is considered alien to these islands (and vice versa). This is because these Arctic areas are located far from mainland Norway (Bjørnøya, 450 km; Spitsbergen, 675 km; Jan Mayen, 900 km) and constitute separate management units.

In terms of geography, mainland Norway extends from 57°58′ N to 71°11′ N and from 4°30′ E to 31°10′ E, covering 323,808 km² (including freshwater bodies). Climatically, 8% of mainland Norway belongs to the boreonemoral zone, 12% to the southern boreal, 20% to the middle boreal, 28% to the northern boreal and 31% to the alpine zones, whereas a minor part

of north-eastern Norway has low-Arctic climate. Svalbard extends from 74°20′ N (Bjørnøya) to 80°50′ N and from 10°28′ E to 33°31′ E, covering 61,022 km², and comprises the zones from the middle-Arctic tundra to the polar desert zone. Jan Mayen is situated at 71°N 8°W, covers 377 km², and probably belongs in the low-Arctic but is difficult to evaluate due to its volcanism. The maritime areas cover 933,000 km² around mainland Norway (Skagerrak, North Sea, Norwegian Sea, Barents Sea), 806,000 km² around Svalbard (Greenland Sea, Norwegian Sea, Barents Sea), and 293,000 km² around Jan Mayen (Norwegian Sea, Greenland Sea).

Expert committees

In 2016, twelve expert committees covering all relevant taxonomic groups were established. Following an open announcement, experts in ecology and taxonomy applied for committee membership. Based on the applications, NBIC appointed 52 experts from 15 different Norwegian research institutions (universities, museums, governmental agencies and private research institutes). The committees commenced their work in December 2016, made a preliminary listing available for public comment in December 2017, and finalised the inventory by May 2018.

Data collection

Spatially and temporally located observations of species occurrences were the key input data for the alien species inventory. Records were mainly gathered from museum collections, published sources (articles, book chapters and reports) and a national online database called Species Map (*Artskart*; Artsdatabanken and GBIF Norway 2018). Species Map contains all records from the Norwegian node of the Global Biodiversity Information Facility (GBIF), currently encompassing more than 600,000 records of non-native species. One of the sources of records in Species Map is the Species Observation System (*Artsobservasjoner*; Artsdatabanken et al. 2018), a citizen-science database where both amateurs and professionals can register their observations of species. For several taxa, these data were supplemented with records kept at the participating or other institutions and with the NOBANIS database (NOBANIS 2018). The methods used for detecting species varied by taxonomic group and included field collection, molecular methods, spore traps and other specialised methods. Records were checked for credibility, and we excluded doubtful records that could not be verified. This was especially important for the citizen-science records from the Species Observation System.

The aim of data collection was an inventory of alien species (neobiota) recorded in Norway as of the year 2017. In addition to spatio-temporal data on occurrences, further information on each species was recorded, including the area of origin and the habitat types colonised. Assignments of species to establishment categories, areas of origin and habitat types were mainly based on the records, or otherwise on literature. Where this kind of information was unavailable (e.g. for old records), assignments to the most likely category were based on expert judgements. The individual evaluations of all species are available in an online database (in Norwegian; Artsdatabanken 2018). Definitions of habitat types and e.g. "heavily modified ecosystems" follow Halvorsen et al. (2016).

Statistical analyses

Taxonomic, geographic and environmental patterns were analysed as contingency tables using Pearson's chi-squared test with simulated *p*-values (based on 100,000 replicates). Table columns and rows that contained fewer than 10 species or were incomparable to the other columns/rows, were excluded from the statistical tests. Many species can originate from more than one continent and occur in more than one habitat type. In order to analyse these data using contingency tables, each species had to be assigned to one group only. For continents, this was done by selecting the closest and/or climatically most similar continent (Europe > Asia > North America > Africa > South America > Oceania; Atlantic Ocean > Pacific Ocean). For habitat types, this was done by selecting the most specialised and/or least modified habitat type or lifestyle (parasitic > alpine > forest > coast > freshwater > wetland > lowland > urban).

The difference of first observation dates between taxonomic groups was analysed using ANOVA (analysis of variance). The geographical variation in the number of alien species recorded per county was analysed using linear regression models (see Online Resource 2 for details). Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). Comparisons with the previous inventory refer to Gederaas et al. (2013; and Artsdatabanken 2012).

Statistical analyses were carried out in the **R** environment (**R** Core Team 2017). Estimates are presented as mean \pm standard error.

Results

A total of 2496 species (including 128 taxa ranked as subspecies, variety, form or section) met the definition of being alien to Norway and fulfilled all four delimitations. These are listed in Online Resource 1. The following four sections summarise the characteristics of the subset of neobiota that have been recorded in mainland Norway, whereas the fifth section describes the neobiota that have been recorded on Svalbard and Jan Mayen. The sixth section analyses the changes since the previous inventory.

Taxonomy

Table 2 shows the distribution of the 2410 neobiota known to occur in mainland Norway across taxonomic groups and establishment categories. Three quarters of the species were plants. The predominant categories were C0, C3 and E (cf. Table 1). The taxonomic representation was highly different among casual and naturalised species (Fig. 1; $\chi_5^2 = 180.40$, p < 0.0001). Whereas plants and vertebrates were better represented among casuals than among naturalised species, the opposite was the case for fungi and invertebrates (Fig. 1). When analysing the establishment categories separately, plants were strongly overrepresented in C0, C2 and C3; vertebrates in C1; fungi in D1 and D2; and algae and invertebrates in E (relative to the total number of alien species of the respective group; Table 2).

The remaining analyses are restricted to naturalised neobiota (categories C3–E, N = 1039), because more data are available for these. Among naturalised plants, 22 families were represented with 10 species or more (Table 3). The best represented taxa among naturalised animals

were arthropods, vertebrates and molluscs (Table 4). The best represented taxa among oomycetes and ascomycetes were *Phytophthora* (15 spp.) and *Erysiphe* (9 spp.), respectively.

The proportion of naturalised neobiota relative to native biota averaged 3% but varied widely among taxonomic groups (Table 5). The highest proportion was obtained by plants, where 22% of the stably reproducing species in Norway were neobiota.

Habitat and origin

Naturalised neobiota are mainly reported from open lowlands, urban environments and woodlands (Table 5). The habitat types colonised were very unevenly distributed among organism groups (Fig. 2). This was mainly due to vertebrates (fishes) being overrepresented in freshwater ecosystems, fungi being overrepresented among parasitic lifeforms, and plants being somewhat overrepresented in urban environments (Fig. 2).

A third of the naturalised species (403 out of 1039) were not found in natural or seminatural ecosystems at all, i.e. they were only recorded from heavily modified ecosystems – such as roadsides, monoculturally forested areas, intensely managed or ploughed systems. An additional 180 species were predominantly found in heavily modified nature but may occasionally (with $\leq 25\%$ of their occurrences) occur in (semi-)natural ecosystems.

The majority of the naturalised neobiota in Norway originated from other parts of Europe (Fig. 3). Asia and North America were also important areas of origin. Taxonomic groups did not differ notably in their continents of origin (Fig. 3); however, species from different continents were unevenly represented in habitat types (Fig. 4). The strongest patterns in this regard were that European species were overrepresented in lowlands and underrepresented in forest ecosystems, whereas North American species were overrepresented in freshwater ecosystems and underrepresented in lowlands (Fig. 4).

Temporal patterns

For most naturalised species, the date of the first observation in Norway has been recorded (N=1011). The oldest observations were from c. 1670, 1685 and 1694 (*Lilium martagon* [martagon lily], *Cyprinus carpio* [common carp], *Sambucus nigra* [elderberry]); the most recent ones were from 2017 (*Janetiella siskiyou* [a cone gall midge], *Symphytum tuberosum* [tuberous comfrey]). The years of first observation were heavily skewed towards the present (Fig. 5). This was especially pronounced among marine organisms, with 87% of marine invertebrates and 70% of algae observed for the first time after 1950 (Fig. 5). For fungi and non-marine invertebrates, the majority (59%) of species was also first observed after 1950. For plants and vertebrates, average observation dates were earlier than for the remaining groups (ANOVA, both t < -2.4, p < 0.02).

The date of the first establishment with at least one stably reproducing population has been recorded for 955 species. The earliest documented establishments of neobiota were in 1740 (*Lilium bulbiferum* [tiger lily]) and 1776 (*Lolium perenne* [perennial ryegrass], *Schedonorus pratensis* [meadow fescue]). The latest establishments were reported in 2017 (*Graphocephala fennahi* [rhododendron leafhopper], $Larix \times marschlinsii$ [Dunkeld larch]).

Among plants, 40 species were included in the inventory because they have had naturalised populations in Norway in the past, even though it is likely that they are not stably reproducing in Norway any more (see Online Resource 1). This entails that the known populations of these species were documented to have disappeared after 1900, and that the existence of unreported populations is unlikely.

Two mammal species were included in the inventory even though they had been native earlier, viz. *Ovibos moschatus* (muskox) and *Sus scrofa* (wild boar). The native populations of both species had gone extinct > 1000 years before their reintroduction.

Spatial patterns

The number of naturalised neobiota recorded in each of 18 Norwegian counties varied between 64 (Finnmark) and 671 (Oslo and Akershus; see Fig. 6), with a median and mean of 326 and 338 species per county, respectively. According to the delimitations, species were reported as alien to a county only if they were alien to mainland Norway as a whole. The number of naturalised species recorded per county was positively related to the human population density in the county and decreased with northern latitude (Fig. 7; linear regression, both |t| > 4.5, p < 0.001; Fig. 7). In mainland Norway, human population densities of counties correlate with their latitude (R = -0.27). Still, both factors independently contributed to the best model, together explaining 91% of the variation among the 18 Norwegian counties. A very similar pattern was found when Svalbard was included (Fig. 7). Details on these analyses are provided in Online Resource 2.

Svalbard and Jan Mayen

On Svalbard, 98 casual and 5 naturalised alien species have been recorded (Table 6). Of the naturalised species, *Echinococcus multilocularis* (a tapeworm) and *Microtus levis* (sibling vole) are alien to Svalbard and not present in mainland Norway. *Chionoecetes opilio* (snow crab) and *Barbarea vulgaris* (bittercress) are alien to, and naturalised in, Svalbard as well as mainland Norway. *Anthriscus sylvestris* (wild chervil) is alien to Svalbard and native to mainland Norway, as are most (83) of the casual species (see Online Resource 1).

Jan Mayen is poorly investigated, but two casual alien species have been reported from the island. The tunicate *Molgula manhattensis* (C1) is most likely alien to Jan Mayen as well as to mainland Norway. *Rumex acetosa* (common sorrel, C2) is alien to Jan Mayen as well as Svalbard, while it is native to mainland Norway.

Comparison with the previous inventory

The previous inventory listed 2300 alien species (2241 for mainland Norway, 79 for Svalbard). 2073 of these were also included in the current inventory (Online Resource 1: List I), while 423 species (17%, N = 2496) were newly included. These additions were due to novel introductions as well as revised knowledge, but also changes in the delimitations.

Several species were included in the 2012 list but not in the current inventory. Of these, 47 species are not regarded as alien to Norway any longer (see Online Resource 1: List II); 34 species have most likely never been present in Norway after all, meaning that some speci-

mens had been misidentified and mistakenly reported as present in Norway at an earlier occasion (see Online Resource 1: List III). The remaining species were omitted due to revised delimitations (87 indoor arthropods, 17 archaeophytes, 11 garden plants, 5 greenhouse fungi) or taxonomic issues (26 spp.).

Discussion

Comparison with other countries

Norway is unusual in a European context, because large parts of the country have boreal, alpine and even Arctic climate. This implies that, on one hand, non-marine habitats in Norway have a relatively low native biodiversity, which may be considered to increase the invasibility of Norwegian nature (Elton 1958; Tilman 1997; but see Fridley et al. 2007). On the other hand, Norway's climate is relatively hostile to alien species, although this situation is about to be lessened by climate change (Iacarella et al. 2015; Dullinger et al. 2017). Climate is the likely cause underlying the global pattern according to which alien species diversity in the extratropics tends to decrease with increasing latitude (Sax 2001; Pyšek and Richardson 2006).

Norway is also unusual in having a human population density of only 16 inhabitants per km², and because < 4% of the Norwegian mainland is urbanised or utilised as arable land. In the light of these special characteristics, it is interesting to compare the Norwegian data with those from other countries. A useful figure, in addition to the absolute number of alien species, is the density of alien species, a unitless index defined as the number of alien species divided by the decadal logarithm of country area in km² (e.g. Lambdon et al. 2008). The number of neobiota in mainland Norway (2410) corresponds to a density index of 437. However, as complete inventories of alien (or neobiotic) species are still rare, we were unable to relate the Norwegian figures to other countries.

When we exclude casual species, the figures for mainland Norway are 1039 naturalised neobiota and a density index of 189. This is a higher number and density than reported from e.g. Austria, Germany, Liechtenstein, Spain, Sweden and Switzerland (Fig. 8a; Essl and Rabitsch 2002; Capdevila Argüelles et al. 2006; Staub 2006; Wittenberg et al. 2006; Nehring et al. 2013, 2015; Rabitsch and Nehring 2017; Strand et al. 2018).

Data from even more countries are available when considering naturalised vascular plants only (for an overview of Europe, see Lambdon et al. 2008). Among the countries included, only Great Britain has more naturalised neophytes than Norway (Fig. 8b; data from Lambdon et al. 2008; supplemented or updated from: Capdevila Argüelles et al. 2006; Staub 2006; de Almeida 2012; Pyšek et al. 2012; Ries et al. 2013; Strand et al. 2018).

Roughly 3% of all stably reproducing species in Norway, and 22% of vascular plant species, are naturalised neobiota. The latter figure corresponds well to the situation in Austria and Czechia (Essl and Rabitsch 2002; Pyšek et al. 2002, 2012). However, if including archaeophytes as well, more than half of the Norwegian flora is of alien origin (Gederaas et al. 2007).

These comparisons suggest that the alien biodiversity, and certainly the alien flora, of Norway is higher than its latitude would suggest. It has been noted earlier (Lambdon et al. 2008) that the Scandinavian countries may be an exception from the global latitudinal gradients (Sax

2001; Pyšek and Richardson 2006). Potential reasons are that agriculture and urbanisation may have introduced a number of species native to Central Europe, or that many species classified as archaeobiota in the rest of Europe reached the northern parts of the continent later (Lambdon et al. 2008). Other possible factors are the Gulf Stream, which renders the Norwegian climate milder than predicted from latitude alone; and the fact that agriculture came very early to northern West Europe compared to similar latitudes in Russia, Alaska and Canada, i.e. there has been a much longer history of alien species following agriculture.

An alternative, or additional, explanation may be found in different sampling efforts in different countries (see Dawson et al. 2017). We are not aware of such estimates across countries, but we note that sampling effort may well have been higher in Norway than in most other countries, given the considerable mapping efforts instigated by NBIC in recent years (ArtDatabanken and Artsdatabanken 2017).

It should be mentioned that the patterns discussed above do not seem to apply to marine species. In these groups, the number and proportion of alien species is low in Norway compared to many other European countries (Katsanevakis et al. 2013).

Geographic, taxonomic and temporal patterns

Within Norway, the number of neobiota recorded in a county varied by one order of magnitude (Fig. 6): whereas 671 species were reported from the area around the capital Oslo in south-eastern Norway, 64 species were reported from the northernmost county (Finnmark). The geographic distribution of neobiota recorded in Norway can be explained by several, not mutually exclusive, factors. The most important are climate, introduction pressure, habitat invasibility and sampling bias (Olsen et al. 2017; cf. Dawson et al. 2017). Climatically, it is not surprising that the number of naturalised species decreases with increasing northern latitude (Fig. 7a), considering that most alien species arriving in Norway originate from countries with a milder climate. The Arctic archipelago of Svalbard represents the extreme in this gradient, with only 5 naturalised species reported (corresponding to a density index of just above 1).

The variation in the numbers of naturalised neobiota per Norwegian county is well described by a model including human population density within a county and its latitude (see Fig. 7 and Online Resource 2). Human population density is directly related to introduction pressure (Dawson et al. 2017), because there are more introductory pathways in densely inhabited areas. This may be due to factors such as the distance to the nearest port or railway, and the density of roads or private gardens (Sharma et al. 2010; Dodd et al. 2016). In addition, disturbance of soil and vegetation is a prerequisite or facilitating factor for the establishment of many species (Lembrechts et al. 2016), and such disturbance can be expected to covary with human population density. Finally, sampling bias has also been shown to be related to human population density, e.g. distance to the nearest herbarium (Dodd et al. 2016). The same factors may explain why the number of naturalised species is highest in lowland, urban and forest ecosystems, as these are the most disturbed and most densely populated habitats.

In terms of taxonomy, the list of naturalised species is heavily dominated by vascular plants. Among animals, vertebrates are better represented than (especially marine) invertebrates, relative to the numbers of native species. This pattern, too, may be due to actual differences in introduction rates or sampling bias. As for the former, plants are overrepresented among species

that have been imported intentionally, e.g. for gardening, agriculture and forestry. Another reasons for the large proportion of plants is that Norway may still be undersaturated with species that have gone extinct during the last glaciation. Many plants that are introduced from Europe may well reach Norway by means of natural dispersal within the next millennia.

As far as sampling bias is concerned, some taxa are inherently more conspicuous than others. In addition, the interest of hobby naturalists is not distributed randomly among taxonomic groups. For these reasons, flowering plants, birds and butterflies probably have higher detection rates than, e.g., flatworms, tunicates or mosses. The lowest detection rates can be expected for parasites and other species that are very small or live within other organisms or in substrates such as soil or water.

Sampling bias may also be an important factor for explaining the taxonomic differences across establishment categories (Fig. 1, Table 2). Higher categories (D2–E) are overrepresented among the 'less conspicuous' groups (fungi, invertebrates and algae). This may be partly because these species are not normally noticed before they have spread to a considerable number of occurrences.

The temporal increase in detections (Fig. 5) may also be due to actual changes in introductions or sampling bias. An instructive example is the substitution of ballast sand and soil by ballast water, when engine-driven ships replaced sailing ships in commercial shipping. This change in practice may explain why certain alien plants are far less common today than during the 19th century (e.g. *Diplotaxis muralis* [annual wall-rocket] and *Verbena officinalis* [common vervain]), and also the recent increase in alien marine invertebrates reported (Fig. 5). Here, too, the underlying patterns in factual changes are to some degree masked by variation in detectability and sampling effort. An increase in awareness has almost certainly contributed to the increase in numbers reported.

The taxonomic differences in temporal trends are similar to the global patterns (Seebens et al. 2017), in that introduction rates of invertebrates, fungi and algae are still increasing, whereas vertebrate introductions seem to have declined in recent decades (Fig. 5). In contrast to the global trend (Seebens et al. 2017), plant introductions seem to decelerate somewhat in Norway, although it is too early to tell whether this is merely a short-term fluctuation.

Conclusion

The third inventory of alien species in Norway showed that 2496 neobiota have been reported from the wild. Of these, 1039 are naturalised in mainland Norway. These numbers are higher than expected from Norway's latitude, which may be due a combination of climatic and historical factors, although differences in sampling effort may complicate the comparison.

A subset of naturalised alien species has adverse ecological effects on native biota. One aim of the inventory has therefore been to create a list that can serve as the basis for ecological impact assessment. Such assessments have been carried out for the naturalised species and a subset of casuals (Artsdatabanken 2018; Sandvik et al. unpubl.).

Notes

Acknowledgements We are grateful to Pål Adolfsen, Helge Bardal (Norwegian Veterinary Institute), Henrik H. Berntsen (Norwegian Institute for Nature Research), Otte Bjelland, Jan H. Sundet (Institute of Marine Research), Kristina Bjureke, Geir Søli (Natural History Museum), Preben S. Ottesen (Norwegian Institute of Public Health), Mikael Svensson (Swedish Species Information Centre) and Eva Vike (Norwegian University of Life Sciences) for help with the inventory.

Funding The inventory was financed by the Norwegian Biodiversity Information Centre.

Author Contributions LG was project leader and organised the inventory; HSa, OH and LG prepared the guidelines; DD, RE, TF, EF, HHa, KH, VH, GK, FØ, HCP, HaSo and BGS headed the expert committees that carried out the inventories; PAÅ, SÅ, T-EB, HE, AE, AF, SF, ØG, JOG, BG, IH, BAH, HHe, TH, AJ, TCJ, SIJ, EK, CM, KN, BN, EO, OP, PAP, KS, JKS, HeSo, LS, JES, POS, VT, VV, KBW, RW and BY were members of these expert committees; OH and LG assisted the expert committees in their work; HSa analysed the data with input from SH, OH and VV; HSa wrote the article with input from the remaining authors.

Conflict of Interest The authors declare that they have no conflict of interest.

Electronic Supplementary Material Online Resource 1: Species inventory (<u>xlsx</u>), Online Resource 2: Naturalised neobiota in Norwegian counties and European countries (pdf)

References

ArtDatabanken, Artsdatabanken (2017) The Swedish and Norwegian Taxonomy Initiatives – collaborating to survey and describe the biodiversity. https://www.biodiversity.no/Pages/236511
Artsdatabanken (2012) Fremmede arter i Norge. http://databanken.no/FremmedArt2012
Artsdatabanken (2018) Fremmedartslista 2018. https://www.artsdatabanken.no/fremmedartslista2018
Artsdatabanken (2019) Artsnavnebasen. Norsk taksonomisk database [Species Nomenclature Database]. http://www2.artsdatabanken.no/artsnavn/Contentpages/Hjem.aspx

Artsdatabanken, GBIF Norway (2018) Artskart [Species Map]. https://artskart.artsdatabanken.no
Artsdatabanken, Sabima, NOF et al (2018) Artsobservasjoner. Rapporteringssystem for arter [Species Observation System]. https://www.artsobservasjoner.no

Blackburn TM, Pyšek P, Bacher S et al (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26:333–339. https://doi.org/10.1016/j.tree.2011.03.023

Blackburn TM, Essl F, Evans T et al (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol 12:e1001850. https://doi.org/10.1371/journal.pbio.1001850

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Capdevila Argüelles L, Iglesias García Á, Orueta y Bernardo Zilleti JF (2006) Especies exóticas invasoras: diagnóstico y bases para la prevención y el manejo. Ministerio de Medio Ambiente, Madrid

D'hont B, Vanderhoeven S, Roelandt S et al (2015) Harmonia⁺ and Pandora⁺: risk screening tools for potentially invasive plants, animals and their pathogens. Biol Invasions 17:1869–1883. https://doi.org/10.1007/s10530-015-0843-1

Dawson W, Moser D, van Kleunen M et al (2017) Global hotspots and correlates of alien species richness across taxonomic groups. Nat Ecol Evol 1:0186. https://doi.org/10.1038/s41559-017-0186

de Almeida JD (2012) Flora exótica subespontânea de Portugal continental (plantas vasculares). Catálogo das plantas vasculares exóticas que ocorrem subespontâneas em Portugal continental e compilação de informações sobre estas plantas, 5th edn. Universidade de Coimbra, Coimbra

- Dodd AJ, McCarthy MA, Ainsworth N, Burgman MA (2016) Identifying hotspots of alien plant naturalisation in Australia: approaches and predictions. Biol Invasions 18:631–645. https://doi.org/10.1007/s10530-015-1035-8
- Dullinger I, Wessely J, Bossdorf O et al (2017) Climate change will increase the naturalization risk from garden plants in Europe. Glob Ecol Biogeogr 26:43–53. https://doi.org/10.1111/geb.12512
- Elton CS (1958) The ecology of invasions by animals and plants. Methuen & Wiley, London & New York
- Essl F, Rabitsch W (eds) (2002) Neobiota in Österreich. Umweltbundesamt, Wien
- Essl F, Nehring S, Klingenstein F, Milasowszky N, Nowack C, Rabitsch W (2011) Review of risk assessment systems of IAS in Europe and introducing the German-Austrian Black List Information System (GABLIS). J Nat Conserv 19:339–350. https://doi.org/10.1016/j.jnc.2011.08.005
- Fridley JD, Stachowicz JJ, Naeem S et al (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2
- Gederaas L, Salvesen I, Viken Å (eds) (2007) Norsk svarteliste 2007 økologiske risikovurderinger av fremmede arter. Artsdatabanken, Trondheim
- Gederaas L, Moen TL, Sandmark H, Skjelseth S (eds) (2013) Alien species in Norway: with the Norwegian Black List 2012. Norwegian Biodiversity Information Centre, Trondheim
- Halvorsen R et al. (2016) NiN typeinndeling og beskrivelsessystem for natursystemnivået. Natur i Norge, artikkel 3, versjon 2.1.0. http://artsdatabanken.no/Files/14539
- Iacarella JC, Dick JTA, Alexander ME, Ricciardi A (2015) Ecological impacts of invasive alien species along temperature gradients: testing the role of environmental matching. Ecol Appl 25:706–716. https://doi.org/10.1890/14-0545.1
- IUCN [World Conservation Union] (2000) IUCN guidelines for the prevention of biodiversity loss caused by alien invasive species. IUCN, Gland
- IUCN [International Union for Conservation of Nature] (2012) Guidelines for application of IUCN Red List criteria at regional and national levels, version 4.0. IUCN, Gland & Cambridge
- Katsanevakis S, Gatto F, Zenetos A, Cardoso AC (2013) How many marine aliens in Europe? Manag Biol Invasions 4:37–42. https://doi.org/10.3391/mbi.2013.4.1.05
- KLD [Royal Norwegian Ministry of Climate and Environment] (2015a) Natur for livet. Norsk handlingsplan for naturmangfold. Meld Storting 2015–2016(14):1–155
- KLD [Royal Norwegian Ministry of Climate and Environment] (2015b) Forskrift om fremmede organismer. Nor Lovtid I 2015:1132–1164
- Lambdon PW, Pyšek P, Basnou C et al (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. Preslia 80:101–149
- Lembrechts JJ, Pauchard A, Lenoir J et al (2016) Disturbance is the key to plant invasions in cold environments. Proc Natl Acad Sci USA 113:14061–14066. https://doi.org/10.1073/pnas.1608980113
- Medvecká J, Kliment J, Májeková J et al (2012) Inventory of the alien flora of Slovakia. Preslia 54:257–309
- Nehring S, Kowarik I, Rabitsch W, Essl F (eds) (2013) Naturschutzfachliche Invasivitätsbewertungen für in Deutschland wild lebende gebietsfremde Gefäßpflanzen. BfN Skr 352:1–202
- Nehring S, Rabitsch W, Kowarik I, Essl F (eds) (2015) Naturschutzfachliche Invasivitätsbewertungen für in Deutschland wild lebende gebietsfremde Wirbeltiere. BfN Skr 409:1–222
- NOBANIS [European Network on Invasive Alien Species] (2018) Gateway to information on invasive alien species in North and Central Europe. http://www.nobanis.org
- Olsen SL, Åström J, Hendrichsen D et al (2017) Fremmede karplanter i Norge: modellering av introduksjonsområder og nåværende utbredelse. NINA Rapp 1393:1–116
- Preston CD, Pearman DA, Hall AR (2004) Archaeophytes in Britain. Bot J Linn Soc 145:257–294. https://doi.org/10.1111/j.1095-8339.2004.00284.x
- Pyšek P, Richardson DM (2006) The biogeography of naturalization in alien plants. J Biogeogr 33:2040–2050. https://doi.org/10.1111/j.1365-2699.2006.01578.x
- Pyšek P, Sádlo J, Mandák B (2002) Catalogue of alien plants of the Czech Republic. Preslia 74:97–186
- Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards a better communication between taxonomists and ecologists. Taxon 53:131–143. https://doi.org/10.2307/4135498

- Pyšek P, Danihelka J, Sádlo J et al (2012) Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. Preslia 84:155–255
- Pyšek P, Pergl J, Essl F et al (2017) Naturalized alien flora of the world: species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia 89:203–274. https://doi.org/10.23855/preslia.2017.203
- Pyšek P, Meyerson LA, Simberloff D (2018) Introducing "Alien Floras and Faunas", a new series in Biological Invasions. Biol Invasions 20:1375–1376. https://doi.org/10.1007/s10530-017-1648-1
- **R** Core Team (2017) **R**: a language and environment for statistical computing, version 3.3.3. **R** Foundation for Statistical Computing, Wien. http://www.r-project.org
- Rabitsch W, Essl W (2006) Biological invasions in Austria: patterns and case studies. Biol Invasions 8:295–308. https://doi.org/10.1007/s10530-004-7890-3
- Rabitsch W, Nehring S (eds) (2017) Naturschutzfachliche Invasivitätsbewertungen für in Deutschland wild lebende gebietsfremde aquatische Pilze, Niedere Pflanzen und Wirbellose Tiere. BfN Skr 458:1–220
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Divers Distrib 6:93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x
- Ries C, Krippel Y, Pfeiffenschneider M, Schneider S (2013) Environmental impact assessment and black, watch and alert list classification after the ISEIA protocol of non-native vascular plant species in Luxembourg. Bull Soc Nat Luxemb 114:15–21
- Ries C, Pfeiffenschneider M, Engel E, Heidt J-C, Lauff M (2014) Environmental impact assessment and black, watch and alert list classification after the ISEIA protocol of vertebrates in Luxembourg. Bull Soc Nat Luxemb 115:195–201
- Sandvik H, Hilmo O, Finstad AG et al (2019) Generic Ecological Impact Assessment of Alien Species (GEIAA): the third generation of assessments in Norway. Biol Invasions: in press. https://doi.org/10.1007/s10530-019-02033-6
- Sax DF (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. J Biogeogr 28:139–150. https://doi.org/10.1046/j.1365-2699.2001.00536.x
- Seebens H, Blackburn TM, Dyer EE et al (2017) No saturation in the accumulation of alien species worldwide. Nat Commun 8:14435. https://doi.org/10.1038/ncomms14435
- Sharma GP, Esler KJ, Blignaut JN (2010) Determining the relationship between invasive alien species density and a country's socio-economic status. S Afr J Sci 106:113. https://doi.org/10.4102/sajs.v106i3/4.113
- Staub R (ed) (2006) Neobiota im Fürstentum Liechtenstein. Ber Bot Zool Ges Liecht Sargans Werdenb 32:89–151
- Strand M, Aronsson M, Svensson M (2018) Klassificering av främmande arters effekter på biologisk mångfald i Sverige ArtDatabankens risklista. ArtDatabanken Rapp 21:1–45
- Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78:81–92. https://doi.org/10.1890/0012-9658(1997)078[0081:CIRLAG]2.0.CO;2
- Vinogradova Y, Pergl J, Essl F et al (2018) Invasive alien plants of Russia: insights from regional inventories. Biol Invasions 20:1931–1943. https://doi.org/10.1007/s10530-018-1686-3
- Wittenberg R, Kenis M, Blick T, Hänggi A, Gassmann A, Weber E (2006) Invasive alien species in Switzerland: an inventory of alien species and their threat to biodiversity and economy in Switzerland. Federal Office for the Environment, Bern

Tables

Table 1 Categories of alien species according to their degree of establishment. Categories and definitions (somewhat shortened) are from Blackburn et al. (2011). The last column details how the definitions have been operationalised in this inventory. Categories C2–E are only assigned to species that also fulfil the definitions of the previous categories (excluding A–C0). If several categories apply, the highest one is assigned (i.e. the one farthest down in the table)

Category	Definition	Implementation
A	Not transported beyond native range	Only used for species that are absent from one region (e.g. Svalbard) but recorded in another
B1	Individuals in captivity or quarantine	Species occurring indoors or in closed installations; only recorded if the species has the potential to reproduce upon release or escape
B2	Individuals in cultivation	Only recorded if the species has the potential to reproduce upon escape
В3	Individuals directly released into the wild	Recorded as C0 or higher
C0	Individuals incapable of surviving for a significant period	The individuals are reported from the wild, but knowledge of their biology makes it unlikely that they are able to reproduce or survive the winter
C1	Individuals surviving in the wild	The individuals reported have survived, or are likely able to survive, the winter in the wild
C2	Individuals reproducing in the wild	The individuals reported are most likely offspring produced in the wild (i.e. they have not been introduced themselves)
С3	Self-sustaining population	At least 1 population (numbering more than 20 individuals) has been producing viable offspring in the wild, without human assistance, and for a period of more than 10 years (cf. IUCN 2012:11)
D1	Individuals surviving a significant distance from the original point of introduction	There is at least 1 occurrence of viable individuals in the wild, at least 2 km from all original points of introduction
D2	Individuals reproducing a significant distance from the original point of introduction	There is at least 1 occurrence in the wild of individuals that are either offspring produced in this location or that are clearly able to produce viable offspring, at least 2 km from all original points of introduction
E	Individuals dispersing, surviving and reproducing at multiple sites	There are at least 10 occurrences that fulfil D2 and that have distances of at least 2 km to all original points of introduction and to each other

Table 2 Survey of the alien species in mainland Norway included in this inventory (Online Material 1). Species counts are provided for neophytes, neozoa, neomycetes and neoalgae, both cumulatively (*N*) and for the establishment categories listed in Table 1. Taxa are sorted by decreasing species counts

Taxon	N	B1 ^a	B2 ^a	C0	C1	C2	C3	D1	D2	Е
Total	2410	24	7	612	363	365	374	12	281	372
Embryophyta (plants)	1892	_	7	571	239	341	337	2	197	198
Magnoliophyta	1835	_	6	569	238	313	326	1	195	187
Pinophyta	52	_	1	1	1	27	10	1	2	9
Marchantiophyta	2	_	_	_	_	_	1	_	_	1
Polypodiophyta	2	_	_	1	_	1	_	-	-	
Bryophyta	1	_	_	_	_	_	_	- (-	1
Metazoa (animals)	411	19	_	38	115	23	28	5	53	130
Hexapoda	222	18	_	35	34	6	19	3	18	89
Vertebrata	104	_	_	1	69	10			17	7
Mollusca	27	1	_	_	5	3	2	1	6	9
Crustacea	18	_	_	_	1	2	4	1	3	7
Arachnida	9	_	_	_	4		_	_	3	2
Nematoda	9	_	_	- /	_	1	1	_	3	4
Monogenea	5	_	_	_	_	_	2	_	2	1
Cnidaria	3	_	-	-	_	_	_	_	3	_
Diplopoda	3	_	_	1	1	_	1	_	_	_
Tunicata	3	-/	\ <u>\</u>	_	_	_	_	_	1	2
Annelida	2	_	-	_	_	1	_	_	_	1
Bryozoa	2	_	_	_	_	_	_	_	_	2
Chilopoda	2	_	_	1	_	_	_	_	_	1
Cestoda	1	_	_	_	1	_	_	_	_	_
Ctenophora	1	_	_	_	_	_	_	_	_	1
"Fungi"b	96	5	_	3	8	1	8	5	27	39
Basidiomycota	41	5	_	2	8	_	3	4	14	5
Ascomycota	38	_	_	1	_	_	_	1	12	24
Oomycota	17	_	_	_	_	1	5	_	1	10
'Algae''b	11	_	_	_	1	_	_	_	1	9
Rhodophyta	8	_	_	_	1	_	_	_	1	6
Phaeophyta	2	_	_	_	_	_	_	_	_	2
Chlorophyta	1	_	_	_	_	_	_	_	_	1

^a The inventory is not exhaustive for categories below C0

b Names in quotation marks are here treated as ecological rather than strictly taxonomical groupings

Table 3 The 22 families of plants that are represented in mainland Norway with ≥ 10 naturalised neophytes, sorted by decreasing number of species. The most frequent genera (and all genera with ≥ 10 naturalised neophytic species) are listed, with number of naturalised species in brackets.

Family	Genera	Species
Rosaceae	Spiraea (18), Rubus (17), Cotoneaster (16)	98
Asteraceae	Senecio (6), Symphyotrichum (6), Doronicum (5)	87
Brassicaceae	Lepidium (8), Camelina (3), Sisymbrium (3)	43
Fabaceae	Lotus (4), Laburnum (3), Lupinus (3)	36
Lamiaceae	Mentha (8), Nepeta (3)	30
Poaceae	Festuca (5), Bromopsis (3)	27
Salicaceae	Salix (17), Populus (10)	27
Apiaceae	Chaerophyllum (6), Eryngium (3), Heracleum (3)	21
Pinaceae	Abies (7), Pinus (6), Larix (4)	21
Boraginaceae	Pulmonaria (6), Symphytum (4)	19
Caryophyllaceae	Dianthus (3)	16
Ranunculaceae	Clematis (4), Anemone (3)	16
Asparagaceae	Hyacinthoides (4), Scilla (4)	15
Iridaceae	Iris (7), Crocus (6)	15
Plantaginaceae	Veronica (10)	15
Polygonaceae	Aconogonon (4), Rumex (4), Reynoutria (3)	15
Crassulaceae	Phedimus (5), Sedum (5), Hylotelephium (3)	14
Amaryllidaceae	Allium (6), Galanthus (3)	13
Onagraceae	Oenothera (7), Epilobium (5)	13
Liliaceae	Tulipa (5)	12
Papaveraceae	Corydalis (4), Papaver (4)	12
Saxifragaceae	Saxifraga (5)	11

Table 4 Animal taxa that are represented in mainland Norway with ≥ 10 naturalised neozoa, sorted by decreasing number of species. The most frequent subordinate taxa are listed (Linnaean ranks differ), with number of species in brackets

Taxon	Subordinate taxa	Species
Hexapoda	Coleoptera (62), Hemiptera (23), Diptera (18), Collembola (14), Hymenoptera (7), Lepidoptera (5)	129
Vertebrata	Actinopterygii (11), Mammalia (8), Aves (3)	24
Mollusca	Gastropoda (15), Bivalvia (3)	18
Crustacea	Isopoda (4), Amphipoda (3), Decapoda (3), Maxillopoda (3)	15

Table 5 Numbers of naturalised neobiota in mainland Norway in relation to native biota (species and habitat types). The total species counts (Artsdatabanken 2019) include native species, neobiota and archaeobiota (for plants, microspecies within *Hieracium*, *Taraxacum* etc. are excluded). The habitat types of neobiota are not mutually exclusive, so that percentages in a column may add up to more than 100%. Percentages are only provided if $N \ge 25$

	N	Algae	Fungi	Marine inverte-brates	Non- marine inverte- brates	Verte- brates	Plants
Total (native + alien)	36,872	700	3,256	5,125	23,120	1,266	3,405
Neobiota	1,039	10	79	24	168	24	734
Percentage neobiota	2.8%	1.4%	2.4%	0.5%	0.7%	1.9%	21.6%
Neobiota with known habitat type	952	10	79	24	140	24	675
Open lowlands	756	_	45 (57%)	1	118 (84%)	9	583 (86%)
Urban environments	498	_	3 (4%)	_	11 (8%)	4	480 (71%)
Woodlands	398	_	46 (58%)	- ,	48 (34%)	5	299 (44%)
Wetlands	71	_	2 (3%)	₇ 1	3 (2%)	5	61 (9%)
Marine habitats / coast	68	10	_	24	_	3	31 (5%)
Parasitic lifestyle	51	_	32 (42%)	2	16 (11%)	_	_
Lakes and rivers	36	_	4 (5%)	1	14 (10%)	14	3 (0%)
Mountains / tundra	4	_			_	2	2 (0%)

Table 6 Survey of the neobiota on Svalbard included in this inventory (see Table 1 for explanations)

	N	B1	B2	C0	C1	C2	C3	D1	D2	Е
Total	103	_	_	73	16	9	3	0	1	1
Magnoliophyta	96	_	_	71	14	9	2	_	_	_
Vertebrata	4	_	_	2	1	_	1	_	_	_
Crustacea	2	_	_	_	1	_	_	_	_	1
Cestoda	1	_	_	_	_	_	_	_	1	_

Figures

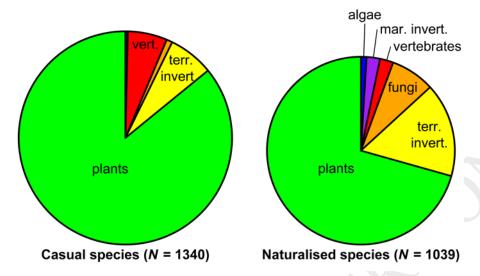


Figure 1 Taxonomic distribution of casual and naturalised neobiota in mainland Norway (mar. invert. = marine invertebrates, terr. invert. = terrestrial and freshwater invertebrates)

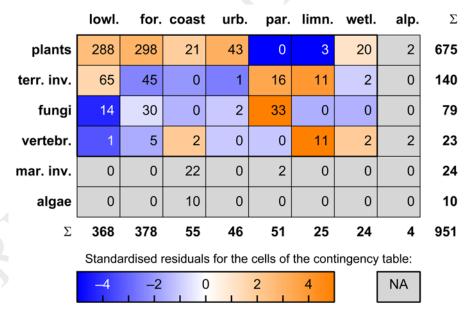


Figure 2 Counts of naturalised neobiota in mainland Norway according to taxonomy and habitat type (lowlands, forests, coasts/marine, urban, parasitic, freshwater, wetlands, alpine/Arctic). Cell colour indicates the standardised residuals of the contingency table ($\chi^2_{18} = 511.54$, p < 0.0001). Grey cells were not included in the contingency table

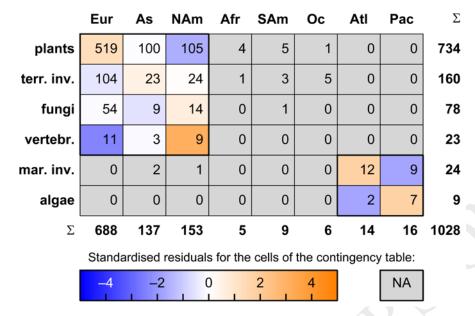


Figure 3 Counts of naturalised neobiota in mainland Norway according to taxonomy and continent of origin (Europe, Asia, North and Central America, Africa, South America, Oceania, Atlantic Ocean, Pacific Ocean). Cell colour indicates the standardised residuals of the contingency table (non-marine species, $\chi_6^2 = 11.42$, p = 0.075; marine species, $\chi_1^2 = 1.84$, p = 0.12). Grey cells were not included in contingency tables

	Eur	As	NAm	Afr	SAm	Ос	Atl	Pac	Σ
lowland	276	43	38	3	5	3	0	0	368
forest	231	68	76	0	1	2	0	0	378
coast	14	7	4	0	0	0	13	16	54
urban	39	2	3	1	1	0	0	0	46
parasite	29	9	8	1	2	0	1	0	50
freshwater	12	1	11	0	0	1	0	0	25
wetland	14	3	7	0	0	0	0	0	24
mountain	1	1	2	0	0	0	0	0	4
Σ	616	134	149	5	9	6	14	16	949

Figure 4 Counts of naturalised neobiota in mainland Norway according to habitat type and continent of origin. Cell colour indicates the standardised residuals of the contingency table ($\chi_{12}^2 = 52.98$, p < 0.0001). See Figure 2 or 3 for further explanations

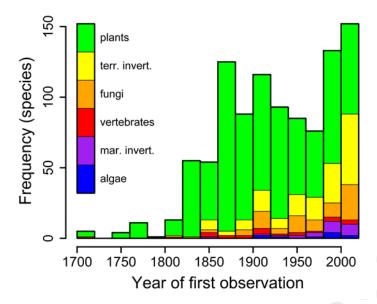


Figure 5 Histogram of the years of first observation of naturalised neobiota in mainland Norway (N = 1011), stratified taxonomically. Bars comprise 20 years, except for the first (1500–1719) and the last bar (2000–2017)

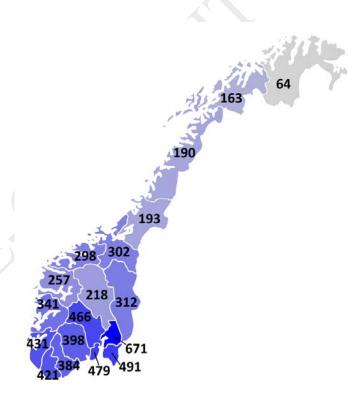


Figure 6 Number of naturalised neobiota in Norwegian counties. Species are regarded as alien in a county only if they are alien to mainland Norway as a whole

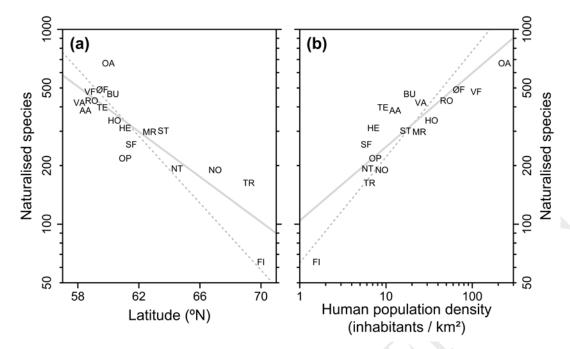


Figure 7 Number of naturalised neobiota in Norwegian counties in relation to the counties' (a) average latitude and (b) human population density. The solid regression lines are based on 18 counties. The broken regression lines include an additional datapoint for Svalbard (which is not shown). Note that, except for latitude, axes are on log-scale. See Online Resource 2 for statistics and for explanations of the abbreviations

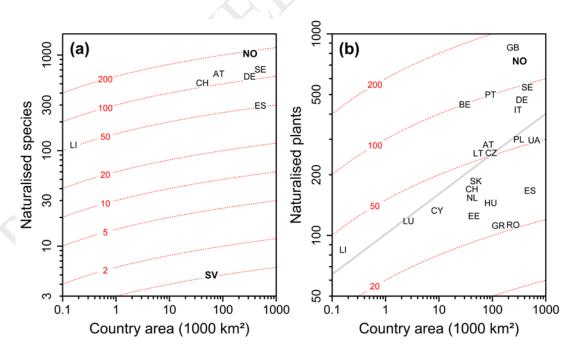


Figure 8 Number of naturalised (a) neobiota and (b) neophytes in different European countries. Countries are identified using their two-letter codes. Dotted contour lines indicate alien species density indices (see text). The grey line in (b) is based on a linear regression. Svalbard is omitted in (b). Note that all axes are on log-scale. See text for data sources, and Online Resource 2 for statistics and for explanations of the abbreviations