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Tanja Kofod Petersen

Biodiversity dynamics in urban areas under changing land-uses

Doctoral thesis

NTNU
Norwegian University of Science and Technology
Thesis for the Degree of
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Faculty of Natural Sciences
Department of Biology

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"Ultimately we need to recognize that while humans continue to build urban landscapes, we share these spaces with other species."

- David Suzuki -

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List of papers

The doctoral thesis is based on the following papers. These will hereafter be referred to by their Roman numerals:

I. **Petersen, T.K.**, Speed, J. D. M., Grøtan, V., Austrheim, G. (2021). „Species data for understanding biodiversity dynamics: The What, Where and When of species occurrence data collection". *Ecological Solutions and Evidence*, 2 (1).

II. **Petersen, T.K.**, Speed, J. D. M., Grøtan, V., Austrheim, G. (2020). „Urban aliens and threatened near-naturals: Land-cover affects the species richness of alien- and threatened species in an urban-rural setting". *Scientific Reports*, 10 (8513).

III. **Petersen, T.K.**, Speed, J. D. M., Grøtan, V., Austrheim, G. (*in press*). „Competitors and ruderals go to town: Plant community composition and function along an urbanisation gradient". *Nordic Journal of Botany*.

IV. **Petersen, T.K.**, Speed, J. D. M., Grøtan, V., Frøyen, Y.K., Austrheim, G. (submitted). „Urbanisation and land-cover change affect the functional turnover of bird communities but not the extent of species composition change". Submitted manuscript to *Journal of Urban Ecology*.

Author contributions

Tanja Kofod Petersen (**TKP**), Gunnar Austrheim (**GA**), James D. M. Speed (**JDMS**), Vidar Grøtan (**VG**), Yngve K. Frøyen (**YKF**). All authors have given their consent to use their work in this thesis.

Paper I, II & III: **TKP**, GA, JDMS and VG conceived the ideas and designed the methodologies; **TKP** retrieved and analysed the data; **TKP** wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Paper IV: **TKP**, GA, JDMS and VG conceived the idea and designed the methodology; **TKP** and YKF retrieved the data, and **TKP** analysed conducted the analyses; **TKP** wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Introduction

Since the dawn of civilisation, humans have altered the physical environment to accommodate their own needs; pristine areas have been converted to agricultural land, cities, and roads. In the past decades, especially urbanisation has increased due to a growing human population (IPBES 2019). In addition, the majority of the world's population now lives in cities, and both further population growth and urbanisation are predicted in the future (United Nations 2018). The growth of cities inevitably happens as the cost of other habitats – the homes to numerous other organisms. Over the last decades, the appreciation of the importance of biodiversity as the basis of ecosystem function and services has increased, as has the understanding of the significance of nature's contributions to people (also known as Ecosystem Services) (IPBES 2018). How to both accommodate the increasing human population and to curb deterioration of biodiversity is an issue of prime importance now and in the immediate future.

Urban ecology

Historically, "urban ecology" has been treated as an oxymoron, and in attempts to study "natural" processes and patterns, researchers actively avoided urban areas (Forman 2014a, Salomon Cavin and Kull 2017). This approach largely adhered to a worldview in which large-scale disturbances (whether they were natural or man-made) were thought to have little long-term impact on a natural system "in balance"; humans were treated as external to biological systems (McDonnell 2011). With growing documentation of anthropogenic impacts on the planet (such as the rise in atmospheric CO_2 levels first published in the early 1960s) and increasing urbanisation, it was acknowledged that such a "humans-outside-of-ecosystems" worldview might hamper our understanding of the ecosphere. With the ever-increasing presence of people, human settlements were recognised as valid foci of ecological studies. From the early 1970s, recognition of the vital part ecology could play in a human context emerged, and a multidisciplinary field reminiscent of current urban ecology budded (McDonnell 2011, Salomon Cavin and Kull 2017, Sukopp 2008).

With the increasing appreciation of urban ecology as an autonomous research field, various biological responses to urbanisation have been recognised, depending on taxonomic-, spatial- and temporal scale (Aronson et al. 2014). Human actions govern biodiversity patterns in urban areas both directly and indirectly; directly through habitat loss and fragmentation, and by introduction of new species; indirectly by changing climate and physiochemical conditions (Kowarik 2011). Through alterations of the physiochemical environment, conditions are made potentially inhospitable for native, locally adapted species, but suitable for generalist and/or alien species. Urban areas thus have a distinct biogeochemistry compared to non-urban areas, driven by human actions (Kaye et al. 2006). Specifically, the urban environment is drier, warmer, more nutrient-rich, polluted and more frequently disturbed compared to more natural counterparts (Forman 2014b, 2014c, Oke 1988, Pellissier et al. 2008). In general, urbanisation can be thought of as a homogenising force on biodiversity (McKinney 2006).

Native vs. alien species in the city

Alien species are frequently introduced to the urban environment (Padayachee et al. 2017). "Alien species" here refers to species (regardless of taxon) which have been introduced to areas outside of their natural range through human action, either deliberately (for example through import of ornamental species and pets), or through "hitch-hiking" (IUCN 2000). Alien species may initially increase local species richness (α diversity[1]), but on a larger, (near-)global scale, cities across biomes become more alike – a decrease in β diversity[2] (McKinney 2006). Alien species are increasingly recognised as drivers of native species extinctions. As the very definition of alien species includes human activity, the link between introductions and cities is obvious. Especially trade, traffic and horticulture are important sources of alien species (Padayachee et al. 2017); urban areas are junctions of all of these. Urban areas thus serve as hotspots for introductions of alien species, and they are particularly susceptible to invasions (Gaertner et al. 2017,

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[1] *α diversity*: species richness/diversity of a local community, as introduced by Whittaker (1972).

[2] *β diversity*: heterogeneity in composition between communities.

van Ham et al. 2013, Padayachee et al. 2017, Salomon Cavin and Kull 2017).

One might be led to believe that cities are depauperate concerning native species, but this is far from the truth. On broad spatial scales, a positive relationship between human population size and biodiversity is seen (Gaston 2005). Cities (and other densely populated areas) can be surprisingly species rich (Cincotta et al. 2000, Gaertner et al. 2017); in some studies, urban areas have even harboured more species than non-urban equivalents, also regarding native and threatened species (Ives et al. 2016, Kühn et al. 2004). It is hypothesised that this is the case as cities generally have been established in productive, species-rich areas – high levels of native biodiversity are thus not necessarily *because of* the urban conditions, but rather *despite of* them (Gaston 2005, Kowarik 2011, Kühn et al. 2004, McKinney 2008). This results in potentially high numbers of native species (including threatened ones) in areas characterised by rapid change, disturbance, and high pressure from alien species – a situation calling for concern. In the worst case, this means that native species inhabiting cities are in reality "living dead" with an extinction debt to pay.

Spatial scale

Studies of biodiversity in an urban context have been performed at multiple scales, including large-scale global studies (Aronson et al. 2014) and single-city ones (Turrini and Knop 2015). Despite the general importance of large-scale studies (e.g. on country- to global level), such investigations are not necessarily appropriate for conservation action, as local management decisions are more often made on a city/county/municipality-level (Luck 2007). Likewise, whereas a positive correlation between species richness and human population density can be seen at large spatial scales, this might not be the case at finer ones (Pautasso 2007); the same mechanisms are not determining large-scale and fine-scale ecological patterns (Gaston 2000, Münkemüller et al. 2014, Uchida et al. 2020). Thus, studies covering the same spatial extent as the one on which actual management decisions are made are needed to inform authorities on the best ways forward regarding biodiversity conservation.

Species occurrence data

To make any statement on the distribution of species in space and time, data on their whereabouts are obviously needed. Scarcity of data is a constant obstacle to overcome, both in space and time (Magurran et al. 2019). Only an estimated 10% of the World's biocollections are available in digital form (Ball-Damerow et al. 2019).

In the past decades, the amounts and availability of species occurrence data have increased immensely (Amano et al. 2016, Gaiji et al. 2013), in no small part due to technological advancements (Powney and Isaac 2015). With the advent of the World-wide Web, handheld GPS's, smartphones and so on, the quantity, quality and accuracy of species occurrence records have increased vastly compared to the early days of biogeographical surveys. These technological advancements have furthermore made species registrations much more attainable for non-professionals, and have thus allowed for an extensive inclusion of "citizen science" in research (August et al. 2015). Likewise, data on species occurrences are increasingly compiled in online portals and databases (Amano et al. 2016, Ball-Damerow et al. 2019). Such portals (the main example being the Global Biodiversity Information Facility, GBIF (GBIF.org 2019, Newbold 2010)) serve as a hodgepodge of different datasets and data types with vastly different origins, scopes and utilities (Speed et al. 2018). A recognised problem with such occurrence records is variation in sampling effort; not all areas nor taxa are investigated to the same degree, neither are the available data evenly spread out in time (Newbold 2010, Powney and Isaac 2015, Tiago et al. 2017). Especially with the increased participation of citizen scientists, taxonomic and spatiotemporal skews can be extensive, based on individual collectors' behaviours and motivations (Boakes et al. 2016). Regardless, these open portals are invaluable sources of spatiotemporal data which would have been otherwise impossible to obtain (Miller-Rushing et al. 2012). Knowledge of the nature of these biases is crucial for developing strategies and methods to account for the issues – this is a field under- and in need of rapid development (Robinson et al. 2018).

Biodiversity and the Sustainable Development Goals

All of the points raised here prove even more crucial in the light of the United Nations' Sustainable Development Goals (SDG) (United Nations 2020b) (Figure 1), and the "Cities and Biodiversity Outlook" by the Convention on Biological Diversity (CBD) (CBD 2012). The SDG include specific targets concerning "Sustainable Cities and Communities" (target 11), and "Life on land" (target 15). In relation to this thesis, three sub-targets of target 15 stand out:

> *"Take urgent and significant action to reduce the degradation of natural habitats, halt the loss of biodiversity and, by 2020, protect and prevent the extinction of threatened species"* (target 15.5),

Figure 1. Conceptual figure from Folke et al. (2016) illustrating the interdependence of the United Nation's Sustainable Development Goals. The goals concerning economy and societal aspects are nested within- and are dependent upon sustainable use and management of the biosphere. Illustration: Azote for Stockholm Resilience Centre, Stockholm University.

> "*By 2020, introduce measures to prevent the introduction and significantly reduce the impact of invasive alien species on land and water ecosystems and control or eradicate the priority species*" (target 15.8),

> "*By 2020, integrate ecosystem and biodiversity values into national and local planning, development processes, poverty reduction strategies and accounts*" (target 15.9).

Neither of these stated targets have been achieved so far, nor are they on the right track to be so (United Nations 2020a). Along the same lines, the 2020 Aichi Biodiversity Targets set by the CBD were not reached either (Brondízio et al. 2019). It is clear that none of these targets can be met without involving city development and biodiversity management within urban boundaries. Cities do not only present issues in this regard, but can also provide opportunities for innovative ways to deal with the relationship between humans and nature (Elmqvist et al. 2013, 2018). To further aid in the completion of the Sustainable Development Goals and the Aichi Targets, and to ensure sustainable use and management of the planets' biological diversity on both global and local levels, understanding in detail how urbanisation and other anthropogenic conversions of land affects other ecosystems and other species is paramount.

Aims

The overall aim of this thesis is to expand our knowledge on the spatiotemporal patterns in biodiversity in urban areas. As the world has experienced increased urbanisation during the last decades, and continue to do so, detailed understanding of how this process affects biodiversity is crucial. As investigations spanning both space and time requires large amounts of (high quality) data, the scope of this thesis is twofold:

1) To evaluate the availability and quality of species occurrence data within Norway and the city of Trondheim, and assess the utility of this data in biodiversity modelling;

2) Investigate how land-use and land-use change affects biodiversity. Particularly the effects of urbanisation were of interest, as were the responses of threatened and/or alien species.

With the studies included in this thesis, I thus aim to assess the availability of data on species occurrences and distributions, examine effects of urbanisation on biodiversity, and provide suggestions on how to develop cities and manage biodiversity within them in a more sustainable fashion. All studies were performed within Norway, most of them limited to Trondheim Municipality. To reach the stated goals, I here attempt to answer the following specific questions:

I. What is the status of openly available species occurrence data in the study area? (**Paper I**)
II. What characterises biodiversity hotspots on an urban-suburban/municipality scale? (**Paper II** & **III**)
III. What are the most important drivers determining the distribution of threatened and alien species? (**Paper II**)
IV. What are the effects of land-use and land-use change on biodiversity, on threatened species and on alien species? **(Paper II, III & IV)**

General methods

The following is a general description and discussion of the methods used in the four papers included in this thesis. Please refer to the "Methods" sections of the individual, appended papers (page I-CCVII) for detailed descriptions.

Study area

For **paper II**, **III** and **IV**, Trondheim municipality served as the study system; for **paper I**, the study area was expanded to encompass all of Norway (Figure 2). Mainland Norway comprises the north-western part of

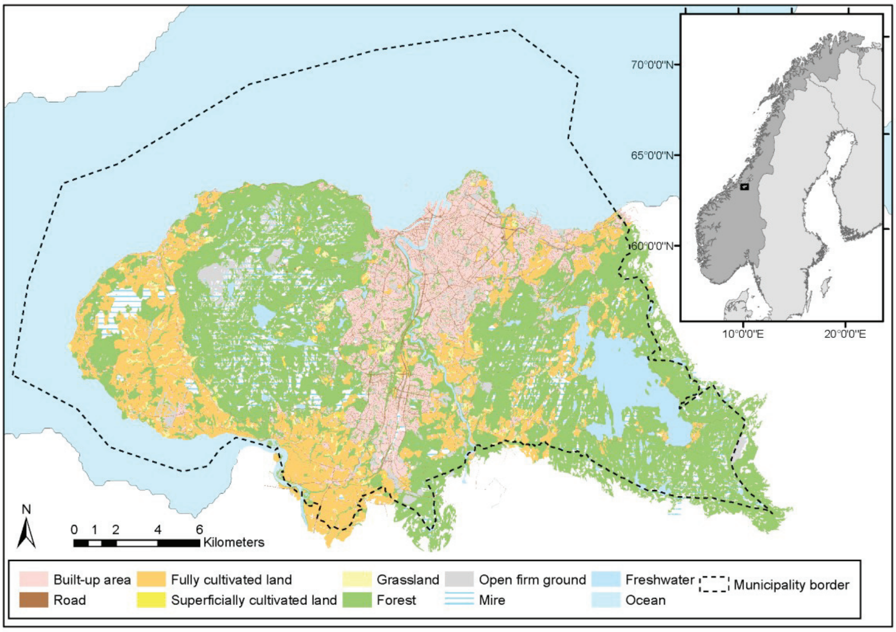

Figure 2. Map of the study area(s) included in all papers. Norway is highlighted in dark grey (upper right inset), and the position of Trondheim Municipality is indicated by a black square. The administrative border of the municipality is illustrated with dashed line, and colours delineate different land-cover types (Norwegian Institute of Bioeconomy Research 2018). Land-cover of the areas surrounding Trondheim has not been included. See **paper I-IV** for more details.

the Scandinavian Peninsula. The country covers ≈323 800 km^2, of which approximately 1.7% is built-up area, and it inhabits ca. 5.4 million people (Statistics Norway 2020). Trondheim[3] is a southern-boreal, coastal municipality, located around 63.42°N, 10.38°E, and it covers approximately 342 km^2. It is the third-most populated municipality in Norway, with approximately 195 000 inhabitants (Statistics Norway 2020). Note that these numbers are from prior to the merger with Klæbu municipality pr. 01.01.2020. In the past decades the municipality has experienced a population increase with subsequent conversions of land-use. The municipality contains large variation in habitats, ranging from industrial- and highly urbanised areas to near-natural forests and mires, and thus presents both extremes of an urbanisation gradient (Trondheim Municipality 2020). In addition, due to the long-term presence of academic institutions such as The Royal Norwegian Society of Sciences and Letters (DKNVS 1760), the university (now named NTNU), the NTNU University Museum, and other research- and management institutions working with biodiversity-related issues (such as NINA (2021) and the Norwegian Biodiversity Information Centre (2021)), Trondheim is fairly well-sampled regarding species occurrence records. Taken together, these circumstances make Trondheim an ideal place to study the effects of urbanisation and land-cover change on biodiversity.

Data

Data on land-cover were based on current and previous land-cover/land-use maps. As we operated on multiple temporal- and spatial scales, several datasets were included, but in all cases the land-cover categories were coded based on land- and tree cover type, timber productivity and soil condition. The outdated DMK ("Digitalt Markslagskart") map was used in **paper III**, previous and updated versions of the AR5 map were used in **paper II**, **III** and **IV**, and the AR50 map were used in **paper I** (Norwegian Institute of Bioeconomy Research 2018, 2019b, 2019a).

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[3] For these studies, Trondheim is defined by the municipal administrative border prior to the merger with Klæbu municipality pr. 01.01.2020. All statistics regarding Trondheim municipality are thus from before this date.

Paper I-IV all included species occurrence data downloaded from the Global Biodiversity Information Facility (GBIF.org 2019). For each paper, different data cleaning steps were applied, generally relating to ensuring data quality, taxonomic- and spatial resolution. DOI's for all downloaded datasets are referenced in the respective papers. For **paper III**, an additional dataset from the NTNU University Museum was included, presenting a structured vegetation survey of 100×100 m^2 vegetation plots along an urbanisation gradient within Trondheim. The full dataset is available through a GBIF public repository (see **paper III** for reference).

A better mechanistic understanding of species' distributions in urban areas, and thus their responses to anthropogenic pressures and land-use changes, can be obtained by examining the functional characteristics and diversity of biological systems rather than focussing on species identities *per se*. In **paper III** and **IV**, we included relevant functional traits of respectively plants and birds to assess the functional responses of the investigated communities (Figure 3). The data were retrieved from various databases, depending on taxon (Billerman et al. 2020, Kattge et al. 2011, Myhrvold et al. 2015, Wilman et al. 2014).

Assessment of spatial and taxonomic biases in species occurrence data

As has been pointed out by several other authors (e.g. Newbold (2010) and Speed et al. (2018)), species occurrence records from databases compiling multiple datasets (including both preserved specimens, structured observational surveys and opportunistic recordings) brings inherent biases and challenges. To address these issues, we examined the status and potential biases of GBIF records in Norway (**paper I**). We studied a subset of ten individual datasets from GBIF differing in origin and thus characteristics. These characteristics included (but were not limited to) taxonomic focus, methodology, number- and skill-level of the reporters. We examined multiple sources of potential skew in the data: taxonomic differences, the distribution of red-listed- and alien species within and between the datasets, temporal patterns, and geographic biases. The potential geographic biases were assessed by repeatedly simulating random distributions of occurrence records across Norway, and comparing these to the distribution of the GBIF data. Dataset name and conservation status of the simulated points were randomly assigned in the same proportions as in the observed dataset. Generalised Linear Models (GLMs) were fitted to the simulated points, providing the expected ranges of number of records falling within each land-cover type.

Predicting species richness by land-cover

In **paper II**, we examined the influence of land-cover variables on species richness patterns among different taxonomic groups, and groups of conservation concern (red-listed and alien species). We constructed spatially dependent Generalised Linear Mixed Effects Models (GLMMs) predicting the total-, threatened- and alien number of species within 500×500 m^2 grid cells across the municipality by habitat, habitat heterogeneity and slope aspect. All grid cells were assigned to habitat categories based on hierarchical cluster analysis of the area of each AR5 land-cover category within the grid cells; thus, the dominating land-cover classes within each grid cell determined "habitat". We identified which variables and variable interactions were able to predict species richness by backwards stepwise model selection based on ΔAIC_c.

Effects of land-cover variables on functional diversity

To examine a more mechanistic relationship between biological communities and (anthropogenic) land-cover, we assessed the differences in functional traits of plants along an urbanisation gradient in **paper III** (Figure 3). We analysed a vegetation survey performed in fifty 100×100 m^2 plots along a suggested urbanisation gradient in Trondheim in 2001-2002. The plots were grouped based on plant community composition using hierarchical cluster analysis, and the differences in slope aspect, age of built structures, proportion of developed area and area of multi-layered forest within the plots were assessed. Rather than assessing the distribution of functional traits of all species recorded in the vegetation plots, we performed Indicator Species Analysis to identify species characteristic of different urbanisation levels, and contrasted functional trait values of the Indicator Species.

To evaluate the identified Indicator Species and their functional responses, we compared the observed patterns with an independent GBIF dataset. In order to evaluate the status of the Indicator Species, we constructed logistic models estimating the probability of presence of an urban- or non-urban indicator species based on the percentage of developed area in 500×500 m^2 grid cells (i.e. a proxy for urbanisation level). We further aimed to evaluate the differences in plant functional traits along an urbanisation gradient, and therefore contrasted the functional trait values of all plant species identified in urban vs. non-urban 500×500 m^2 grid cells. The differences in functional traits identified in the two datasets were compared to identify overall trait syndromes.

Land-cover change effects on functional diversity

Within most ecosystems a degree of "ecological memory" exists. This means that community composition depends not only on the current conditions and interactions, but also by what conditions and disturbances happened in the past. In **paper IV**, we examined the effects the land-cover changes

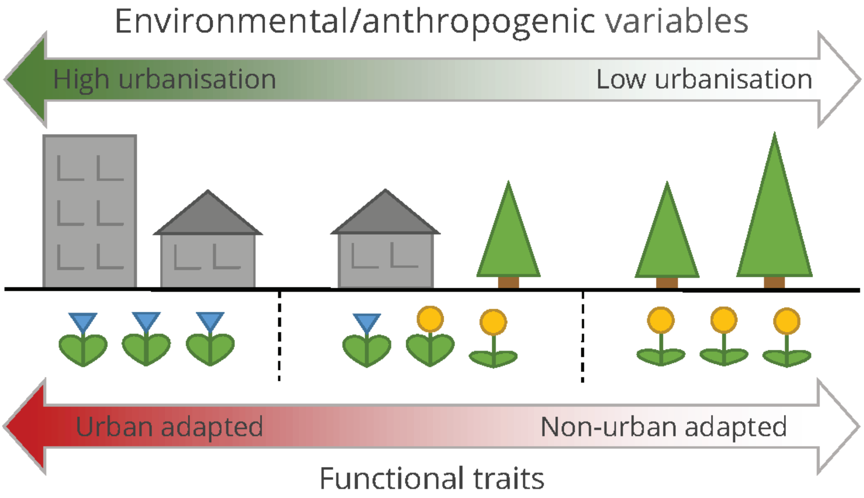

Figure 3. Conceptual figure illustrating the species turnover and interspecific trait variation along a gradient of environmental and anthropogenic variables. Figure modified from **paper III**.

on bird communities in Trondheim. Using land-cover maps from 2011 and 2018, we calculated an index of land-cover change within the 500×500 m^2 grid cells; changes in bird community composition were denoted as the turnover component of the Jaccard dissimilarity index ($\beta_{turnover}$) between the two time steps. We tested whether land-cover change could be used as a reliable predictor of species turnover. However, stability in community level metrics can mask deviations in species composition (MacLean et al. 2018) – measures of β diversity make no claims regarding the characteristics of the communities. To assess the responses of different functional groups of birds, we constructed spatially explicit models of the probability of a species either disappearing from or appearing in a grid cell, based on the functional traits of the species and land-dissimilarity.

To put the results in a conservation context, we evaluated potential future land-cover changes within the municipality, based on the land-use element of the municipal master plan. These potential future land-cover conversions were then held against the identified responses by different avian functional groups.

Summary of the main results

Paper I

Species data for understanding biodiversity dynamics: The What, Where and When of species occurrence data collection

We examined the potential differences in taxonomic-, time-, and land-cover biases in observational GBIF records from ten different datasets, focussing on red-listed and alien species. Specifically, we tested whether the spatial distribution of observational records differed from what could be seen in randomly simulated datasets.

The studied datasets differed taxonomically and temporally, with datasets predominately consisting of citizen science records being dominated by birds. The number of GBIF records have increased over time, with citizen science records providing the bulk of the increase in the later years. The datasets differed in their geographical coverage, with anthropogenic land-covers having more records than what would be expected by chance in most cases. The prevalence of a roadside bias was underlined by a scarcity of records from remote areas, compared to what was to be expected by chance.

Paper II

Urban aliens and threatened near-naturals: Land-cover affects the species richness of alien- and threatened species in an urban-rural setting

We examined the effects of fine-scale land-cover variables (land-cover, habitat heterogeneity and mean slope aspect) on species richness of different taxonomic groups (birds, non-avian animals, plants and fungi) and groups of conservation concern (threatened- and alien species) within 500×500 m^2 grid cells across Trondheim municipality.

The total number of species predicted depended on both mean aspect, habitat and –heterogeneity, all varying by taxon, illustrating highly complex dynamics in the relationships between species richness and the predictor variables. The number of plant species increased with increasing habitat heterogeneity, whereas other taxa showed no clear responses. Across taxa, the highest number of species were seen in relatively undisturbed habitats, and the lowest numbers were predicted in urban areas. The highest numbers of threatened species were predicted in habitats relatively unaffected by human activity and by mean aspect. On the contrary, the number of alien species depended only on taxon and spatial autocorrelation. Conclusively, the study showed how land-cover variables within an administrative border could be used to predict species richness within taxonomic groups.

Paper III

Competitors and ruderals go to town: Plant community composition and function along an urbanisation gradient

We explored plant species turnover along an urbanisation gradient by examining how species indicative of diverging urbanisation levels varied in their functional traits. To evaluate the identified patterns in functional traits, we compared the differences in functional traits of urban- and non-urban Indicator Species to the differences in functional trait distributions of all plants registered in urban- and non-urban areas in a GBIF dataset.

We identified differences in community composition between two different urbanisation levels, mirroring a shift in environmental- and anthropogenic variables, thus indicating how environmental conditions function as an ecological filter. Species indicative of urban areas had higher Specific Leaf Areas, higher affinities for nitrogen and light, had lower seed dry mass, were taller, were more likely to be annual and were more disturbance tolerant than species indicative of non-urban areas. The probability of presence of a non-urban Indicator Species in a grid cell in the independent dataset showed a linear, negative relationship within increasing percentage of developed area, validating their status as indicators. The probability of presence of an urban Indicator Species showed a hump-shaped relationship with increasing proportion of developed area, peaking at intermediate levels. Large confidence intervals around predictions however weakened the indicative value of these indicators.

The exact same functional traits could not be identified among all plant species registered in urban- vs. non-urban areas in the independent dataset, but traits related to the same functional trait syndrome were observed: species in urban areas had lower moisture affinity, higher nitrogen and alkaline affinity, were taller and had a larger specific leaf area. In conclusion, disturbance-tolerance and rapid resource acquisition is favoured in highly urbanised areas, compared to species adapted for stress-tolerance and resource conservation.

Paper IV

Urbanisation and land-cover change affect turnover of bird functional groups but not the extent of species composition change

We studied the characteristics of land-cover change seen in Trondheim between 2011 and 2018, and how the species- and functional diversity of birds in 500×500 m^2 grid cells across Trondheim municipality have been affected by these changes. We examined the probability of a bird species from the local species pool either disappearing from or appearing in a grid cell, based on the land-cover dissimilarity index and functional traits of the bird species.

The changes in land-cover and land-use in the past decade were dominated by urbanisation; in particular, conversion of cultivated land and open firm ground to developed area. The degree of species turnover could not be explained by the land-cover change index. However, the probability of (dis-)appearance of a bird species was affected by both the traits of the species (longevity), and interaction between traits and land-cover dissimilarity: forage stratum, habitat association and main dietary component; increasing longevity decreased the probability of disappearance and increased the probability of appearance. Generally, granivorous species and species associated with urban- and open areas showed decreasing probabilities of disappearing with increasing land-cover dissimilarity, whereas urban- and open-associated, non-ground-feeding species showed an increasing probability of appearing with increasing land-cover change. Overall, predicted probabilities of disappearing were much higher than the probabilities of appearing, indicating that increasing land-cover change has the potential of impoverishing local avifauna. Considering the land-cover conversions planned within the municipality, local avian communities will likely be impoverished given continued urbanisation and land-cover change.

Discussion

Not all datasets are created equal

In **paper I**, we evaluated the status of openly available species occurrence data. Specifically, we tested a subset of data available through GBIF to assess whether biases in taxonomic-, temporal- and geographic scope differed between datasets, and related those differences to the origins of the datasets. This study showed, unsurprisingly, that the datasets in GBIF differ in taxonomic and temporal coverage; particularly datasets dominated by citizen science records focused on birds, and had a sharper increase in abundance in recent years. The most interesting highlight of this study was the difference in geographical coverage by the different datasets: anthropogenic land-covers (such as urban/built-up areas) had many more records than expected by chance, whereas remote areas generally had fewer records than expected. Likewise, the different datasets also showed varying biases regarding red-listed- and alien species records, with citizen science-dominated datasets skewed towards red-listed species. This underlines that caution must be taken when dealing with compiled datasets. The disproportionate taxonomic distribution of records have been documented in previous studies as well (Amano et al. 2016), but relating this to both conservation status of the records and the characteristics of the (likely) collectors emphasises the importance of careful evaluation of data quality and suitability (Ball-Damerow et al. 2019). Developed areas (i.e. cities) generally had more records than would be expected through random sampling for most datasets – particularly datasets dominated by citizen science records, or datasets focussing on alien species. Thus, such compiled datasets have great potential as data sources within urban areas. The main caveats then become the taxonomic skew(s) and disentangling whether the disproportionate number of alien- and red-listed records are due to true abundances, or simply reflects the interests of the collectors. If species occurrence data from open databases are to be used for comparisons across habitats, measures to account for the differences in sampling effort (taxonomically, geographically and by conservation status group) needs to be developed and implemented.

Where the wild things are

In **paper II**, we examined the effects of land-cover and land-cover variables on species richness of four different taxonomic groups, both in total and for threatened- or alien species. This study revealed that the different taxonomic- and conservation groups did not respond similarly to different habitat types. This illustrates the complex relationships between biodiversity and land-cover, and how there is no "silver bullet" approach for predicting species richness across taxonomic- and conservation groups. This is in concordance with the meta-analysis performed by Beninde et al. (2015), who found multiple significant predictors of species richness within urban areas, both at local- and landscape level. Similarly, a study by Matthies et al. (2017) concluded multivariate analyses of biodiversity to be essential, as different predictor variables were retained as significant for different taxonomic groups. Nevertheless, our study showed that on a municipality-wide scale, the highest numbers of species across taxa and conservation groups were found in habitats relatively unaffected by humans, whereas the lowest numbers were seen in urban areas (with few exceptions).

We found a similar result in **paper III**, using a finer spatial scale and focussing on plants: more species were registered in non-urban areas compared to urban areas with a higher anthropogenic pressure. This is in agreement with what has been shown by other studies (e.g. Melliger et al. (2018)). However, dissimilar results have been reported as well, ranging from increasing species richness with urbanisation (e.g. Kühn et al. (2004)) or peaking species richness at moderate levels of urban development (e.g. McKinney (2008)). These responses depend heavily on spatial resolution, taxonomic scope, conservation status, and choice of urbanisation metrics (see for example Pautasso (2007), McKinney (2008), Aronson et al. (2014) and Concepción et al. (2016)).

Nevertheless, some general points regarding the effects of urbanisation and land-cover on biodiversity can be made: overall, intense urbanisation (using sharp increases in built-up area as a proxy) affects species richness negatively. If intermediate levels of urbanisation are found to be most beneficial for biodiversity, this effect can in part be the result of an increase in generalist and/or alien species. Our studies agree with the general consensus that if (native) species richness is to be favoured by management, urban sprawl should be decreased as far as possible, and more natural habitat types should be relieved of anthropogenic pressure whenever possible (Concepción et al. 2016, Geschke et al. 2018, Sushinsky et al. 2013).

For whom the bell tolls

To study the effects of urbanisation on biodiversity in more detail, we examined the effects of land-cover variables and land-cover change on the functional traits of biological communities in **paper III** and **IV** (for plants and birds, respectively). This allowed for a more mechanistic understanding of the factors and processes determining community composition along an urbanisation gradient in Trondheim. Natural systems undergo continuous compositional change (Darwin 1859); our study indicates that increasing levels of land-cover change do not necessarily affect the extent of this compositional change, but rather the functional direction. The degree of land-cover change (measured by a land-cover change index) could not be linked directly to the extent of community composition change (species replacement). Thus, community level metrics can mask deviances in species compositions (MacLean et al. 2018). We showed that environmental- and anthropogenic conditions (indicating different urbanisation levels) filter plant species according to their functional traits. Likewise, the extent of changes in land-cover over time, dominated by increases in built-up area, affects the probability of bird species either appearing in or disappearing from grid-cells depending on their functional traits. The plant species benefitting from high urbanisation levels are species adapted for rapid resource acquisition and disturbed environments. The bird species responding positively to increasing levels of land-cover change (i.e. urbanisation) are likewise pre-adapted for the urban conditions: they are generally associated with urban- or open areas, are non-ground-feeding and granivorous. In a broad sense, urbanisation thus function as an ecological filter across taxa (Figure 4). It is reasonable to assume that the "urban filter" (dis-)favours the same traits across large spatial scales. Our studies thus support the notion that urbanisation can serve as biologically homogenising force over extensive spatial scales (McKinney 2006).

Fantastic data and where to find them

Data availability has always been, and continues to be, a major obstacle to biodiversity research (Dornelas et al. 2013). Despite the large amount of species occurrence records available at the moment, and the increasing number of records continuously being published, these are still merely a drop in the ocean compared to all sampled species data, which are again just samples. There are no definitive estimates of how much of the world's species data are currently available in digital form; this is in part driven by the fact that no inventory of the world's natural history collections exists (Ariño 2010). Likewise, the amount of data stored in private collections is unknown. Some precautious estimates have been inferred, such as: 6-10% of specimen-based data held in biological collections are available through GBIF

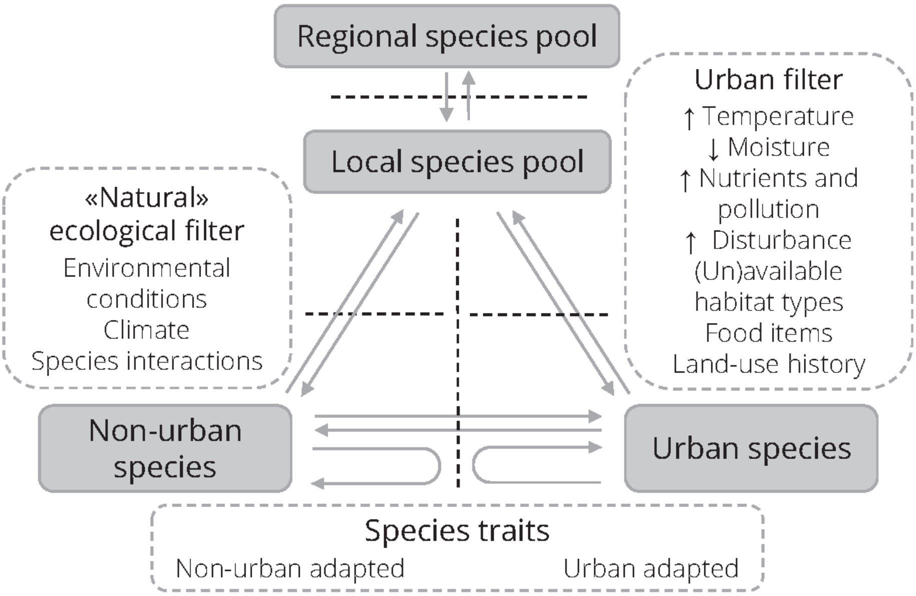

Figure 4. Conceptual figure of the filtering effect of urbanisation. The local species pools are subsets of the regional species pool (solid, grey boxes). The local species pools are filtered (arrows and dashed lines) based on local biogeochemical conditions and existing communities, according to the (functional) traits of the species, which determine whether the species are (pre-)adapted for the local conditions (dashed boxes).

(Townsend Peterson et al. 2018) and 10% of biocollections are digitally available (Ball-Damerow et al. 2019). Much of the data are however incomplete: they miss spatial-, temporal- or taxonomic information (Townsend Peterson et al. 2018). The uneven taxonomic distribution of the digitally available data is of prime importance: in particular, invertebrates and non-vascular plants are underrepresented in databases, despite their abundances in nature (Beck et al. 2012). The excess or shortfall of records for different taxa generally depend on whether the included species are considered "charismatic" (Troudet et al. 2017).

The papers included in this thesis further illustrate these issues by the immense decrease in number of species occurrence records between initial data download and the final analyses. Data shortage hampered both the taxonomic- and the temporal scope of the studies, as well as the habitat coverage (in particular for **paper II** and **paper IV**, and further illustrated in **paper I**).

Along the same lines, the availability of fine-grain land-cover data (and other relevant biogeographical factors) constitutes a bottleneck for research advancements. Several initiatives for making such data available exist (such as Landsat from NASA (National Aeronautics and Space Administration 2021), the CORINE Land Cover from the European Environment Agency (Copernicus 2021), and the Copernicus Sentinel programs by the European Space Agency (European Space Agency 2021)). See also Randin et al. (2020) for a review on the use of remote sensing for biodiversity monitoring. However, the spatial resolution of such data is often either too coarse to be useful for detailed mechanistic studies, or the land-cover categories are not recognised in sufficient detail. Without a common standard for how to categorise land-cover, comparisons across space and time becomes increasingly difficult. As demonstrated in **paper III**, if the classification scheme within a limited area changes over time, temporal studies are complicated as well. Thus, digital biogeographical studies cannot replace local, field studies with classification of the habitats done in real time.

Unfortunately, detailed knowledge on land-cover and related variables cannot be created retroactively, but future efforts should be made to ensure available, high-quality land-cover data, preferably adhering to a common standard to aid future research. Currently, a god candidate for future tracking of land-cover and land-cover changes is the Sentinel-2 satellites; the images have already been used in various ecological studies (European Space Agency 2021, Murayama and Ranagalage 2020).

The crux

The four papers included in this thesis tie together to advance the field of urban ecology by multiple strands (Figure 5): the assessment of GBIF data quality and bias in **paper I** lays the foundation for the use of GBIF data in the remaining papers by illustrating the general abundance of available data in urban- and anthropogenic habitats. It further connects with **paper II** by illustrating the importance of examining groups of conservation concern separately. The main contribution to the field of urban ecology by this particular study is the demonstration of the usefulness of compiled GBIF data for urban studies, if appropriate measures are taken to account for taxonomic- and temporal variation in sampling effort. **Paper II**, **III** and **IV** jointly illustrate the varying responses to land-cover and land-cover change displayed by different taxa, groups of conservation concern, and functional groups. In particular, the responses to urban areas and urbanisation are highlighted. These papers thus underline how urbanisation functions as an ecological filter. The main contribution to the field is the indication that the filtering effect of urbanisation is evident across taxa and consistent across spatial resolutions, confirming the generality of the concept. **Paper IV** show how increasing land-cover change (i.e. urbanisation) will likely cause impoverishment local avifauna, which in turn might signal biotic homogenisation over large scales. Thus, the papers included in this thesis jointly emphasise the importance of minimising pressure on- and urbanisation of non-anthropogenic habitats, if a management goal is to favour native biodiversity.

The collective findings of the included papers advance the field of urban ecology by showing how land-cover data, as categorised and classified by management institutions, relate to biodiversity, and how urbanisation functions as an ecological filter in a broad sense. Simultaneously, new questions and directions for future research

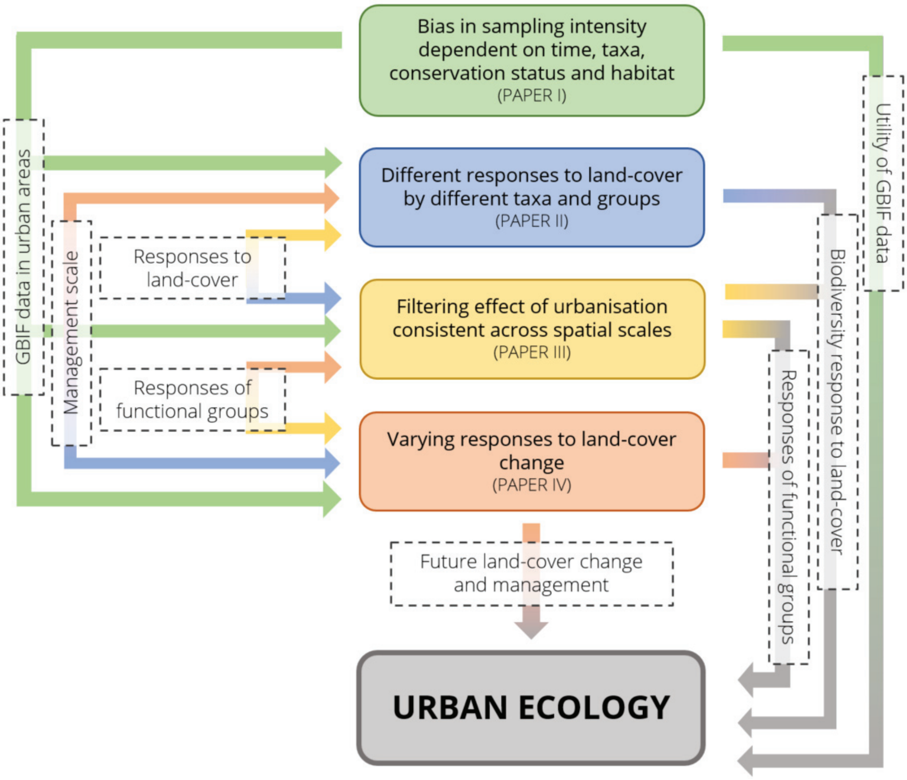

Figure 5. Synthetic diagram illustrating how the four papers included in the thesis tie together, and how they relate to and advance the field of urban ecology in general. The individual papers and their respective main themes and results relevant to the broader scope are indicated by the coloured boxes. The coloured arrows on the left-hand side of the diagram illustrate how the papers are connected, the coloured/grey arrows on the right-hand side of the diagram illustrate how they relate to urban ecology (grey box). Detailed descriptions of the connections and contributions can be found in the main text

within urban ecology arise; whether the results are repeatable over multiple spatial scales and -resolutions warrants further investigation. This includes both fine-scale, mechanistic studies to investigate local drivers, and national- to global scale studies to elucidate the general patterns. Further refinement of the models, including (but not limited to) climatic factors and soil properties, could disentangle biodiversity dynamics even further (McDonnell and Hahs 2013). As pointed out by McDonnell and Hahs (2013), urban ecologists need to translate the questions asked by practitioners (such as "How much urban green space is needed to to support biodiversity?"), into ecologically relevant questions (such as: "What are the ecological processes determining population viability and what are the attributes of green spaces that drive these processes?").

To include the important temporal aspects evident in urban ecology, the field would benefit from long-term experiments, rather than the use of opportunistic data, as pointed out by Ramalho and Hobbs (2012). Additionally, a greater integration with evolutionary ecology to answer how urbanisation affects selection processes, as pointed out by Rivkin et al. (2019), warrants attention. To handle the shifting biases in species occurrence records, additional work on how to dynamically account for these issues is necessary.

Conclusions

In recent years, Trondheim has experienced increasing urbanisation, illustrated by an increase in built-up area, similar to what is seen on both a national- and global level. The available open-source species occurrence datasets available for Norway and Trondheim are greatly skewed in their taxonomic representation, with an overabundance of birds in particular. The sharp increase in yearly number of records is mainly driven by an increase in the number of volunteer citizen science records. Likewise, the numbers of available records are skewed between groups of conservation concern, with a seemingly greater motivation to report red-listed species compared to alien ones. Geographically, anthropogenic land-covers have many more records than would be expected by chance, whereas the opposite is true for remote areas. To bridge the knowledge-gaps, future sampling should be directed towards less sampled areas and for infrequently investigated taxa. Along the same lines, further work on how to account for inherent bias in such opportunistic data is needed.

Land-cover and related environmental variables determine the distribution- and number of species in an urban-rural context, but different taxa and groups of conservation concern do not respond similarly to the same variables. A greater number of threatened species are found in habitats relatively unaffected by humans, whereas alien species are mainly determined by the location of their initial introduction. On a more mechanistic level, the observed responses of plants along an urbanisation gradient indicate that increasing urbanisation favours species adhering to a disturbance-tolerant, resource-acquisitive life strategy, compared to a more stress-tolerant, conservative strategy seen among plant species characteristic of non-urban areas. In a similar fashion, the probability of bird species either disappearing from or appearing within an area over time depends on the degree of land-cover change, with birds from different functional groups responding contrastingly: granivores, generalists and species associated with urban- and open areas respond positively to increasing land-cover change, whereas the opposite is true for forest- and wetland specialists. However, the overall probabilities for species disappearance are far higher than the probability of colonisation by new species.

Recommendations for future biodiversity management in Trondheim, in the light of continued urban expansion, are to minimise the conversion of vulnerable habitat as much as possible, and to monitor urban areas closely to mitigate the introduction and spread of alien species.

Synthesis and future perspectives

This thesis have documented how the diversity of species, including the diversity within threatened and alien ones, depends on current land-cover and -use, and how land-use history (i.e. changes in land-cover over time) affects the functional composition of biological communities on a municipality scale. Despite the growing availability of species occurrence data, great care must be taken to ensure data quality, and to counteract inherent skews and biases within the compiled data available through open data portals. Despite the contributions from this thesis to the collective knowledge of biodiversity dynamics in urban areas, further studies are still warranted.

Paper I illustrated aspects of the potential issues with using compiled species occurrence records from open databases, due to inherent differences in scope and sampling effort. With the increasing use of such data (Powney and Isaac 2015), new and robust methods to account for these differences would advance multiple research fields. As high-quality data is evidently a constant obstacle to overcome, further efforts to make biodiversity data available are encouraged. Fortunately, a general paradigm of openness regarding data sharing and reuse is forming within the ecological communities (August et al. 2015), an example of these efforts being the Living Norway Ecological Data Network (2020):

> "*(…) a joint effort to promote management of ecological data from Norwegian research institutions in agreement with FAIR principles.*"

The FAIR principles refer to the efforts of making data "*F*indable, *A*ccessible, *I*nteroperable and *R*eusable" (Wilkinson et al. 2016). This thesis (in particular **paper I**) underlined great variation in data availability over time, and thus emphasises the concerns raised by Dornelas et al. (2018, 2013) and Magurran et al. (2019): time-series data are lacking, despite it being of crucial importance to elucidate how the planet's ecosystem are responding to anthropogenic pressures. Due to the unfortunate uni-directionality of time, we cannot start time-series surveys retroactively, but will have to make the best of what imperfect data we have available (Dornelas et al. 2013). A relatively small fraction of the world's biocollections are currently digitised (and thus available for reuse) (Ball-Damerow et al. 2019) – it can therefore be advocated that effort be put into digitising specimens from e.g. herbaria and museums (both physical specimens and observational records), and making them more easily available to the ecological research communities.

As already pointed out, further development of (statistical) tools for accounting for differences in sampling effort, whether that be taxonomically, temporally or spatially, is a front worth venturing.

As for local management practices, **paper II** and **paper IV** illustrated how, in broad terms, biodiversity will be affected by further urbanisation. The results presented in this thesis suggest that to favour the diversity of native and/or threatened species, and to prevent a potential impoverishment of local biological communities, the grand themes should be to limit further anthropogenic pressure, particularly when this happens at the cost of vulnerable habitat types. Specifically, **paper II** identified coastal areas (i.e. ecotones) and mires to be of prime importance for the local biodiversity of Trondheim; thus on a local management level, such areas should be prioritised. To mitigate the spread of alien species, the main tool is to prevent introductions in the first place (Skarpaas and Økland 2009). Hampering urban sprawl while at the same time accommodating human welfare will be a challenging, but essential and interesting field in the future.

The Fifteenth meeting of the Conference of the Parties to the Convention on Biological Diversity is currently in preparation (CBD 2021); these preparations are done in the light of the unfulfilled Aichi Biodiversity Targets and SDGs. This includes the development of a "Post-2020 Global Biodiversity Framework" – this framework builds on the Strategic Plan for Biodiversity 2011-2020, and will be the successor of this and the Aichi Targets (CBD 2020). According to the zero draft of the Post-2020 Global Biodiversity Framework, the action targets in this framework includes specifically:

> "*Target 11. By 2030, increase benefits from biodiversity and green/blue spaces for*

> *human health and well-being, including the proportion of people with access to such spaces by at least [100%], especially for urban dwellers.*"

In this target, the importance of biodiversity for human health and well-being is articulated; if the access to green/blue spaces are to be increased, especially for urban dwellers, the immediate interpretation is that these spaces should be located within city boundaries[4]. Thus, as biodiversity in cities is a UN target in itself, understanding the dynamics of urban biological communities becomes essential, and especially how these dynamics relate to human welfare (CBD 2020).

Urban ecology is still a relatively young field, and its scopes and paradigms need to be refined. A shift from studies of "ecology *in* cities" to "ecology *of* cities"[5] is slowly emerging (McDonnell and Hahs 2008), but the paradigm of humans as external to ecosystems is still widely prevalent. Either time must pass for this shift to happen, or an in-depth discussion of under which circumstances either view is appropriate is warranted. Repeating the statement made by McDonnell & Hahs (2013), the questions asked by managers and decision-makers might not match the ones asked by researchers; the former likely asking questions regarding day-to-day decisions. These aspects should be incorporated into urban ecological research, and we should aim at making it possible to translate practical questions into ecologically relevant research questions, and *vice versa*, to aid in evidence-based conservation and biodiversity management. Along those lines, it is worth venturing into more detailed predictors and response variables; rather than focussing on aggregate measures

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[4] In addition, the terms "green/blue spaces" and "green/blue infrastructure" are most frequently used in connection with urban structures and areas (IPBES 2019). The urban aspect of this target is thus implicit.

[5] As described by Grimm et al. (2000) and Pickett et al. (2008): ecology *in* in the city focusses on the physical environment, frequently taking a case study approach addressing questions akin to "how do ecological patterns and processes differ in vs. outside city boundaries?". Ecology *of* cities represent a more holistic framework, treating entire cities as ecosystems in themselves, thus often incorporating multiple disciplines; human activities are in this framework not considered as external disturbances to an ecosystem, but as an important driver within the system.

(such as species richness), both site-specific and large-scale studies of mechanistic relationships and processes (e.g. fecundity and recruitment success) could provide direct, useful answers to management questions and concerns (McDonnell and Hahs 2008, 2013).

It is clear that the future of urban ecology must take even more advantage of its already multifaceted nature. Close collaborations between multiple disciplines and stakeholders are necessary to accommodate the needs of both humans and other organisms (Kaye et al. 2006). Specifically, in addition to ecologists, also actors from social sciences are needed to further understand how nature and society interacts, and thus shed light on the potential problems and synergies (Folke et al. 2016). City planners are needed to put the conclusions of academics into a real-world context. Such involvement of multiple fields has been described as both "multidisciplinary", "interdisciplinary" and "transdisciplinary, but no clear definition of these expressions exist, and they are frequently used interchangeably (Figure 6) (Choi and Pak 2006, Jahn et al. 2012, von Wehrden et al. 2019), and are defined with various levels of complexity (Max-Neef 2005). However, attempts at disentangling the concepts are provided by e.g. Choi and Pak (2006) and Jahn

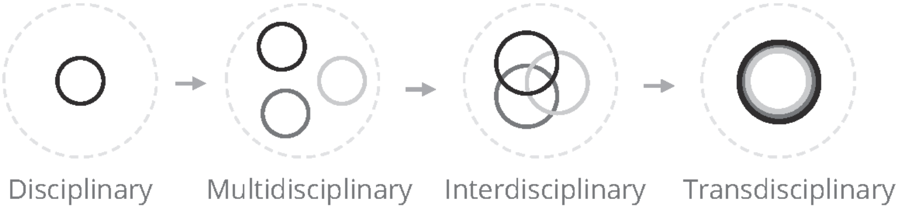

Figure 6. Visualisation of the (simplified) relations between different disciplines in different disciplinary frameworks. In a multidisciplinary approach, the individual fields operate individually, working within the boundaries of the field. In an interdisciplinary framework, the disciplines share knowledge and methodologies, creating synergies and blurring the boundaries; the individual fields are however still recognisable. In a transdisciplinary framework, the collaborations transcend the disciplinary boundaries, forming a new, holistic field. Examples of potential fields relevant to the envisioned field of "*Ecology of cities*" can be ecology, sociology and economy.

et al. (2012), and a version of these interpretations will be the definitions used here: “multidisciplinary” is an interplay and collaboration between disciplines, but each one stays and operates within the boundaries of the respective field. “Interdisciplinary” refers to a synthesis of multiple disciplines in which a transfer of knowledge and methodology happens between fields, blurring the boundaries. “Transdisciplinary” indicates a holistic framework in which both scientists and stakeholders transcend the boundaries between disciplines and operates in a new, unified field (Choi and Pak 2006) (Figure 6). Despite the fact that transdisciplinarity has been a known concept for a long time (Jahn et al. 2012), practical appliance is still rare (Angelstam et al. 2013). To fully achieve sustainable city development in the future, urban ecology needs to move from multi- and interdisciplinary research and management, to a fully transdisciplinary field.

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Paper I

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Species data for understanding biodiversity dynamics: The What, Where and When of species occurrence data collection.

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Alien species; Citizen science; GBIF; Land cover; Museum collections; Sampling bias; Threatened species

Abstract

1. The availability and quantity of observational species occurrence records have greatly increased due to technological advancements and the rise of online portals, such as the Global Biodiversity Information Facility (GBIF), coalescing occurrence records from multiple datasets. It is well-established that such records are biased in time, space and taxonomy, but whether these datasets differ in relation to origin has not been assessed. If biases are specific to different types of datasets, and the relative contribution from these datasets have changed over time, these shifting biases would have implications for interpretations of results, and consequentially for management and conservation measures.

2. We examined observational GBIF records from Norway to test potential differences in taxonomic-, time-, and land-cover biases between ten different datasets, with a focus on red-listed and non-native species.
3. The datasets differ in their taxonomic coverage, with datasets dominated by citizen scientist recorders focusing greatly on birds. The number of records has increased over time, in particular, citizen science datasets have had a sharp increase in recent years.
4. The different datasets (including division of the datasets by conservation status) showed differences in geographical coverage. Anthropogenic land-covers have more records than would be expected by chance in the majority of cases. Remote areas have fewer records than would be expected, underlining the prevalence of a roadside bias.
5. Accounting for biases in opportunistic species occurrence records need to be a dynamic- rather than static process, as the taxonomic- and geographical biases have changed over time, and differ between datasets, depending on origin and inherent characteristics. Data-collection programmes should be designed to counteract the biases of the specific datasets, and methods to account for the biases in existing data should be developed. When utilising compiled, open-source data, care must be taken to ensure complementarity between the datasets, both regarding time and space. Incorporating strengths and accounting for biases between datasets can strengthen the integration between species occurrence records with different origins for science-policy impact and management.

Introduction

The amount and availability of data on species occurrences have increased tremendously in recent years (Gaiji *et al.*, 2013), as have their use in applied conservation and biodiversity management (Powney and Isaac, 2015). Registering species occurrences have become far easier than in the early days of biogeographical surveys due to technological advancements, and can be done with the help of volunteer amateurs ("citizen scientists") (Boakes *et al.*, 2016). Online portals, e.g. the Global Biodiversity Information Facility (GBIF) (GBIF.org, 2019a), have further increased the public availability and interest (Amano *et al.*, 2016). These portals gather data from various sources, ranging from digitised natural history collections to observations made by citizen scientists. Thus, these records are a mixture of data on preserved specimens and observational records from both structured surveys and opportunistic sightings (Speed *et al.*, 2018). Volunteers participating in citizen science programs (or autonomously reporting species occurrences) likely have different motivations for reporting than do institutional recorders registering species according to a specified aim, covering both intrinsic and extrinsic factors. For participants in citizen science programs, the most important motivational factors have been reported as a personal connection, interest and concern for nature, a wish to contribute to science and (biodiversity- and nature-) conservation, and the value/usefulness of their contributions (Ganzevoort *et al.*, 2017; Tiago *et al.*, 2017; Larson *et al.*, 2020).

These mixed datasets thus suffer from various biases and errors due to their diverse origins and underlying motivations (Newbold, 2010). A frequently recognised bias for occurrence records is the "roadside" bias; observations are reported more frequently short distances from roads and paths, due to easier accessibility (Kadmon *et al.*, 2004; Tye *et al.*, 2017). The term can be expanded to include areas near densely populated areas (Luck, 2007; Robinson *et al.*, 2018). Concern has been raised repeatedly over this bias, especially if sampled areas cover significantly different environmental conditions than do un-sampled areas (Phillips *et al.*, 2009; Bystriakova *et al.*, 2012; Speed *et al.*, 2018). This potentially leads to faulty conclusions regarding biodiversity patterns (Kramer-Schadt *et al.*, 2013). More importantly, if such potential biases are not similar among data providers (e.g., datasets mainly consisting of purely opportunistic citizen science records vs. datasets from structured, targeted institutional surveys), conclusions can differ depending on the proportional contribution from the different datatypes (Tye *et al.*, 2017). Even more so, if this relative contribution from various types of datasets has changed over time.

In terms of biodiversity management, attention is frequently focused on specific taxonomic groups or on species of conservation concern (e.g. red-listed and alien species). However, different data providers might prioritise differently regarding taxonomic groups, and species' management status (red-listed vs. alien). Citizen scientists can be biased towards charismatic, easily recognisable taxa (Amano *et al.*, 2016), and have a greater incentive to report red-listed and rare species (Tulloch, Mustin, *et al.*, 2013). Speed *et al.* (2018) showed that observational plant records and preserved specimens have different biases regarding taxonomic coverage, time and space, and hypothesised that these differences can be translated somewhat to whether the data originate from structured surveys or opportunistic records, thus illustrating some of the potential issues with these mixed datasets. Note however, the distinction between observation- and specimen records is not equivalent to the distinction between citizen science- and institutional records; vegetation plot data will be registered as observations and some specimens in natural history collections are supplied by citizens (Miller-Rushing *et al.*, 2012; NTNU University Museum, 2018). Geldmann *et al.* (2016) showed that spatial bias in citizen science records, depended on the sampling scheme, distance to roads, and the human population density.

Understanding spatio-temporal dynamics of biodiversity is paramount to achieve sustainable management of biodiversity issues, e.g. red-listed- and alien species; for example, there is a general lack of understanding on how land-use, a main but complex driver, affects biodiversity change, as detailed data on species occurrences associated with different land-use types often are limited. Fine-grain data on species distributions and -associations from local- to global spatial scales, and over long time periods are required – a task virtually impossible to achieve through targeted surveys alone (Bonney *et al.*, 2009; Dickinson *et al.*, 2010; Theobald *et al.*, 2015). Opportunistic citizen science records are frequently used as a data source for e.g. Species Distribution Modelling (SDM) (Jetz *et al.*, 2012; Beck *et al.*, 2014), which can be used in decision-making for managing red-listed- and alien species (Thuiller *et al.*, 2005; Guisan *et al.*, 2013; Syfert *et al.*, 2014). As these models are sensitive to bias in the data (Yañez-Arenas *et al.*, 2014), methods to account for varying forms of bias in SDM's are still being explored (e.g. Kramer-Schadt *et al.* (2013), Dorazio (2014) and Robinson *et al.* (2018)). A general caveat of using GBIF records in SDM is that only few of datasets report species absences, thus requiring the use of presence-only modelling.

If the inherent biases differ markedly between datasets collected through institutional surveys, as citizen science, or as a mixture of the two, and the proportional contribution from these groups has changed over time, this raises the additional issue of how to deal with shifting biases, rather than simply static ones.

To our knowledge, limited attention has been given to whether taxonomic-, temporal- and geographical sampling biases are similar for datasets with varying origins (i.e. predominantly from citizen science programs or institutionally organised surveys), and whether these different datasets complement or amplify each other's biases. The same holds for records of conservation concern within these datasets (but see Beck *et al.* (2014) for a comparison of GBIF- original source data, Tye *et al.* (2017) for comparison of SDMs based on citizen science- or institutional observation records, Troudet *et al.* (2017) for an assessment of taxonomic bias in GBIF records, and Speed *et al.* (2018) for comparison of spatial-, environmental-, temporal-, and taxonomic coverage of observational records vs. preserved specimens). Awareness of such differences can elucidate how such mixed datasets should be utilised in the future to ensure complementarity, and what biases to account for. Specifically, it will provide guidance to (1) what geographical areas, taxonomic- and conservation groups should be targeted to balance sampling effort (and by whom); (2) whether certain datasets (with specified origins and characteristics) are representative of all collected data, and if not: (3) how to ensure complementarity between datasets to obtain maximum coverage.

In this study, we aim to test the ten datasets with the most records within the study region from GBIF, detailing their differences and biases in taxonomy, time and land-cover associations, and relating these to the various origins and characteristics of the datasets. The datasets range from “pure” opportunistic citizen science records, to observations from structured, targeted surveys by scientific institutions. To relate the results to biodiversity management, focus will be put on red-listed and alien species.

We hypothesise the following:

H1: The distribution of records between the three main kingdoms (H1a) and alien- vs. red-listed species (H1b) differ between the datasets; also within the datasets not explicitly focussing on a particular taxonomic group.

H2: There has been an increase in the number of records over time, primarily reflecting an increase in the activity of Citizen Scientists.

H3: The different datasets will be unevenly distributed among different land-cover types, with areas heavily influenced by humans (e.g. urban areas and agricultural land; areas classified as “Developed area” and “Cultivated” in Table S.1 (Fig. 1, Fig. S.1)) sampled more than would be expected by random chance; this oversampling is expected to be greater for datasets primarily consisting of Citizen Science records than for more targeted datasets.

Materials and methods

Land-cover and species occurrence records

The study was limited to Norway (Fig. 1). This is a well-surveyed region regarding species occurrence records in GBIF (Chandler *et al.*, 2017), covering great variation in land-cover, climate, human population density, and with detailed land-cover data available (Statistics Norway, 2020).

Land-cover was based on the Norwegian AR50 maps from NIBIO (Norwegian Institute of Bioeconomy Research, 2019), downloaded through Geonorge (2019). Land-cover is categorised based on land- and tree cover type, timber productivity and soil condition (Supporting Information S.1, Table S.1, Fig. S.1). Areas smaller than 1.5 ha are not visible in the dataset. The AR50 data were last updated in year 2016.

All georeferenced records of all taxa (regardless of taxonomic level) within Norway were downloaded from GBIF on 19.11.2019 (GBIF.org, 2019b). The full dataset consisted of 31 091 434 species occurrence records. Of these, 23 586 634 belonged to the kingdom Animalia, 1 275 533 belonged to Fungi, 5 872 214 belonged to Plantae, 283 924 belonged to Archaea, Bacteria, Chromista or Protozoa, 46 were viruses, and 73 083 had no reported kingdom or were *incertae sedis*. The records ranged temporally from 1686 to 2019.

The following criteria were used for improving the dataset quality and -comparability: (1) Records with the occurrence status “`absent`” were removed, as very few of the dominant datasets included information on absences. Thus, including absence records would reduce the comparability of the datasets; (2) records with no registered species-level information were removed to standardise the taxonomic resolution of the datasets; (3) potential duplicate records for species, date, basis of record, coordinates and coordinate uncertainty were removed, as there is no guarantee that the same records have not been registered multiple times by different data providers; (4) records from later than 31.12.2018 were removed, thus only including full sampling years. This was done in consideration of the temporal analyses; (5) only records classified as “`HUMAN_OBSERVATION`” were retained; as the distribution of data types differed greatly between datasets, only comparing data within a single basis of record increased the comparability among datasets. Only records from the kingdoms Animalia, Plantae and Fungi were retained. For the comparison of different datasets, the analyses were limited to datasets including >50,000 records. The final dataset for analyses consisted of 10 datasets holding a total of 7,560,590 records (Table 1, see Supporting

Information S.2, Table S.2 for detailed descriptions of the individual datasets). Most species were only observed sporadically (Supporting Information S.3, Figs. S.2-S.3). The ten datasets were not evenly distributed across Norway, neither individually nor in unison. However, as part of the aim of the study was to assess skews in geographical distribution, this was not considered an issue.

The datasets included in the analyses differ in origin and in several characteristics, including (but not limited to) taxonomic focus, methodology, number- and skill level of the reporters. Two of the datasets can be regarded as "pure" citizen science datasets (NBIC_{CS}: Citizen science species observations from the Species Observation Service in Norway (The Norwegian Biodiversity Information Centre and Hoem, 2020b). eBird: citizen science records of birds (Levatich and Padilla, 2019)). Five datasets originated from museums and/or universities (KMN: vascular plant registrations from the Agder Museum of Natural History and Botanical Garden (Åsen, 2019). NTNU: vascular plant registrations according to standardised cross-lists (NTNU University Museum, 2020). $\text{UiO}_{\text{Lichen}}$: lichen registrations from the University of Oslo Natural History Museum (Natural History Museum, 2020). $\text{UiO}_{\text{Plant Obs}}$: vascular plant registrations (observational records) (Natural History Museum, 2019b). $\text{UiO}_{\text{Plant Notes}}$: vascular plant registrations (field notes) (Natural History Museum, 2019a)), and can be regarded to cover somewhat structured surveys and observations by institutional recorders. Two datasets stemmed from a private consultant and –organisation (Jordal: consultant within biology and management (Jordal, 2019) and BioFokus: non-profit organisation providing survey information (Blindheim, 2020)), which both provide biodiversity survey information for decision makers, and can thus be regarded as mainly structured surveys and observations done by institutional recorders. Likewise, the final dataset ($\text{NBIC}_{\text{Other}}$) included datasets and databases from providers not hosting their own GBIF Integrated Publishing Toolkit (IPT) services, such as the Norwegian Environmental Agency – these are likewise regarded as mainly structured, institutional surveys. Data from NBIC are quality controlled internally: the data owner is responsible for the quality of the data. Dubious records are validated by experts, and the data owner is asked to provide evidence (e.g. photos) of the record. If these cannot be provided, the record is deleted (Norwegian Biodiversity Information Centre, 2018; Norwegian Species Observation Service, 2020).

The latest Norwegian Red List of Species was finalised in 2015, 10 years after the first national assessment. The list includes species evaluated as being at risk of extinction in Norway, if conditions remain unchanged. The classification follows the same criteria as the IUCN Red List (Henriksen and Hilmo, 2015). In total, ≈4,500 species are currently red-listed; of these are ≈2,550 animals (mainly invertebrates), ≈750 plants and ≈1,200 fungi. The first version of the Alien Species List was compiled in 2007 (Gederaas *et al.*, 2012), and the latest version was refined and published in 2018 (Sandvik *et al.*, 2017; The Norwegian Biodiversity Information Centre, 2018b). In total, ≈3,000 species are listed as alien to mainland Norway, ≈1,500 of these have a risk assessment. Of these, ≈390 are animals, ≈990 are plants and ≈100 are fungi. As per the guidelines published by the Norwegian Biodiversity Information Centre (Sandvik *et al.*, 2017), we here use the term "alien species" rather than the frequently used "invasive species". "Alien" refers to *"(…) a species introduced outside its natural past or present distribution."* (IUCN, 2020). The term "invasive" suggest invasion potential and negative ecological effects, which is not necessarily the case for all alien species. To avoid subjective decisions as to which alien species to classify as "invasive", all species classified as "alien" on the Alien Species List (Gederaas *et al.*, 2012) were included, and the term "alien" was used rather than "invasive".

Species names of the GBIF records were matched with the Norwegian Red List, and the Norwegian Alien Species List, using synonyms from the GBIF backbone taxonomy, using the package `'rgbif'` (Chamberlain and Boettiger, 2017). Species within the Red List categories "Regionally Extinct", "Critically Endangered", "Endangered", "Vulnerable", "Near Threatened" and "Data Deficient" are classified as "red-listed". As the majority of "Data

Deficient" species are potentially threatened (Bland *et al.*, 2015), and old records are included in the analyses, inclusion of the remaining Red List categories is warranted. Species alien to Svalbard, but native to mainland Norway were not listed as alien, neither were alien species which have not yet established, but are evaluated to have the potential to do so within 50 years (The Norwegian Biodiversity Information Centre, 2018)).

Maps and occurrence records were transformed to the geodetic coordinate reference system WGS84/UTM zone 32 (epsg: 32632).

Statistical analyses

Taxonomic differences within and between datasets were examined using X^2- tests (base package: `'stats'`), testing the null hypothesis of equal distribution of the kingdoms between and within the datasets. Likewise, the distribution of red-listed and alien species between the datasets was tested with a X^2-test.

To test for temporal patterns in the data, a Mann-Kendall test for a monotonic trend was applied (package:`'trend'` (Pohlert, 2020)). The median sampling year of the datasets were compared with a Kruskal-Wallis-test, followed by a posthoc pairwise Dunn-test with Bonferroni-correction for multiple comparisons (packages: `'stats'` and `'FSA'` (Ogle *et al.*, 2020)).

For examining geographical biases, the data were further reduced to match the timeframe of the land-cover data. Only data from year 2004 to (and including) year 2018 were used. Changes in land-cover are assumed to be minimal within this 15-year span. The remaining 5,622,260 records were overlaid on the AR50 map (package:`'sp'` (Pebesma and Bivand, 2005)). The null hypotheses was that the species occurrence records are randomly distributed across Norway, and the number of records is a function of the area of each land-cover type.

5,622,260 points were randomly overlaid on the map 100 times, giving ranges of expected number of points associated with each land-cover type. Dataset names and conservation status (“red-listed”-, and “alien”) were assigned randomly to the points in the same proportions as in the original data. Generalised Linear Models (Poisson error distribution, “`identity`” link function) (base package: `'stats'`) were fitted to the number of records predicted by area of each land-cover type for the simulated data, providing the null models; one separate model for each of the combinations of dataset and conservation status. Sampling bias was concluded if the observed number fell outside the 0.95 confidence interval of the model. To compare the extent of sampling bias for the different groups, the absolute- and relative residuals were calculated as:

$$Absolute\ residual = No.records_{observed} - No.\ records_{predicted}$$

and

$$Relative\ residual = \frac{Absolute\ residual}{mean(No.records_{observed}, No.\ records_{predicted})}.$$

To evaluate the differences in biodiversity patterns obtained using occurrence records from the different datasets, or all in combination, individual-based species accumulation curves were made for each dataset × conservation status group, and the asymptotic species richness calculated (package: `'iNEXT'` (Hsieh *et al.*, 2020)).

All data preparation and analyses were performed in R, version 3.6.1 (R Core Team, 2020). Maps were made in ArcMap version 10.6 (ESRI, 2018).

Results

Taxonomic differences

The number of records from each dataset differed *($X^2 = 26\ 019\ 773$, df = 9, p-value <0.001)* with the vast majority of the records belonging to the $NBIC_{CS}$ dataset, followed by the $UiO_{Plant\ Notes}$ (see Table 1 for description of dataset names). The kingdoms were not equally distributed between and within the datasets ($X^2 = 3\ 813\ 957$, $df = 18$, $p\text{-value} <0.001$). Obviously, the datasets with a specified taxonomic scope were dominated by records belonging to the particular kingdom, but the datasets including several kingdoms differed as well; the BioFokus- and NBIC$_{\text{CS}}$ datasets had an overabundance of animals and fungi, whereas the NBIC$_{\text{other}}$ dataset only had an overabundance of animal records. The Jordal dataset had an overabundance of plants and fungi (Fig. 2). Within the animal kingdom, birds was the most frequently recorded class, followed by insects and mammals overall. For the multi-taxa datasets, the distribution within the animal kingdom differed: the BioFokus datasets held most records of insects, followed by birds and mammals, the Jordal dataset was dominated by birds, followed by insects and bivalves, and the NBIC$_{\text{CS}}$- and NBIC$_{\text{Other}}$ datasets were dominated by records of birds, followed by insects and mammals (Fig. S.4). When accounting for the different sample sizes, the distribution of red-listed- and alien species differed between the datasets, with the BioFokus-,eBird-,NBIC$_{\text{CS}}$-,NBIC$_{\text{other}}$-, and UiO$_{\text{Lichen}}$ holding more red-listed-, and the KMN-, Jordal-, NTNU-, UiO$_{\text{Plant Nores}}$- and UiO$_{\text{Plant Obs}}$ datasets holding more alien species than what would be expected by random ($X^2 = 104\ 807$, $df = 9$, $p\text{-value} < 0.001$) (Fig. 2b).

Temporal differences

The Mann-Kendall test detected a tendency in the overall dataset; the number of records had increased over time ($z = 16.732$, $n = 200$, $p\text{-value} <0.001$) (Fig. 3a). Median year differed for all datasets, (medians: KMN = 1986, BioFokus = 2011, eBird = 2015, Jordal = 2007, NBIC$_{\text{CS}}$ = 2014, NBIC$_{\text{other}}$ = 2014, NTNU = 1985, UiO$_{\text{Lichen}}$ = 2000, UiO$_{\text{Plant Notes}}$ = 1961, UiO$_{\text{Plant Obs}}$ = 2009, Kruskal-Wallis = 496.44, $df = 9$, $p\text{-value} = <0.001$. $p\text{-value} < 0.001$ for all pairwise comparisons) (Fig. 3b).

Geographic differences

The simulated numbers of records within the groups (conservation status × dataset) were predicted by the area of the specified land cover type (Table 2, Fig. 4).

Each land-cover type was relatively over- or under-sampled for different datasets (the observed number of records fell outside of the 0.95 Confidence Interval of models based on the simulated data), except for Snow/ice, which was under-sampled by all datasets. The results are summarised in Table 3, and the full table can be seen in the Supporting Information S.6.

Models and results regarding datasets (regardless of conservation status) can be seen in the Supporting Information (Supporting Information S.5).

Comparing the absolute residuals between predicted and observed number of records within each land-cover type, the largest numerical discrepancies were seen for open firm ground, developed areas and cultivated land (Fig. 5a). However, comparing the relative residuals (disregarding un-mapped areas and snow/ice), only alien records associated with open firm ground showed a consistent pattern between datasets (under-sampling) (Fig. 5b).

Asymptotic species richness

The asymptotic species richness differed for most of the datasets (Supporting Information S.7). For both red-listed- and alien species, only the estimates for the NBIC_{CS} datasets (NBIC_{CS} red-listed = *2 412* (*C.I. = 2 333 – 2 513*), NBIC_{CS} alien = *867* (*C.I. = 833 - 920*)) overlapped with the estimates for all datasets combined (Combined red-listed = *2 550* (*C.I. = 2 469 – 2 654*), Combined alien = *861* (*C.I. = 836 - 902*)).

Discussion

Various forms of biases have been shown for the increasing amount of species data available from open databases, such as GBIF. However the potential taxonomic-, temporal-, and geographical biases differ between datasets according to the origin and characteristics of the datasets, and how these different datasets might complement each other, have not been addressed. Additionally, whether these biases extend to red-listed and alien species remain un-investigated. We found that multi-taxa datasets from GBIF are biased towards different kingdoms (supporting H1a). More records of red-listed species are registered than alien species; (supporting H1b). When categorising the records according to datasets and conservation status, the geographical biases differ between the datasets, with a few general patterns. Anthropogenic land-covers are generally oversampled (with a few exceptions), whereas less directly human-affected- and/or remote areas are under-sampled (somewhat supporting H3).

Differences in taxonomic groups and conservation status between datasets

The taxonomic bias within and between the datasets differ markedly, both in the sense that several of the datasets are concerned with a single taxonomic group, and in that the multi-taxa datasets are skewed towards a single group. The datasets originating from museums all focus on plants (except for $\text{UiO}_{\text{Lichen}}$; lichens are here classified as fungi). These patterns are reflected when comparing the multi-taxa datasets: the two datasets from the Norwegian Biodiversity Information Centre (NBIC) are both dominated by animal records, whereas the BioFokus and Jordal are both dominated by plants. Interestingly, only two out of the ten datasets can be regarded as citizen science, but yet they make up the bulk of the records. The dominance of birds within these datasets reflect the long-term popularity of ornithology (Devictor *et al.*, 2010), the incentive for people to report on charismatic, recognisable species, and that many citizen science programmes have focused on birds (Tulloch, Mustin, *et al.*, 2013). However, if the datasets dominated by citizen science records are not considered, the avian dominance is much less pronounced. This echoes the taxonomic differences observed by Troudet *et al.* (2017) and Speed *et al.* (2018). Theobald *et al.* (2015) found the taxonomic bias in citizen science- and institutional datasets to be consistent; however, they did see an overweight of respectively birds and plants in the two groups. This underlines the careful considerations which much be taken eventually when using citizen science in multi-taxa analyses – nevertheless, within popular taxa, citizen science records can be a useful supplement to institutional observations, as this allows for otherwise impossible sample sizes (Tulloch, Possingham, *et al.*, 2013; Powney and Isaac, 2015). Citizen science data on popular taxa have proven useful for discovering population trends, conservation and management (e.g. for birds: Lehikoinen *et al.* (2019) and examples in Sullivan *et al.* (2009)).

The datasets with more alien- than red-listed records were all datasets focused on vascular plants; for all other datasets, more red-listed- than alien records were registered. This illustrates that most species on the Alien Species List are plants (The Norwegian Biodiversity Information Centre, 2018). The dominance of red-listed- compared to alien species among half of the datasets, in particular in the datasets dominated by citizen science records (NBIC$_{\mathrm{CS}}$ and eBird) points to a greater interest for rarities among citizen scientists and a potential lack of interest or knowledge regarding alien species. Among the other datasets, the difference can be due to a traditionally larger focus on red-listed species, or that red-listed species are likely registered as observations (i.e. not destructively sampled) (NTNU University Museum, 2018), whereas alien species are potentially sampled as specimens to ensure validation later. The numerical difference between the conservation status groups can nevertheless be an artefact of the number of species in either status group: approximately three times as many species are on the Norwegian Red List compared to the Alien Species List (The Norwegian Biodiversity Information Centre, 2015, 2018).

Geographical biases

The most anthropogenic land-cover types have higher numbers of records than what would be expected for most, but not all groups. Developed areas were oversampled overall in all but three datasets (KMN, NTNU and Jordal); when focussing on either red-listed- or alien records, the same pattern emerges, with the exception of the Jordal dataset being oversampled and the UiO$_{\mathrm{Plant\ Obs}}$ being under-sampled for red-listed species. This pattern likely has multiple underlying causes: despite a general omission of cities in ecological history (reviewed by Salomon Cavin and Kull (2017)), the last decades have seen increased focus on urban ecology, especially on cities as centres of spread for alien species (Gaertner *et al.*, 2017). This has likely amplified the oversampling of alien species in urban areas. The oversampling of red-listed species are likely a combined effect of roadside bias and interest/prestige, as the oversampling is particularly large for datasets dominated by citizen science records.

Agricultural areas are similarly oversampled for most groups. This again reflects the roadside bias, as agricultural areas are generally found near developed areas (Fig. S.1), and thus have high accessibility. Grazing land is particularly oversampled, reflecting how such areas are regarded as of conservation concern, thus warranting attention from different recorders (Pärtel *et al.*, 2005).

The picture is highly nuanced regarding the different forest categories. The cases of oversampling may reflect that sampling tends to be done where high species richness is expected *a priori* (Boakes *et al.*, 2016), the high amount of woodland in Norway (>35%), and the high species richness of forests (≈60% of Norwegian species are associated with woodlands). The highest number and concentration of red-listed species are found in coniferous woodlands and broad-leaved deciduous woodland, respectively (Gjerde *et al.*, 2010), which is somewhat seen in the positive residuals of red-listed records from most datasets. Some of the datasets hold fewer red-listed records than expected for coniferous- (KMN, eBird, Jordal NBIC$_{\text{CS}}$ (red-listed), and UiO$_{\text{Plant Obs}}$) and deciduous (eBird, NBIC$_{\text{CS}}$ (red-listed), NTNU (red-listed), UiO$_{\text{Lichen}}$, and UiO$_{\text{Plant Obs}}$) forests. This discrepancy presumably stems from the taxonomical difference between the datasets: red-listed woodland species in Norway are mainly fungi, insects and lichens (Gjerde *et al.*, 2010; Henriksen and Hilmo, 2015), and the number of red-listed plants outnumber red-listed animals; according to the Norwegian Biodiversity Information Centre (2015), only 14 out of 82 red-listed birds are associated with forests. Both datasets mainly collected by citizen scientists are heavily dominated by (or exclusively consists of) birds, which are easier to observe in open areas. Unclassified forests have fewer records than predicted for almost all datasets, except NBIC$_{\text{Other}}$ and UiO$_{\text{Plant Obs}}$, reflecting that this forest type is found in more remote, inaccessible areas; these two datasets have likely targeted such areas specifically. The land-covers with fewer records than predicted for most of the datasets are characterised by being located in more remote and/or inaccessible areas, less directly affected by humans: snow/ice-covered areas, mires and open firm ground. In some instances, this reflects genuine low species richness and –abundance (discussed below), as is likely the case for "snow/ice" (having the largest relative residuals) and the most alpine cases of "open firm ground". However, some areas are likely under-sampled due to inaccessibility (e.g. mires), genuine difference in spatial- and taxonomic focus and interest of the datasets.

The discrepancies between predicted and observed number of records should be interpreted with caution. Some land-cover types are naturally more species poor than others. It can thus be expected that a lower number of records should be reported, than would be expected solely from area. This is the case of alpine areas; it is estimated that only ≈14% of the native vascular plants of Norway occur in mountains (Austrheim *et al.*, 2010). Alpine areas are here found within the land-cover types "Open firm ground" and "Snow/ice", both of which have fewer records than predicted by the null models. Consequently, parts of the differences between observations and predictions can be attributed to the null models not taking intrinsic differences in species richness and abundances into account. Nevertheless, as we were not modelling species richness, but number of records (a proxy of sampling effort), the main signals are mainly attributable to differences in sampling effort.

Dataset complementarity

The general quality of the data found in open databases, such as GBIF is a point worth general discussion. Various opinions on the matter exist (Newbold, 2010; Gaiji *et al.*, 2013; Powney and Isaac, 2015). The biases shown underlines how the individual datasets stored in GBIF are not all compiled with the intention of covering all taxa, periods or habitat. Thus, indiscriminately using such compiled datasets without accounting for the differences in sampling effort (whether this is spatial, temporal or taxonomic) will inevitably lead to flawed results. The differences in both taxonomic- and geographic focus of different datasets from open databases shown in this study raise the question on how to compile such datasets to ensure optimal coverage, and whether datasets with certain origin and characteristics are complementary. If multi-taxa management decisions are to be made based on analyses including e.g. GBIF data, several considerations must be taken into account.

1. Regarding taxonomic complementarity, it is clear that careful examination of the included datasets is necessary, as indiscriminate data use will result in taxonomic imbalances.

2. Likewise, as the temporal coverage of the datasets is highly variable, timespan of individual datasets should be considered in relation to the questions asked.

3. Considering the geographical dissimilarities between the datasets, it is evident that if conclusions regarding the importance of different land-cover types for species of conservation concern are drawn upon analyses of single datasets, contrasting results will follow.

4. The geographic coverage of the single datasets used in analyses should be investigated to ensure that certain areas are nor over- or under-represented.

The overarching theme of these points can be summarised as not to assume a greater quality and validity of the available data than what is warranted. Care must be taken as to not stretch the conclusions based on single datasets further than the extents of the individual datasets, geographically or taxonomically.

Integrating multiple datasets for understanding and managing biodiversity

Data availability thus remains the main challenge for understanding biodiversity patterns, and ultimately for how we manage biodiversity (Magurran *et al.*, 2019). This study has examined how different datasets, with different origins and characteristics, can complement each other in filling data availability gaps, specifically the gaps for three kingdoms (animals, plants and fungi), red-listed and alien species, and their distributions across land-covers and time.

Despite the emerging paradigm of data reuse and sharing among scientists, lack of data publishing is still an issue; only 10% of biocollections are estimated to be digitally available, including data used prior to recent changes in data publishing policies provided by funding agencies and journals (Ball-Damerow *et al.*, 2019). Traditionally, most collected data have been stored locally, and data not directly used in publications have remained unused and potentially forgotten with time (Osawa, 2019). This also leaves the worst case scenario that not all parts of datasets are published. Likewise, standardisation of biodiversity data among data providers is important to ensure interoperability (Poisot *et al.*, 2019). An attempt at this is to use the Darwin Core Archive format adopted by GBIF (Wieczorek *et al.*, 2012; Osawa, 2019). Despite these efforts, substantial quantities of primary biodiversity data (and metadata) remain undiscovered (Chavan and Penev, 2011). This leaves a gap in the foundation of biodiversity research. In the light of the results presented here, if the lack of data sharing is uneven among datasets with different origins, the gap is even more severe.

Open source, compiled biodiversity data have potential to be used for biodiversity modelling, if spatially biased sampling effort can be corrected for (Higa *et al.*, 2015). Unfortunately, a recent review found that only 69% of the examined papers addressed some aspect of data quality (Ball-Damerow *et al.*, 2019). Our results caution that careful considerations of the data used in such studies are needed; as the contribution from different datasets have changed over time, so has the geographical bias. Therefore, accounting for bias should be a dynamic process, dependent on timespan of the included data and the data contributors. If observational datasets of mixed origins are used indiscriminately, the reported spatio-temporal patterns could merely reflect spatio-temporal shifts in bias. Future surveys and citizen science programmes should aim to include otherwise neglected taxonomic groups, especially in under-sampled land-cover types, such as remote mountainous areas. In particular, non-avian animals are underrepresented compared to their actual abundance, and open firm ground and mires should be investigated more closely. Citizen science programmes focussing on non-avian taxa should be designed, learning from the success of previous programmes for e.g. birds (Sullivan *et al.*, 2009), butterflies (Butterfly Conservation, 2020), and bumblebees (Bumblebee Conservation Trust, 2019), and use their established frameworks. Both citizen scientists and institutional recorders should be encouraged to record observations in secluded areas, and to include observations of "less prestigious" species.

The quality of data from respectively institutional recorders and citizen scientists will vary immensely depending on methods and organism group. Whereas trained professionals likely exhibit greater skills regarding some of the more challenging groups, this is not necessarily the case for all taxa. If quality can be ensured, citizen scientists can provide otherwise impossible amounts of data to facilitate science-policy impact of the sustainable biodiversity management. This study has shown the different biases from different datasets, and illustrate some of the challenges with accounting for all of them in a single study.

Authors' contributions

TKP, GA, JDMS and VG conceived the idea and designed the methodology; TKP retrieved and analysed the data; TKP wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

All relevant data are available from public repository (GBIF Occurrence Download – 19.11.2019, doi: 10.15468/dl.dmdxne) (GBIF.org, 2019b).

Land-cover data are available through Kartkatalogen (Geonorge, 2019), and was downloaded on 23.11.2019.

All R code written to perform the data download- and analyses can be viewed and downloaded in a public repository: https://doi.org/10.5281/zenodo.4455460.

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Figures and tables

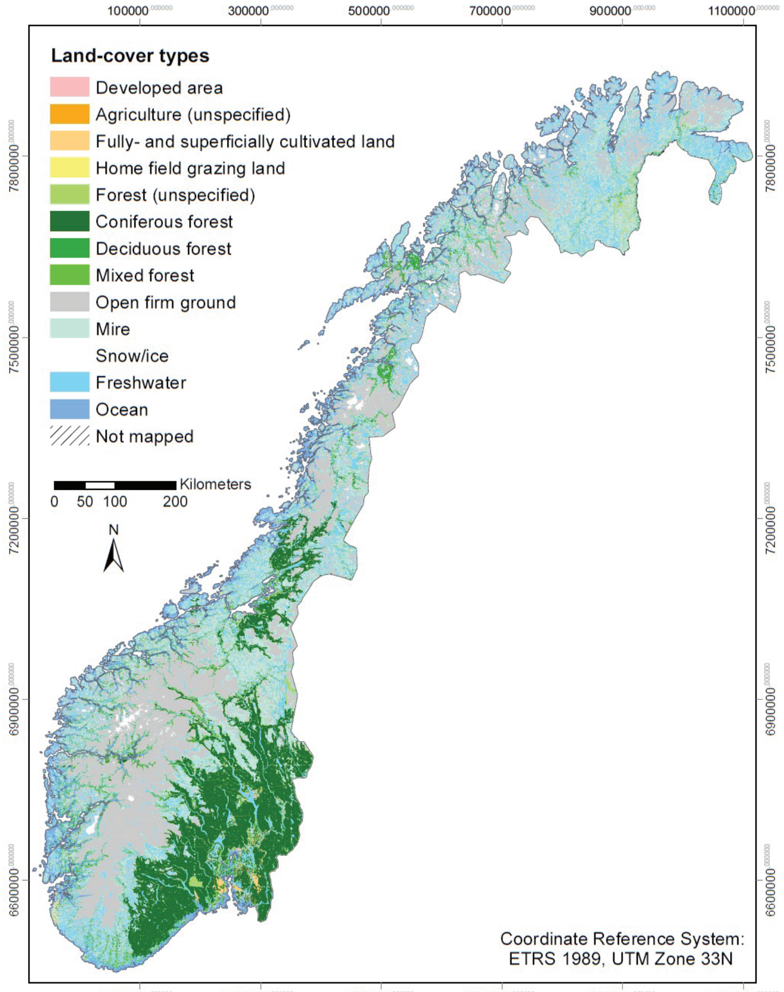

Figure 1. Map of Norway. Detailed maps of the individual land-cover types are shown in the Supporting Information S.1, Fig. S.1.

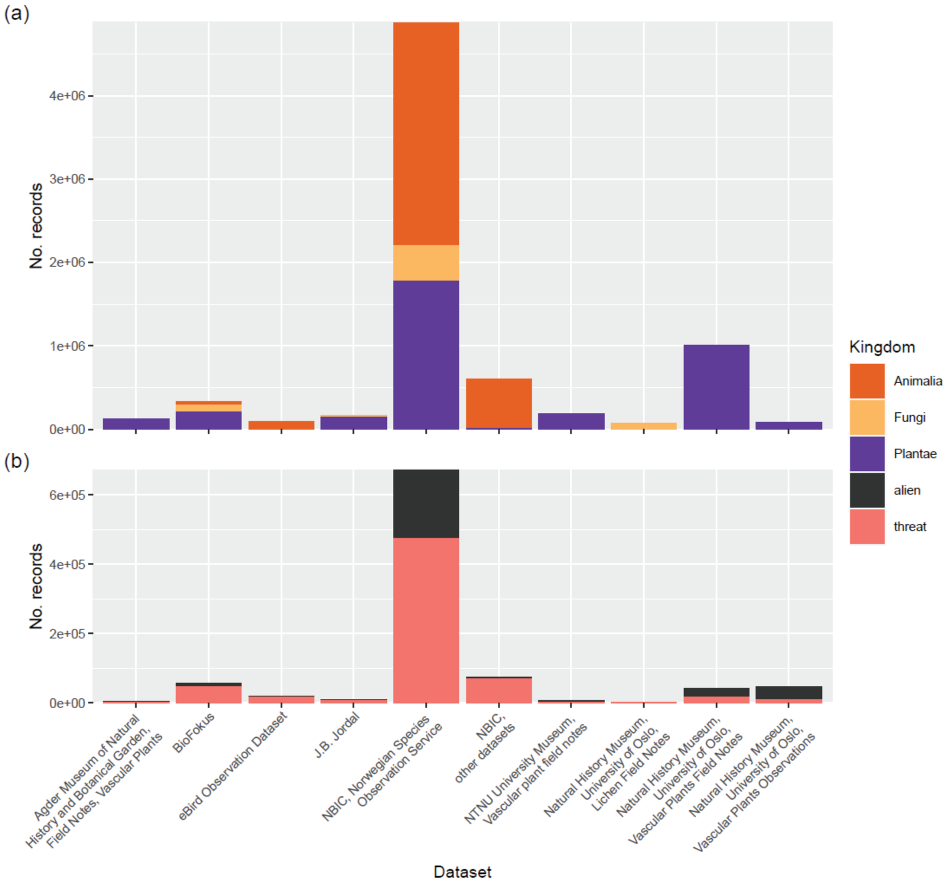

Figure 2. Number of records within each of the datasets used in the analyses. *(a)* Number of records from the included kingdoms in each dataset; *(b)* number of red-listed- or alien species records in each dataset. Note the differences in y-axis values due to species neither on the Red List nor the Alien Species List included in *(b)*.

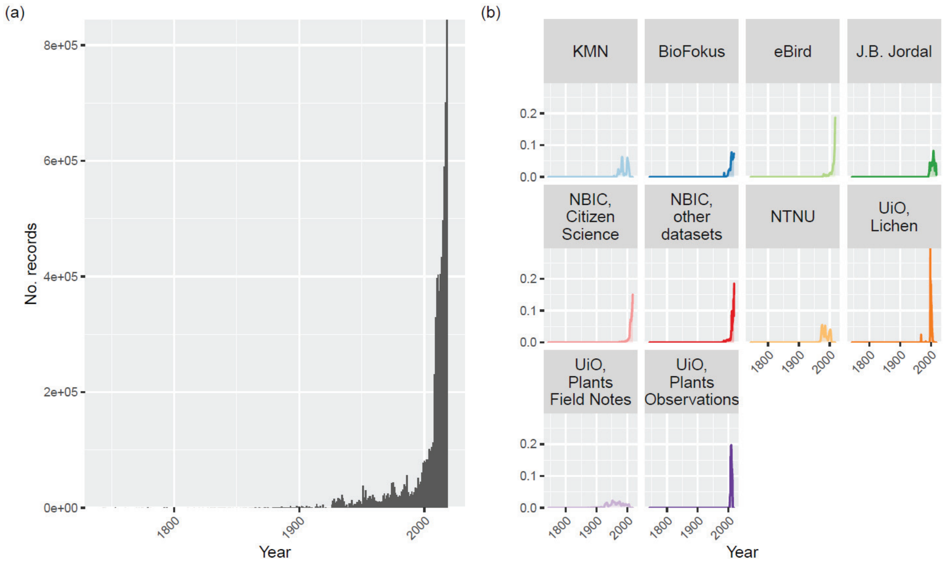

Figure 3. *(a)* Number of GBIF records across years in total. *(b)* Density plots of the number of records, divided by datasets. Note that the y-axis in *(b)* indicate proportion rather than absolute number. Acronyms refers to the datasets described in Table 1.

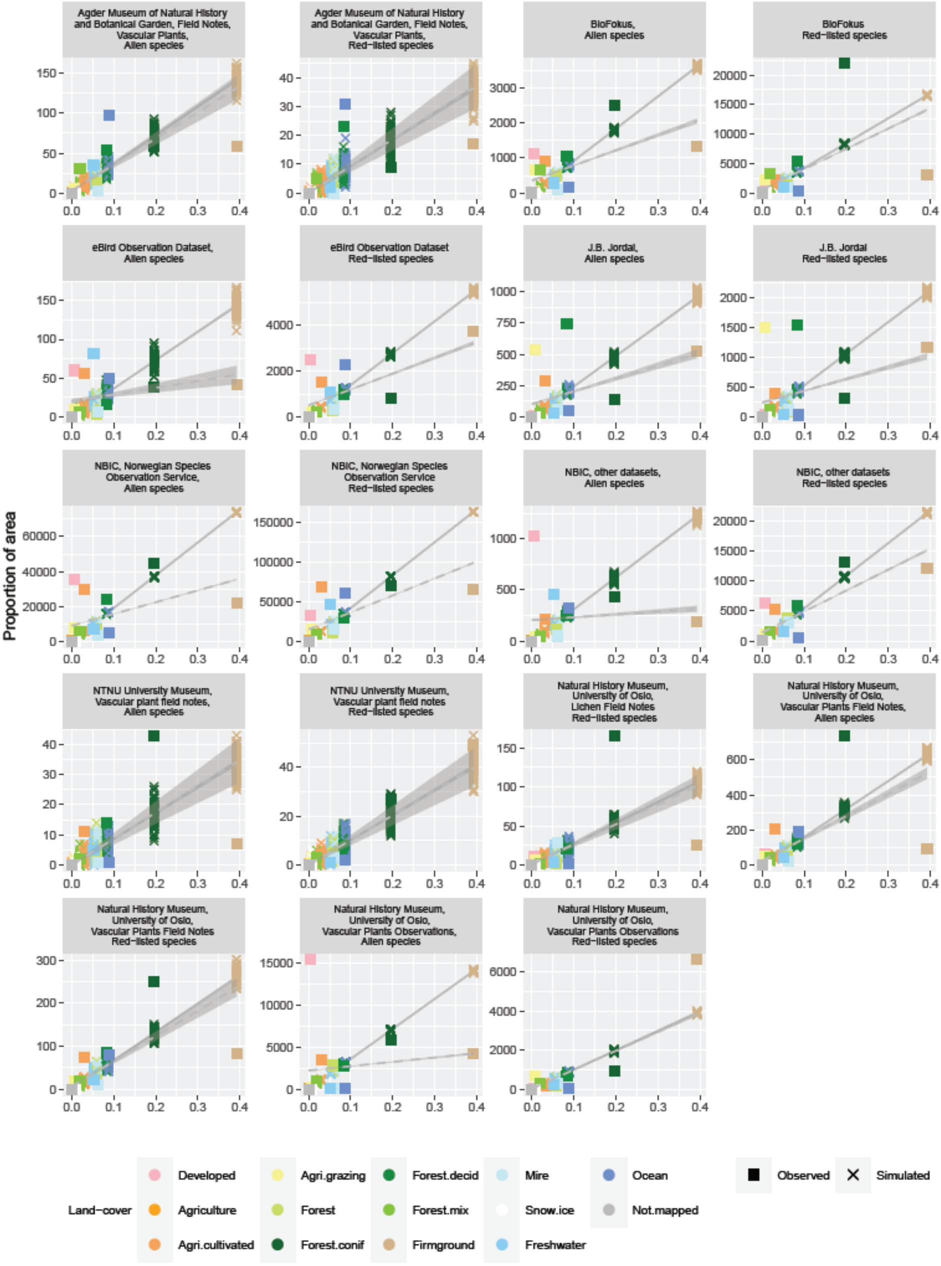
Agder Museum of Natural History and Botanical Garden, Field Notes, Vascular Plants, Alien species
Agder Museum of Natural History and Botanical Garden, Field Notes, Vascular Plants, Red−listed species
BioFokus, Alien species
BioFokus Red−listed species
eBird Observation Dataset, Alien species
eBird Observation Dataset Red−listed species
J.B. Jordal, Alien species
J.B. Jordal Red−listed species
NBIC, Norwegian Species Observation Service, Alien species
NBIC, Norwegian Species Observation Service Red−listed species
NBIC, other datasets, Alien species
NBIC, other datasets Red−listed species
NTNU University Museum, Vascular plant field notes, Alien species
NTNU University Museum, Vascular plant field notes Red−listed species
Natural History Museum, University of Oslo, Lichen Field Notes Red−listed species
Natural History Museum, University of Oslo, Vascular Plants Field Notes, Alien species
Natural History Museum, University of Oslo, Vascular Plants Field Notes Red−listed species
Natural History Museum, University of Oslo, Vascular Plants Observations, Alien species
Natural History Museum, University of Oslo, Vascular Plants Observations Red−listed species
Proportion of area
0.0
0.1
0.2
0.3
0.4
Land−cover
Developed
Agriculture
Agri.cultivated
Agri.grazing
Forest
Forest.conif
Forest.decid
Forest.mix
Firmground
Mire
Snow.ice
Freshwater
Ocean
Not.mapped
Observed
Simulated

Figure 4. Null models (GLM) of the number of records as a function of area (proportion of total area within Norway) for the simulated data (crosses), vs. the observed number of records for each land-cover type (squares). Solid lines indicate model predictions; gray ribbons indicate the 0.95 confidence interval. Dashed lines indicate regressions similar to the null-models fitted through the observed values.

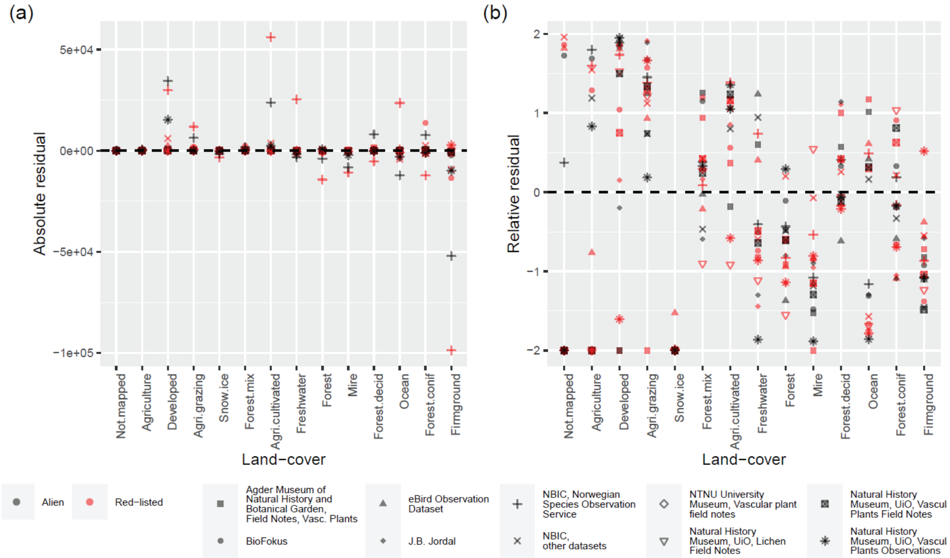

Figure 5. Differences between observed number of records within each land-cover type, and the number of records predicted by area. *(a)* Absolute residuals ($No.records_{observed} - No.\ records_{predicted}$); *(b)* relative residuals ($\frac{Absolute\ residual}{mean(No.records_{observed}\ ,No.\ records_{predicted}\ )}$). Colours indicate conservation status, shapes indicate dataset. The land-cover types are ordered increasingly with respect to area.

Table 1. Datasets included in the analyses. The datasets are displayed in descending order according to the total no. records. The description is simplified from the description and methodology as presented on the GBIF webpage. More detailed descriptions can be found in Supporting Information S.2., Table S.2.

Dataset Name **(abbreviation)**	**Publisher (reference)**	**# Animals** **# Plants** **# Fungi**	**Description**
Norwegian Species Observation Service, (NBIC$_{CS}$)	Norwegian Biodiversity Information Centre (The Norwegian Biodiversity Information Centre and Hoem, 2020b)	2 678 373 1 776 878 422 930	Citizen science species observations (Artsobservasjoner.no)
Vascular Plants, Field notes, Oslo (UiO$_{Plant\ Notes}$)	Natural History Museum, University of Oslo (Natural History Museum, 2019a)	0 1 006 937 0	Vascular Plants, Field notes from Norway
Norwegian Biodiversity Information Centre - Other datasets (NBIC$_{other}$)	Norwegian Biodiversity Information Centre (The Norwegian Biodiversity Information Centre and Hoem, 2020a)	585 898 17288 289	Other data providers sharing occurrence data via the Norwegian Species Map Service
BioFokus (BioFokus)		39 179 212 265	

	BioFokus (Blindheim, 2020)	82724	A non-profit organisation providing biodiversity survey information on biological diversity to decision makers and the public in Norway.
Vascular plant field notes, NTNU University Museum (NTNU)	NTNU University Museum (NTNU University Museum, 2020)	0 188 910 0	Vascular plant field notes, Norway, using standardised cross-lists. The dataset is a collection of observations made during various research projects at the NTNU University Museum
Jordal (Jordal)	Biolog J.B. Jordal AS (Jordal, 2019)	282 150 411 21 856	John Bjarne Jordal, sole proprietor. Consultant within biology and nature management)
Vascular Plants, Field notes, Agder naturmuseum (KMN) (KMN)	Agder Museum of Natural History and Botanical Garden (Åsen, 2019)	0 125 115 0	Vascular Plants, Field notes from Norway
EOD - eBird Observation Dataset (eBird)	Cornell Lab of Ornithology (Levatich and Padilla, 2019)	93 109 0 0	eBird: a collective enterprise taking a novel approach to citizen science by developing cooperative partnerships among experts in a wide range of fields
		0	Vascular Plants, Observations, Oslo

Vascular Plants, Observations, Oslo ($\text{UiO}_{\text{Plant Obs}}$)	Natural History Museum, University of Oslo (Natural History Museum, 2019b)	82 634 0	
Lichen field notes, Oslo ($\text{UiO}_{\text{Lichen}}$)	Natural History Museum, University of Oslo (Natural History Museum, 2020)	0 0 75 512	Lichens, Field notes from Norway

Table 2. Model output. Simulated occurrence data randomly distributed across the AR50 map; conservation status and dataset name assigned in the same proportions as for the GBIF data (100 repetitions). Generalised linear models (Poisson error distribution, “`identity`”-link function) of the simulated data were fitted, predicting number of records falling within each land-cover by the area of the respective land-cover type. P-values below 0.05 are highlighted in bold text. Acronyms refers to the datasets described in Table 1.

(a) Red-listed species occurrence records				
	Estimate	**Std. error**	**z-value**	**p-value**
Dataset: KMN				
Intercept	3.337e-04	3.618e-06	-92.25	**<0.001**
Proportion of total area	9.218e+01	9.601e-01	96.00	**<0.001**
Dataset: BioFokus				
Intercept	-4.525e-02	3.253e-02	-1.39	0.164
Proportion of total area	4.223e+04	2.056e+01	2054.50e	**<0.001**
Dataset: eBird				
Intercept	-2.288e-03	2.173e-02	-0.105	0.916
Proportion of total area	1.397e+04	1.182e+01	1181.673	**<0.001**
Dataset: Jordal				
Intercept	1.002e-02	1.681e-02	0.596	0.551
Proportion of total area	5.324e+03	7.300e+00	729.297	**<0.001**
Dataset: NBIC$_{CS}$				
Intercept	-8.217e-02	1.181e-01	0.696	0.486
Proportion of total area	4.165e+05	6.456e+01	645.341	**<0.001**
Dataset: NBIC$_{Other}$				
Intercept	-1.640e-03	4.370e-02	-0038	0.97
Proportion of total area	5.451e+04	2.335e+01	2333.829	**<0.001**
Dataset: NTNU				
Intercept	-3.694e-04	3.680e-06	-100.4	**<0.001**
Proportion of total area	1.020e+02	1.010e+00	101.0	**<0.001**

Dataset: $\text{UiO}_{\text{Lichen}}$				
Intercept	-9.760e-04	6.637e-06	-147.1	**<0.001**
Proportion of total area	2.696e+02	1.642e+00	164.2	**<0.001**
Dataset: $\text{UiO}_{\text{Plant Notes}}$				
Intercept	-2.406e-03	2.899e-05	-83.01	**<0.001**
Proportion of total area	6.647e+02	2.578e+00	257.81	**<0.001**
Dataset: $\text{UiO}_{\text{Plant Obs}}$				
Intercept	2.763e-02	2.474e-02	1.117	0.264
Proportion of total area	9.981e+03	9.996e+00	998,450	**<0.001**

(b) Alien species occurrence records				
	Estimate	**Std. error**	**z-value**	**p-value**
Dataset: KMN				
Intercept	-1.310e-03	7.510e-05	-17.45	**<0.001**
Proportion of total area	3.620e+02	1.903e+00	190.27	**<0.001**
Dataset: BioFokus				
Intercept	4.047e-02	2.651e-02	1.527	0.127
Proportion of total area	9.240e+03	9.619e+00	960.567	**<0.001**
Dataset: eBird				
Intercept	1.471e-02	1.137e-02	1.294	0.196
Proportion of total area	3.658e+02	1.919	190.657	**<0.001**
Dataset: Jordal				
Intercept	2.351e-02	1.726e-02	1.362	0.173
Proportion of total area	2.442e03	4.948e+00	493.657	**<0.001**
Dataset: NBIC_{CS}				
Intercept	5.979e-04	8.174e-02	0.007	0.994
Proportion of total area	1.889+05	4.347e+01	4344.328	**<0.001**
Dataset: $\text{NBIC}_{\text{Other}}$				
Intercept	8.834e-03	1.390e-02	0636	0.525
Proportion of total area	3.120e+03	5.598e+00	558.283	**<0.001**
Dataset: NTNU				
Intercept	-3.128e-04	2.901e-05	-10.78	**<0.001**

Proportion of total area	8.640e+01	9.296e-01	92.95	**<0.001**
Dataset: UiO$_{\text{Plant Notes}}$				
Intercept	-5.791e-03	2.618e-05	-221.2	**<0.001**
Proportion of total area	1.600e+03	4.000e+00	399.9	**<0.001**
Dataset: UiO$_{\text{Plant Obs}}$				
Intercept	1.108e-02	3.710e-02	0.299	0.765
Proportion of total area	3.595e+04	1.897e+01	1895.303	**<0.001**

Table 3. Over- vs. under-sampled land-cover types for each dataset. A summary of which land-cover types has either more or fewer observed records than expected by the Generalised Linear Models summarised in Table 2. ↑ indicates more records than expected, ↓ indicates fewer records than expected. “n.s.” indicates that the observed number of records fell within the 0.95 C.I. of the model predictions. See Supporting Information, Table S.6 for detailed numbers. Acronyms refers to the datasets described in Table 1.

	KMN	Bio-Fokus	eBird	Jordal	NBIC$_{\text{CS}}$	NBIC$_{\text{Other}}$	NTNU	UiO$_{\text{Lichen}}$	UiO$_{\text{Plant Notes}}$	UiO$_{\text{Plant Obs}}$
	Red-listed	*Red-listed*	*Red-listed*	*Red-listed*	*Red-listed*	*Red-listed*	*Red-listed*	*Red-listed*	*Red-listed*	*Red-listed*
	Alien	*Alien*	*Alien*	*Alien*	*Alien*	*Alien*	*Alien*	-	*Alien*	*Alien*
Developed area	↓	↑	↑	↑	↑	↑	↓	↑	↑	↓
	↓	↑	↑	↓	↑	↑	↓	-	↑	↑
Agriculture (unsp.)	↓	↑	↓	↓	↑	↑	↓	↓	↓	↓
	↓	↑	↓	↓	↑	↑	↓	-	↓	↑
Cultivated land	↑	↑	↑	↑	↑	↑	↑	↓	↑	↓
	↓	↑	↑	↑	↑	↑	↑	-	↑	↑
Home fields grazing land	↓	↑	↑	↑	↑	↑	↑	↑	↑	↑
	↑	↑	↑	↑	↑	↑	↓	-	↑	↑
Forest (unsp.)	↓	↓	↓	↓	↓	↑	↓	↓	↓	↓
	↓	↓	↓	↓	↓	↓	↓	-	↓	↑
Coniferous forest	↓	↑	↓	↓	↓	↑	↑	↑	↓	↓
	↓	↑	↓	↓	↑	↓	↑	-	↓	↓

Deciduous forest	↑	↑	↓	↑	↓	↑	↓	↓	↑	↓
	↑	↑	↓	↑	↑	↓	↑	-	↓	↓
Mixed forest	↑	↑	↓	↑	↑	↑	↑	↓	↑	↑
	↑	↑	↓	↓	↑	↓	↑	-	↑	↑
Open firm ground	↓	↓	↓	↓	↓	↓	↑	↓	↓	↓
	↓	↓	↓	↓	↓	↓	↓	-	↓	↑
Mire	↓	↓	↓	↓	↓	↓	↓	↑	↓	↓
	↓	↓	↓	↓	↓	↓	↓	-	↓	↓
Snow/ice	↓	↓	↓	↓	↓	↓	↓	↓	↓	↓
	↓	↓	↓	↓	↓	↓	↓	-	↓	↓
Freshwater	↓	↓	↑	↓	↑	↓	↓	↓	↓	↓
	↑	↓	↑	↓	↓	↑	↑	-	↓	↓
Ocean	↑	↓	↑	↓	↑	↓	↓	↓	↑	↓
	↑	↓	↑	↓	↑	↑	↓	-	↑	↓
Not mapped	n.s.	↑	↑	n.s.	↓	↑	n.s.	n.s.	n.s.	↓
	n.s.	↑	n.s.	n.s.	↑	n.s.	n.s.	-	n.s.	↓

Supplementary material

Tanja K. Petersen, James D. M. Speed, Vidar Grøtan, Gunnar Austrheim

Species data for understanding biodiversity dynamics: The What, Where and When of species occurrence data collection.

S.1. Land-cover categories in AR50

Table S.1. Land-cover categories in the AR50 maps for Norway used in the analyses. The descriptions of the land-cover types are based on the descriptions from the AR50 product specification (Norwegian Institute of Bioeconomy Research, 2016)[1]. "Percentage of total area" describes the percentage of the entire AR50 map covered by the respective land-cover type.

AR50 category	Name	Description	Area (km^2)	Percentage of total area (%)
10	Developed area	Area which is used for traffic or houses	1 945.5	0.55
20	Agriculture	Fully cultivated land, superficially cultivated land, and home fields grazing land; exact use not specified	56.9	0.016
24	Fully- and superficially cultivated land	Fully cultivated land be used for agriculture or meadows, and be renewed by ploughing.	10 612.6	3.0

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[1] Norwegian Institute of Bioeconomy Research. 2016. 50 *Produktspesifikasjon: Arealressurskart.*

		Superficially cultivated land is mostly evened out on the surface, allowing for mechanical harvesting		
25	Home fields grazing land	Home fields which can be used for grazing, but cannot be mechanically harvested. At least 50% of the area is covered by grasses	2 249.5	0.6
30	Forest	Forest type unregistered	20 844.7	5.9
31	Coniferous forest	At least 50% of the area is covered by conifers	69 424.4	19.5
32	Deciduous forest	Less than 20% of the forested area is covered by conifers	29 440.8	8.3
33	Mixed forest	Between 20 and 50% of the forested area is covered by conifers	6 956.7	2.0
50	Open firm ground	Firm ground which is not farmland, forest, developed or used for communications purposes	139 314.5	39.2
60	Mire	Area with marsh vegetation and a peat layer at least 30 cm thick	21 833.9	6.1
70	Snow/ice	Mix of snow and ice which does not melt during the summer	2 831.1	0.80
81	Freshwater	Lakes and rivers	18 511.4	5.2
82	Ocean	Ocean	31 150.1	8.8
99	Not mapped	Area of unknown character	1.3	0.00036

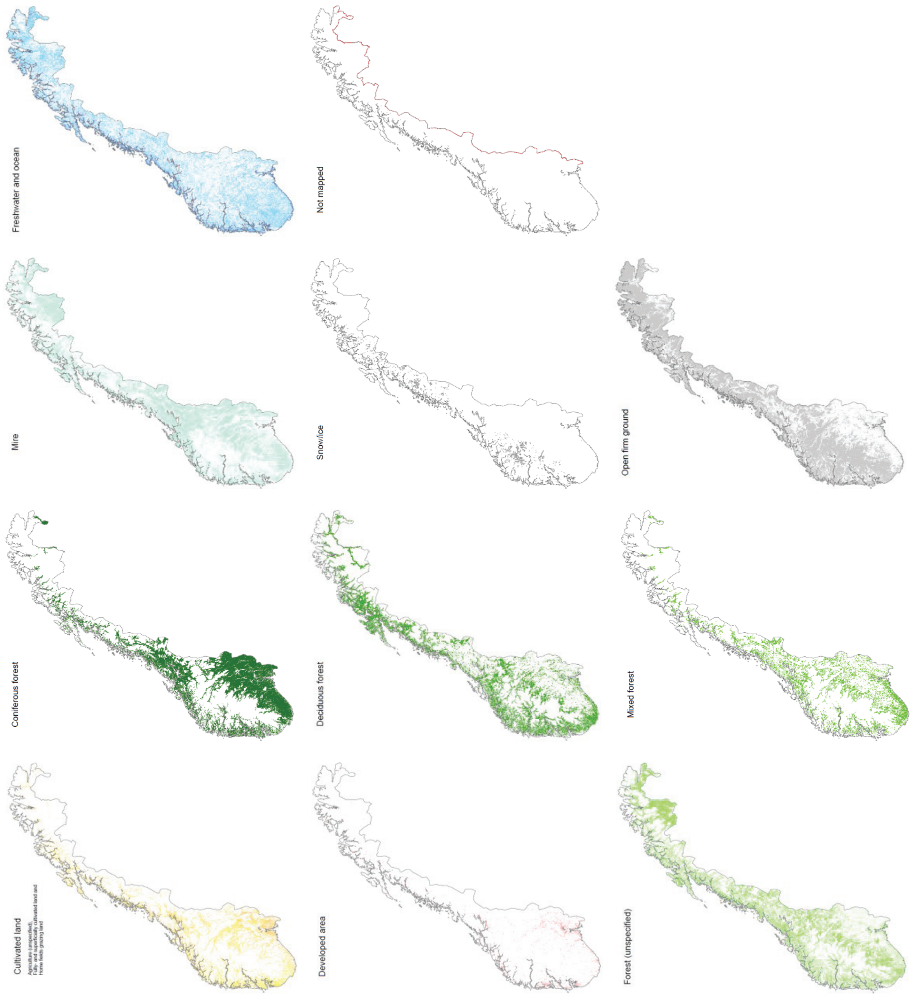

Figure S.1 Detailed maps of the individual land-cover categories included in the analyses. Scale, geographic scope and colour legend are similar to Fig. 1, except snow/ice (light grey) and unmapped areas (red), which were changed here to increase visibility.

S.2. Datasets included in analyses

Table S.2 Datasets included in the analyses. The datasets are displayed in descending order according to the total no. records.

The description is modified from the description and methodology as presented on the linked GBIF webpage.

Dataset Name (abbreviation)	Citation	Publisher	# Animals # Plants # Fungi	Description
Norwegian Species Observation Service (NBIC$_{\text{CS}}$)	The Norwegian Biodiversity Information Centre, Hoem S (2020). Norwegian Species Observation Service. Version 1.82. The Norwegian Biodiversity Information Centre (NBIC). Occurrence dataset https://doi.org/10.15468/zjbzel accessed via GBIF.org on 2020-05-15	Norwegian Biodiversity Information Centre	2 678 373 1 776 878 422 930	Citizen science species observations from the Species Observation Service in Norway (Artsobservasjoner.no)
Vascular Plants, Field notes, Oslo (O) (UiO$_{\text{Plant Notes}}$)	Natural History Museum, University of Oslo (2019). Vascular Plants, Field notes, Oslo (O). Version 1.186. Occurrence dataset https://doi.org/10.15468/w8gru5 accessed via GBIF.org on 2020-05-15.	Natural History Museum, University of Oslo	0 1 006 937 0	Vascular Plants, Field notes from Norway
	Norwegian Biodiversity Information Centre, Hoem S (2020).		585 898	

Norwegian Biodiversity Information Centre - Other datasets ($\text{NBIC}_{\text{other}}$)	Norwegian Biodiversity Information Centre - Other datasets. Version 13.132. The Norwegian Biodiversity Information Centre (NBIC). Occurrence dataset https://doi.org/10.15468/tm56sc accessed via GBIF.org on 2020-05-15	Norwegian Biodiversity Information Centre	17 288 289	Other data providers sharing occurrence data via the Norwegian Species Map Service, allowing NBIC to share their data as they do not provide their own IPT service. This includes datasets/databases from the following providers: The Norwegian Environment Agency (http://www.miljodirektoratet.no/): *Predator database, water species database, naturedatabase* and *salmon registry.* Sustain.no (http://www.miljolare.no/en/): *Alien species, plants, butterflies, earthworms, snails, water species, garden birds, coastal species, ponds species and stream species*
BioFokus (BioFokus)	Blindheim T (2020). BioFokus. Version 1.1384. BioFokus. Occurrence dataset https://doi.org/10.15468/jxbhqx accessed via GBIF.org on 2020-05-15	BioFokus	39 179 212 265 82 724	BioFokus is a non-profit organization for providing biodiversity survey information on biological diversity to decision makers and the public in Norway. BioFokus focuses on field work to secure updated and relevant data on botany, zoology, ecology, and survey for respective areas. BioFokus employees cover a wide range of species-groups and have broad understanding of ecology in the respective nature types, including

				forest, cultural landscapes and fresh water
Vascular plant field notes, NTNU University Museum (NTNU)	NTNU University Museum (2020). Vascular plant field notes, NTNU University Museum. Version 1.97. Sampling event dataset https://doi.org/10.15468/jxbhqx accessed via GBIF.org on 2020-05-15	NTNU University Museum	0 188 910 0	Vascular plant field notes, Norway. Observation of vascular plants from more several thousand localities using standardised cross-lists. The dataset is a collection of observations made during various research project, including surveys and shorter field trips, at the NTNU University Museum from the first part of the 1900s and onwards. Included are also a few observations made by skilled amateurs. The dataset contains observation from several thousand localities throughout Norway. The observations were recorded in the field using standardised cross-list forms covering most vascular plants to be found in Norway.
Jordal (Jordal)	Jordal J B (2019). Jordal. Version 1.91. Biolog J.B. Jordal AS. Occurrence dataset https://doi.org/10.15468/wqsad9 accessed via GBIF.org on 2020-05-15	Biolog J.B. Jordal AS	282 150 411 21 856	John Bjarne Jordal, sole proprietor. Consultant within biology and nature management (http://www.jbjordal.no/)
Vascular Plants, Field notes, Agder naturmuseum (KMN) (KMN)	Åsen P (2019). Vascular Plants, Field notes, Agder naturmuseum (KMN). Version 1.160. Agder Museum of Natural History and Botanical Garden. Occurrence	Agder Museum of Natural History and Botanical Garden	0 125 115 0	Vascular Plants, Field notes from Norway

	dataset https://doi.org/10.15468/gja4jo accessed via GBIF.org on 2020-05-15			
EOD - eBird Observation Dataset (eBird)	Levatich T, Padilla F (2019). EOD - eBird Observation Dataset. Cornell Lab of Ornithology. Occurrence dataset https://doi.org/10.15468/aomfnb accessed via GBIF.org on 2020-05-15	Cornell Lab of Ornithology	93 109 0 0	eBird is a collective enterprise that takes a novel approach to citizen science by developing cooperative partnerships among experts in a wide range of fields: population ecologists, conservation biologists, quantitative ecologists, statisticians, computer scientists, GIS and informatics specialists, application developers, and data administrators
Vascular Plants, Observations, Oslo (O) ($\text{UiO}_{\text{Plant Obs}}$)	Natural History Museum, University of Oslo (2019). Vascular Plants, Observations, Oslo (O). Version 1.181. Occurrence dataset https://doi.org/10.15468/tvnjk7 accessed via GBIF.org on 2020-05-15	Natural History Museum, University of Oslo	0 82 634 0	Vascular Plants, Observations, Oslo (O)
Lichen field notes, Oslo (O) ($\text{UiO}_{\text{Lichen}}$)	Natural History Museum, University of Oslo (2020). Lichen field notes, Oslo (O). Version 1.180. Occurrence dataset https://doi.org/10.15468/zrfxcu accessed via GBIF.org on 2020-05-15	Natural History Museum, University of Oslo	0 0 75512	Lichens, Field notes from Norway

S.3 Taxonomical differences in GBIF records

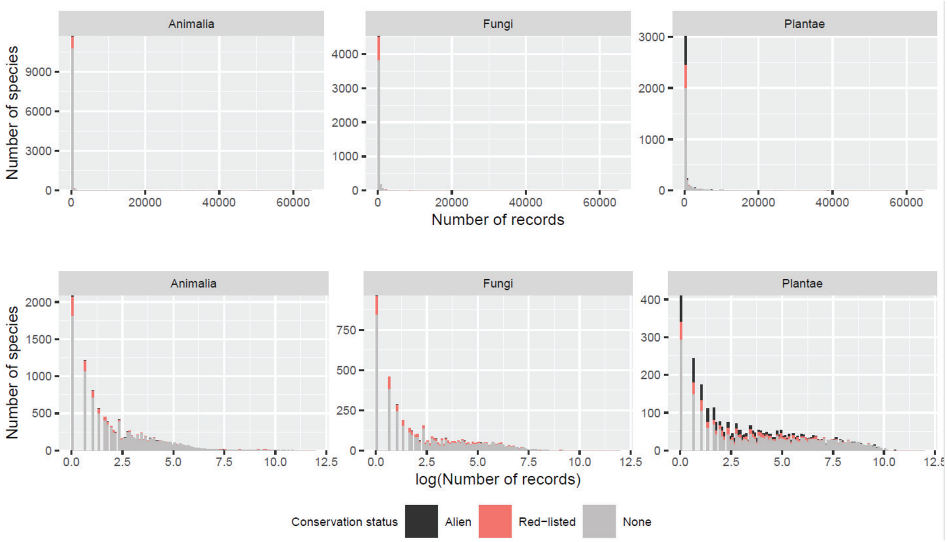

Figure S.2. Number of species by number of records in the analysed GBIF records within each kingdom. The number of species by total number of records (top panels), and by log(number of records) (bottom panels). Conservation status is indicated by colour.

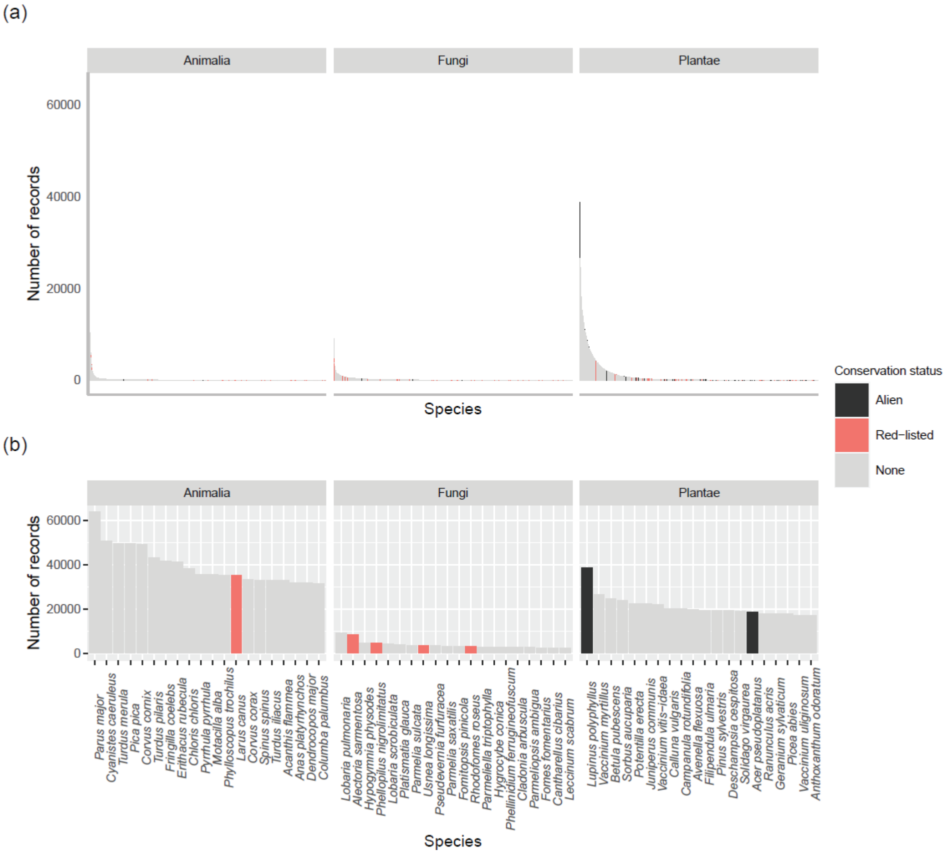

Figure S.3. Number of records for each species within the kingdoms. *(a)* For all species (species names not indicated), and *(b)* the 20 most frequent species within each of the kingdoms. Conservation status is indicated by color.

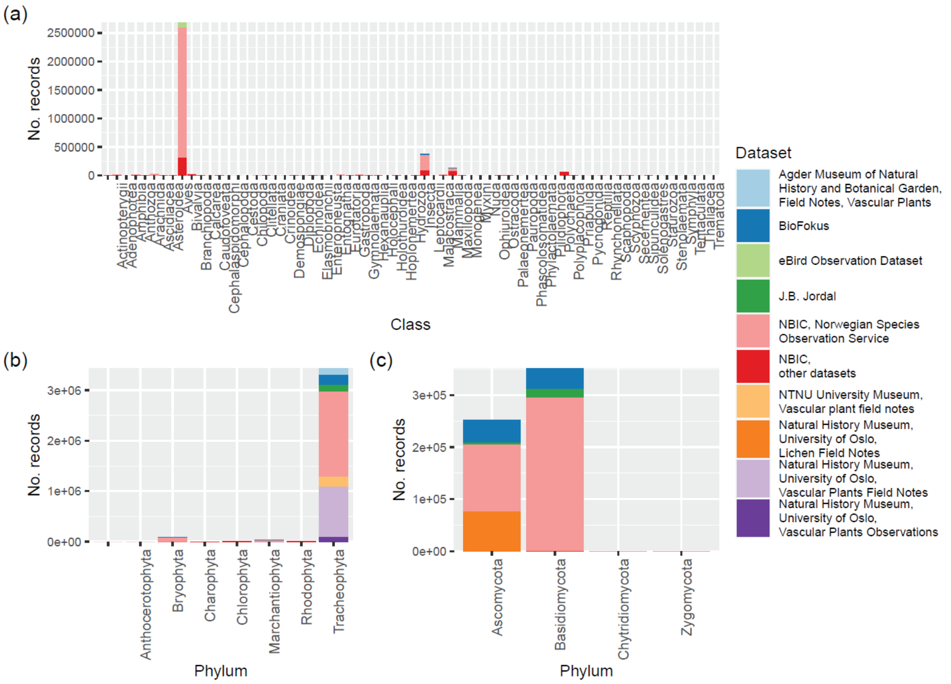

Figure S.4. Number of records at lower taxonomic levels within the kingdoms *(a)* Animalia, *(b)* Plantae and *(c)* Fungi.

S.4 Interannual variation in GBIF records for the two recorder groups

To compare the within-year variation between the datasets, the proportion of records registered in each month was calculated (separately for each dataset and each kingdom to account for the uneven sampling sizes). Treating "month" as numerical values, the median months of sampling were compared with a Kruskal-Wallis test, and posthoc pairwise comparisons were performed with a Dunn Test with Bonferroni correction for multiple comparisons. The median sampling month differed between datasets for all taxonomic groups (Animals: Kruskal-Wallis X^2 = *53.245, df = 4, p-value < 0.001;* Plants: Kruskal-Wallis X^2 = *23.718, df = 7, p-value = 0.001;* Fungi: Kruskal-Wallis X^2 = *46.051, df = 4, p-value < 0.001;* All: Kruskal-Wallis X^2 = *46.247, df = 9, p-value < 0.001*). All pairwise comparisons were significantly different (adjusted p-value < 0.001), except for the Jordal and BioFokus datasets for animal records.

Table S.3. Interannual temporal variation between datasets. Mean and median sampling month, including standard deviation and interquartile range.

	Dataset	**Mean**	**S.D.**	**Median**	**IQR**
Animals	BioFokus	6.88	1.70	7	2
	eBird	6.15	2.32	6	2
	Jordal	6.66	2.13	7	3
	NBIC$_{CS}$	6.03	2.63	6	4
	NBIC$_{Other}$	4.20	3.50	3	6
Plants	KMN	7.13	1.03	7	2
	BioFokus	7.54	1.42	8	3
	Jordal	7.85	1.38	8	2

	NBIC$_{\text{CS}}$	6.91	1.61	7	2
	NBIC$_{\text{Other}}$	7.57	1.44	8	2
	NTNU	7.42	1.06	7	1
	UiO$_{\text{Plant Notes}}$	7.22	0.932	7	1
	UiO$_{\text{Plant Nores}}$	7.22	1.44	7	2
Fungi	BioFokus	8.16	1.81	9	2
	Jordal	8.64	1.42	9	1
	NBIC$_{\text{CS}}$	7.57	2.60	8	3
	NBIC$_{\text{Other}}$	6.56	2.68	7	4
	UiO$_{\text{Lichen}}$	6.92	2.34	7	4
All	KMN	7.13	1.03	7	2
	BioFokus	7.61	1.60	8	3
	eBird	6.15	2.32	6	2
	Jordal	7.95	1.41	8	2
	NBIC$_{\text{CS}}$	6.48	2.37	7	3
	NBIC$_{\text{Other}}$	4.30	3.50	3	6
	NTNU	7.42	1.06	7	1
	UiO$_{\text{Lichen}}$	6.92	2.34	7	4
	UiO$_{\text{Plant Notes}}$	7.22	0.93	7	1
	UiO$_{\text{Plant Nores}}$	7.22	1.44	7	2

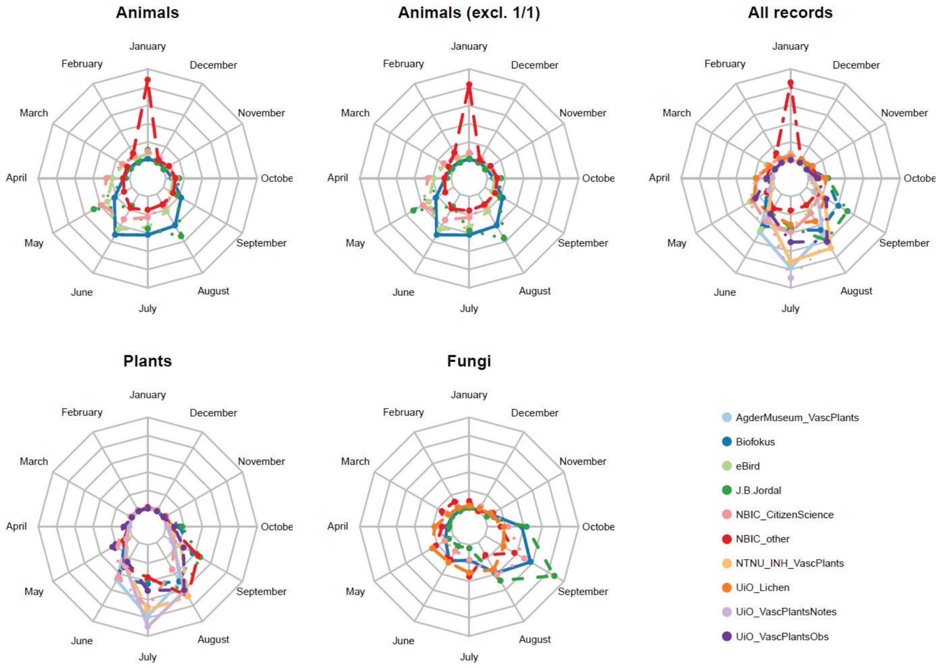

Figure S.5. Proportion of records in total and within each of the three kingdoms registered each month. Dataset is indicated by colour. Records without information of month of recording are not included. “Animals (excl. 1/1)” is excluding animal records registered to January 1st.

S.5 Separate models for individual datasets

For the simulated data, the number of records within each land-cover type is predicted by the area of the specified land cover type (Table S.2).

Only open firm ground, mires and snow/ice showed consistent patterns across all datasets; all had fewer records that would be expected by the area. Developed areas were under-sampled in the KMN-, NTNU-, and Jordal datasets, and oversampled for all others. Unspecified agricultural areas were under-sampled (i.e. had no records) in the KMN-, NTNU-, $\text{UiO}_{\text{Lichen}}$- and $\text{UiO}_{\text{Plant Notes}}$ datasets, but were oversampled for all others. Cultivated areas and grazing land were under-sampled in the KMN- and NTNU dataset, respectively, otherwise oversampled in all cases. Coniferous forest was oversampled in the NBIC_{CS}-, BioFokus-, NTNU-, $\text{UiO}_{\text{Lichen}}$- and $\text{UiO}_{\text{Plant Notes}}$ datasets, under-sampled for all others. Deciduous- and mixed forest were both under-sampled in the $\text{NBIC}_{\text{other}}$ dataset, otherwise consistently oversampled, whereas unspecified forest was oversampled in the NTNU- and $\text{UiO}_{\text{Plant Obs}}$ datasets, otherwise consistently under-sampled. Freshwater was oversampled in the $\text{NBIC}_{\text{other}}$-, NBIC_{CS}-, eBird- and KMN datasets, otherwise under-sampled. Ocean was oversampled in the $\text{UiO}_{\text{Plant Notes}}$-, eBird-, KMN- and $\text{NBIC}_{\text{other}}$ datasets, otherwise under-sampled. Unmapped areas were oversampled in the $\text{UiO}_{\text{Plant Obs}}$-, $\text{NBIC}_{\text{other}}$-, eBird- and BioFokus datasets, and under-sampled for the NBIC_{CS}-, KMN-, Jordal- and $\text{UiP}_{\text{Plant Notes}}$ datasets, and the number of records from the $\text{UiO}_{\text{Lichen}}$. NTNU datasets fell within the 0.95 CI.

Comparing the absolute residuals between predicted and observed number of records within each land-cover type, the largest numerical discrepancies were seen for open firm ground, developed area and cultivated land (Figure S.6-S.9). When comparing the relative residuals, no other consistent patterns are seen (Figure S.9).

Table S.4. Generalised linear models (Poisson error distribution, “`identity`”-link function) of the simulated, random data, predicting the number of records for each land-cover type as a function of the area of the specified land-cover type in Norway.

	Estimate	**Std. error**	**z value**	**p value**
KMN				
Intercept	4.675e-02	3.010e-02	1.553	0.12
Proportion of area	1.326e+04	1.152e+01	1150.920	<0.001
BioFokus				
Intercept	1.200e-02	1.001e-01	0.12	0.905
Proportion of area	2.800e+05	5.293e+01	5289.24	<0.001
eBird				
Intercept	9.353e-03	5.294e-02	0.177	0.86
Proportion of area	7.675e+04	2.771e+01	2769.340	<0.001
Jordal				
Intercept	-6.343e-02	5.745e-02	-1.104	0.27
Proportion of area	1.105e+05	3.326e+01	3323.834	<0.001
NBIC$_{CS}$				
Intercept	4.839e-01	4.015e-01	1.205	0.228
Proportion of area	4.429e+06	2.105e+02	21038.426	<0.001
NBIC$_{Other}$				
Intercept	-5.170e-02	1.346e-01	-0.384	0.701
Proportion of area	5.266e+05	7.259e+01	7254.215	<0.001
NTNU				
Intercept	-1.192e-02	1.412e-02	-0.844	0.398

Proportion of area	8.879e+03	9.425e+00	942.060	<0.001
$\mathbf{UiO}_{\mathbf{Lichen}}$				
Intercept	1.164e-02	1.697e-02	0.686	0.493
Proportion of area	5.041e+03	7.104e+00	709.638	<0.001
$\mathbf{UiO}_{\mathbf{Plant\ Notes}}$				
Intercept	1.287e-03	3.977e-02	0.032	0.974
Proportion of area	4.439e+04	2.108e+01	2106.276	<0.001
$\mathbf{UiO}_{\mathbf{Plant\ Obs}}$				
Intercept	6.962e-02	5.961e-02	1.168	0.243
Proportion of area	8.186e+04	2.862e+01	2859.838	<0.001

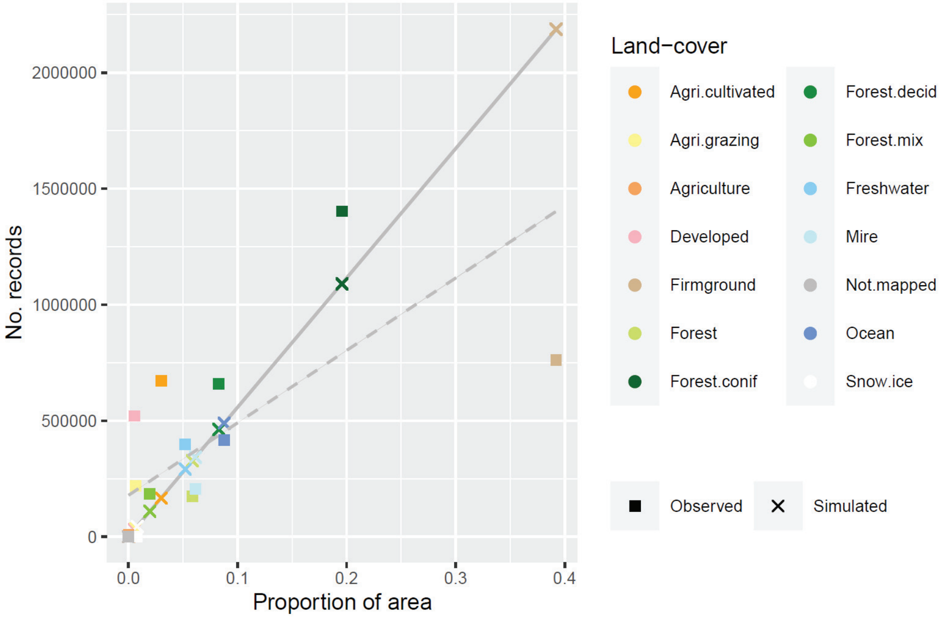

Figure S.6. Null model (GLM) of the total number of records as a function of area (proportion of the total area within the study area) for the random, simulated data (crosses), vs. the observed number of records for each land-cover type (squares), not including information on dataset or conservation status. The solid line indicate the predicted values by the null-model, gray ribbons indicate the 0.95 C.I..

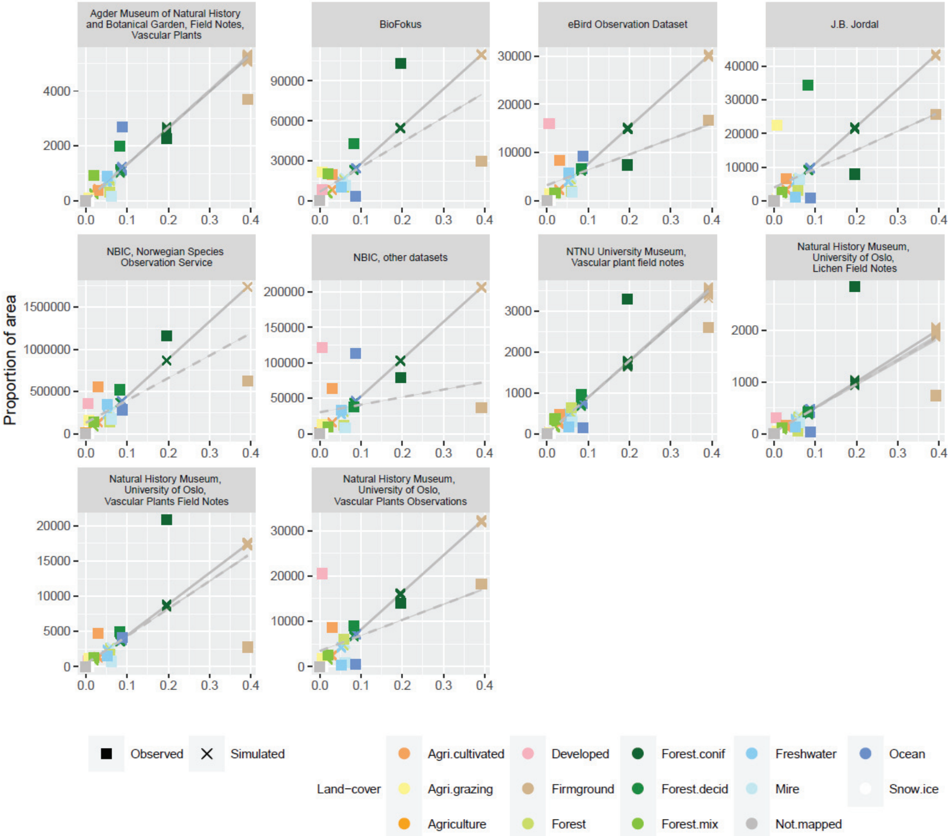

Figure S.7. Null models (GLM) of the number of records as a function of area (proportion of the total area within the study area) for the random, simulated data (crosses), vs. the observed number of records for each land-cover type (squares). Solid lines indicate the predicted values by the null-model, gray ribbons indicate the 0.95 C.I.

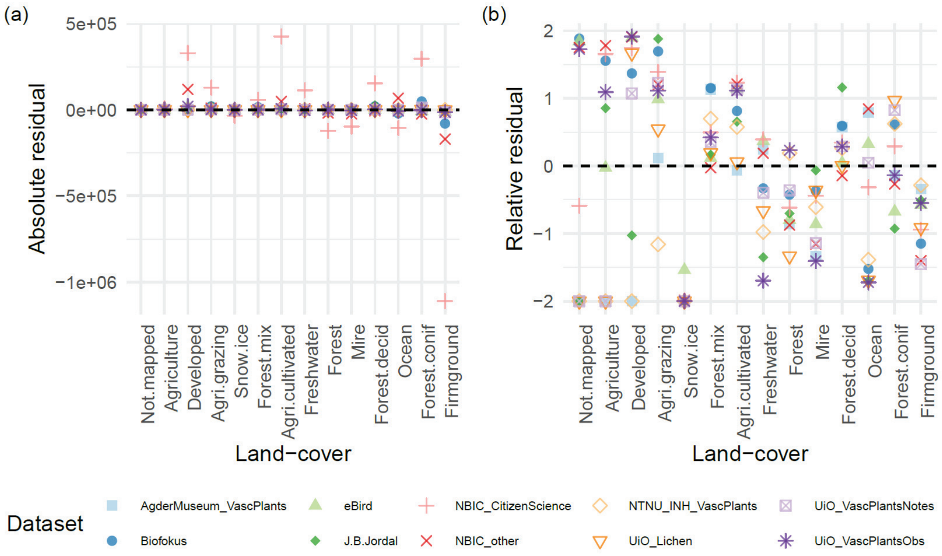

Figure S.9. *(a)* Absolute and *(b)* relative residuals between observed number of species occurrence records, and the predicted number of records, based on the area of each land-cover type. Colours/shapes indicate dataset.

Table S.5. Observed number of records for each land-cover type, the number of records predicted for each land-cover type based on area, and the absolute and relative difference between the two. Negative residuals are highlighted in gray. * indicates that the observed number of records falls within the 0.95 confidence interval.

Land-cover	**Dataset**	**Observed**	**Predicted**	**Absolute residual**	**Relative residual**
Developed area	KMN	0.00	72.83	-72.83	-2.00
	BioFokus	8202.00	1536.21	6665.79	1.37
	eBird	16080.00	421.14	15658.86	1.90
	Jordal	195.00	606.52	-411.52	-1.03
	NBIC_{CS}	353357.00	24305.34	329051.66	1.74
	$\text{NBIC}_{\text{Other}}$	121287.00	2889.51	118397.49	1.91
	NTNU	0.00	48.71	-48.71	-2.00
	$\text{UiO}_{\text{Lichen}}$	305.00	27.67	277.33	1.67
	$\text{UiO}_{\text{Plant Notes}}$	807.00	243.61	563.39	1.07
	$\text{UiO}_{\text{Plant Obs}}$	20516.00	449.23	20066.77	1.91
Agriculture (unsp.)	KMN	0.00	2.18	-2.18	-2.00
	BioFokus	360.00	44.94	315.06	1.56
	eBird	12.00	12.32	-0.32	-0.03
	Jordal	44.00	17.68	26.32	0.85
	NBIC_{CS}	7543.00	711.24	6831.76	1.66
	$\text{NBIC}_{\text{Other}}$	1452.00	84.45	1367.55	1.78
	NTNU	0.00	1.41	-1.41	-2.00
	$\text{UiO}_{\text{Lichen}}$	0.00	0.82	-0.82	-2.00
	$\text{UiO}_{\text{Plant Notes}}$	0.00	7.13	-7.13	-2.00
	$\text{UiO}_{\text{Plant Obs}}$	45.00	13.20	31.80	1.09
Cultivated land	KMN	371.00	396.85	-25.85	-0.07

	BioFokus	19845.00	8375.70	11469.30	0.81
	eBird	8373.00	2296.12	6076.88	1.14
	Jordal	6529.00	3307.18	3221.82	0.66
	NBIC$_{\text{CS}}$	557986.00	132515.66	425470.34	1.23
	NBIC$_{\text{Other}}$	64208.00	15754.44	48453.56	1.21
	NTNU	481.00	265.62	215.38	0.58
	UiO$_{\text{Lichen}}$	160.00	150.84	9.16	0.06
	UiO$_{\text{Plant Notes}}$	4763.00	1328.20	3434.80	1.13
	UiO$_{\text{Plant Obs}}$	8603.00	2449.00	6154.00	1.11
Home fields grazing land	KMN	95.00	84.30	10.70	0.12
	BioFokus	21515.00	1778.38	19736.62	1.69
	eBird	1434.00	487.53	946.47	0.99
	Jordal	22524.00	702.15	21821.85	1.88
	NBIC$_{\text{CS}}$	156314.00	28136.80	128177.20	1.39
	NBIC$_{\text{Other}}$	13422.00	3345.02	10076.98	1.20
	NTNU	15.00	56.39	-41.39	-1.16
	UiO$_{\text{Lichen}}$	56.00	32.04	23.96	0.54
	UiO$_{\text{Plant Notes}}$	1181.00	282.01	898.99	1.23
	UiO$_{\text{Plant Obs}}$	1824.00	520.04	1303.96	1.11
Forest	KMN	310.00	776.68	-466.68	-0.86
	BioFokus	10656.00	16392.88	-5736.88	-0.42
	eBird	1929.00	4493.95	-2564.95	-0.80
	Jordal	3109.00	6472.87	-3363.87	-0.70
	NBIC$_{\text{CS}}$	136870.00	259358.86	-122488.86	-0.62
	NBIC$_{\text{Other}}$	12076.00	30834.60	-18758.60	-0.87
	NTNU	629.00	519.89	109.11	0.19
	UiO$_{\text{Lichen}}$	59.00	295.21	-236.21	-1.33
	UiO$_{\text{Plant Notes}}$	1804.00	2599.55	-795.55	-0.36
	UiO$_{\text{Plant Obs}}$	6057.00	4793.12	1263.88	0.23
Coniferous forest	KMN	2260.00	2595.81	-335.81	-0.14

	BioFokus	103112.00	54790.45	48321.55	0.61
	eBird	7443.00	15020.26	-7577.26	-0.67
	Jordal	7934.00	21634.64	-13700.64	-0.93
	NBIC$_{\text{CS}}$	1162695.00	866862.89	295832.11	0.29
	NBIC$_{\text{Other}}$	78797.00	103059.66	-24262.66	-0.27
	NTNU	3309.00	1737.67	1571.33	0.62
	UiO$_{\text{Lichen}}$	2841.00	986.65	1854.35	0.97
	UiO$_{\text{Plant Notes}}$	20885.00	8688.57	12196.43	0.82
	UiO$_{\text{Plant Obs}}$	13922.00	16020.04	-2098.04	-0.14
Deciduous forest	KMN	1985.00	1099.58	885.42	0.57
	BioFokus	42799.00	23208.55	19590.45	0.59
	eBird	6656.00	6362.40	293.60	0.05
	Jordal	34497.00	9164.12	25332.88	1.16
	NBIC$_{\text{CS}}$	520766.00	367192.44	153573.56	0.35
	NBIC$_{\text{Other}}$	37835.00	43654.74	-5819.74	-0.14
	NTNU	956.00	736.05	219.95	0.26
	UiO$_{\text{Lichen}}$	420.00	417.94	2.06	0.00
	UiO$_{\text{Plant Notes}}$	4925.00	3680.37	1244.63	0.29
	UiO$_{\text{Plant Obs}}$	9061.00	6785.93	2275.07	0.29
Mixed forest	KMN	936.00	260.18	675.82	1.13
	BioFokus	20395.00	5490.77	14904.23	1.15
	eBird	1693.00	1505.25	187.75	0.12
	Jordal	2560.00	2168.03	391.97	0.17
	NBIC$_{\text{CS}}$	144012.00	86872.08	57139.92	0.49
	NBIC$_{\text{Other}}$	10060.00	10327.96	-267.96	-0.03
	NTNU	361.00	174.13	186.87	0.70
	UiO$_{\text{Lichen}}$	120.00	98.89	21.11	0.19
	UiO$_{\text{Plant Notes}}$	1247.00	870.72	376.28	0.36
	UiO$_{\text{Plant Obs}}$	2466.00	1605.49	860.51	0.42
Open firm ground	KMN	3684.00	5199.70	-1515.70	-0.34

	BioFokus	29709.00	109752.61	-80043.61	-1.15
	eBird	16658.00	30087.59	-13429.59	-0.57
	Jordal	25778.00	43337.14	-17559.14	-0.51
	NBIC$_{\text{CS}}$	624927.00	1736442.04	-1111515.04	-0.94
	NBIC$_{\text{Other}}$	36376.00	206442.37	-170066.37	-1.40
	NTNU	2610.00	3480.81	-870.81	-0.29
	UiO$_{\text{Lichen}}$	738.00	1976.39	-1238.39	-0.91
	UiO$_{\text{Plant Notes}}$	2764.00	17404.37	-14640.37	-1.45
	UiO$_{\text{Plant Obs}}$	18263.00	32090.22	-13827.22	-0.55
Mire	KMN	163.00	814.94	-651.94	-1.33
	BioFokus	11842.00	17200.45	-5358.45	-0.37
	eBird	1874.00	4715.34	-2841.34	-0.86
	Jordal	6367.00	6791.75	-424.75	-0.06
	NBIC$_{\text{CS}}$	174161.00	272135.72	-97974.72	-0.44
	NBIC$_{\text{Other}}$	8667.00	32353.62	-23686.62	-1.15
	NTNU	291.00	545.50	-254.50	-0.61
	UiO$_{\text{Lichen}}$	215.00	309.75	-94.75	-0.36
	UiO$_{\text{Plant Notes}}$	747.00	2727.61	-1980.61	-1.14
	UiO$_{\text{Plant Obs}}$	880.00	5029.24	-4149.24	-1.40
Snow/ice	KMN	0.00	105.89	-105.89	-2.00
	BioFokus	5.00	2234.19	-2229.19	-1.99
	eBird	80.00	612.49	-532.49	-1.54
	Jordal	0.00	882.13	-882.13	-2.00
	NBIC$_{\text{CS}}$	93.00	35348.36	-35255.36	-1.99
	NBIC$_{\text{Other}}$	16.00	4202.39	-4186.39	-1.98
	NTNU	0.00	70.85	-70.85	-2.00
	UiO$_{\text{Lichen}}$	0.00	40.24	-40.24	-2.00
	UiO$_{\text{Plant Notes}}$	0.00	354.29	-354.29	-2.00
	UiO$_{\text{Plant Obs}}$	0.00	653.31	-653.31	-2.00
Freshwater	KMN	889.00	691.48	197.52	0.25
	BioFokus	10443.00	14594.59	-4151.59	-0.33
	eBird	5807.00	4000.97	1806.03	0.37

	Jordal	1118.00	5762.79	-4644.79	-1.35
	NBIC$_{\text{CS}}$	344041.00	230907.42	113133.58	0.39
	NBIC$_{\text{Other}}$	33102.00	27452.06	5649.94	0.19
	NTNU	159.00	462.86	-303.86	-0.98
	UiO$_{\text{Lichen}}$	132.00	262.82	-130.82	-0.66
	UiO$_{\text{Plant Notes}}$	1552.00	2314.38	-762.38	-0.39
	UiO$_{\text{Plant Obs}}$	349.00	4267.32	-3918.32	-1.70
Ocean	KMN	2680.00	1163.40	1516.60	0.79
	BioFokus	3335.00	24555.65	-21220.65	-1.52
	eBird	9327.00	6731.69	2595.31	0.32
	Jordal	797.00	9696.04	-8899.04	-1.70
	NBIC$_{\text{CS}}$	282800.00	388505.50	-105705.50	-0.31
	NBIC$_{\text{Other}}$	113587.00	46188.61	67398.39	0.84
	NTNU	141.00	778.77	-637.77	-1.39
	UiO$_{\text{Lichen}}$	37.00	442.20	-405.20	-1.69
	UiO$_{\text{Plant Notes}}$	4085.00	3893.99	191.01	0.05
	UiO$_{\text{Plant Obs}}$	537.00	7179.80	-6642.80	-1.72
Not mapped	KMN	0.00	0.09	-0.09	-2.00
	BioFokus	34.00	1.03	32.97	1.88
	eBird	7.00	0.29	6.71	1.84
	Jordal	0.00	0.34	-0.34	-2.00
	NBIC$_{\text{CS}}$	9.00	16.52	-7.52	-0.59
	NBIC$_{\text{Other}}$	28.00	1.85	26.15	1.75
	NTNU	0.00	0.02	-0.02	-2.00*
	UiO$_{\text{Lichen}}$	0.00	0.03	-0.03	-2.00*
	UiO$_{\text{Plant Notes}}$	0.00	0.16	-0.16	-2.00
	UiO$_{\text{Plant Obs}}$	5.00	0.37	4.63	1.73

S.6 Observed and predicted number of records

Table S.6. Observed- and predicted number of records for each land-cover type, and absolute and relative difference between the two. Negative residuals are highlighted in gray. * indicates that the observed number of records falls within the 0.95 confidence interval.

Land-cover	Dataset	Conservation status	Observed	Predicted	Absolute residual	Relative residual
Developed area	KMN	Red-listed	0	0.51	-0.51	-2.00
		Alien	0	1.99	-1.99	-2.00
	BioFokus	Red-listed	736	231.69	504.31	1.04
		Alien	1122	50.74	1071.26	1.83
	eBird	Red-listed	2490	76.67	2413.33	1.88
		Alien	60	2.02	57.98	1.87
	Jordal	Red-listed	34	29.23	4.77	0.15
		Alien	11	13.43	-2.43	-0.20
	NBIC$_{\text{CS}}$	Red-listed	32192	2285.22	29906.78	1.73
		Alien	35475	1036.34	34438.66	1.89
	NBIC$_{\text{Other}}$	Red-listed	6355	299.08	6055.92	1.82
		Alien	1027	17.13	1009.87	1.93
	NTNU	Red-listed	0	0.56	-0.56	-2.00
		Alien	0	0.47	-0.47	-2.00
	UiO$_{\text{Lichen}}$	Red-listed	11	1.48	9.52	1.53
	UiO$_{\text{Plant Notes}}$	Red-listed	8	3.65	4.35	0.75
		Alien	61	8.77	52.23	1.50
	UiO$_{\text{Plant Obs}}$	Red-listed	6	54.79	-48.79	-1.61
		Alien	15501	197.27	15303.73	1.95
Agriculture (unsp.)	KMN	Red-listed	0	0.01	-0.01	-2.00
		Alien	0	0.06	-0.06	-2.00
	BioFokus	Red-listed	31	6.73	24.27	1.29
		Alien	18	1.52	16.48	1.69
	eBird	Red-listed	1	2.24	-1.24	-0.77

		Alien	0	0.07	-0.07	-2.00
	Jordal	Red-listed	0	0.86	-0.86	-2.00
		Alien	0	0.42	-0.42	-2.00
	NBIC$_{CS}$	Red-listed	600	66.75	533.25	1.60
		Alien	575	30.31	544.69	1.80
	NBIC$_{Other}$	Red-listed	68	8.74	59.26	1.54
		Alien	2	0.51	1.49	1.19
	NTNU	Red-listed	0	0.02	-0.02	-2.00
		Alien	0	0.01	-0.01	-2.00
	UiO$_{Lichen}$	Red-listed	0	0.04	-0.04	-2.00
	UiO$_{Plant\ Notes}$	Red-listed	0	0.10	-0.10	-2.00
		Alien	0	0.25	-0.25	-2.00
	UiO$_{Plant\ Obs}$	Red-listed	0	1.63	-1.63	-2.00
		Alien	14	5.78	8.22	0.83
Cultivated land	KMN	Red-listed	4	2.76	1.24	0.37
		Alien	9	10.83	-1.83	-0.18
	BioFokus	Red-listed	2248	1263.42	984.58	0.56
		Alien	904	276.48	627.52	1.06
	eBird	Red-listed	1539	418.03	1120.97	1.15
		Alien	56	10.96	45.04	1.35
	Jordal	Red-listed	396	159.30	236.70	0.85
		Alien	289	73.10	215.90	1.19
	NBIC$_{CS}$	Red-listed	68657	12459.86	56197.14	1.39
		Alien	29489	5650.36	23838.64	1.36
	NBIC$_{Other}$	Red-listed	5301	1630.67	3670.33	1.06
		Alien	218	93.37	124.63	0.80
	NTNU	Red-listed	4	3.05	0.95	0.27
		Alien	11	2.58	8.42	1.24
	UiO$_{Lichen}$	Red-listed	3	8.06	-5.06	-0.92
	UiO$_{Plant\ Notes}$	Red-listed	75	19.88	55.12	1.16
		Alien	203	47.85	155.15	1.24
	UiO$_{Plant\ Obs}$	Red-listed	164	298.63	-134.63	-0.58

		Alien	3453	1075.51	2377.49	1.05
Home fields grazing land	KMN	Red-listed	0	0.59	-0.59	-2.00
		Alien	5	2.30	2.70	0.74
	BioFokus	Red-listed	2236	268.22	1967.78	1.57
		Alien	654	58.74	595.26	1.67
	eBird	Red-listed	243	88.76	154.24	0.93
		Alien	10	2.34	7.66	1.24
	Jordal	Red-listed	1502	33.83	1468.17	1.91
		Alien	540	15.54	524.46	1.89
	NBIC$_{\text{CS}}$	Red-listed	14502	2645.48	11856.52	1.38
		Alien	7549	1199.72	6349.28	1.45
	NBIC$_{\text{Other}}$	Red-listed	1232	346.23	885.77	1.12
		Alien	43	19.83	23.17	0.74
	NTNU	Red-listed	1	0.65	0.35	0.43
		Alien	0	0.55	-0.55	-2.00
	UiO$_{\text{Lichen}}$	Red-listed	7	1.71	5.29	1.21
	UiO$_{\text{Plant Notes}}$	Red-listed	20	4.22	15.78	1.30
		Alien	51	10.16	40.84	1.34
	UiO$_{\text{Plant Obs}}$	Red-listed	693	63.43	629.57	1.66
		Alien	275	228.37	46.63	0.19
Forest (unsp.)	KMN	Red-listed	2	5.40	-3.40	-0.92
		Alien	13	21.20	-8.20	-0.48
	BioFokus	Red-listed	1311	2472.81	-1161.81	-0.61
		Alien	485	541.09	-56.09	-0.11
	eBird	Red-listed	294	818.18	-524.18	-0.94
		Alien	4	21.43	-17.43	-1.37
	Jordal	Red-listed	84	311.77	-227.77	-1.15
		Alien	61	143.04	-82.04	-0.80
	NBIC$_{\text{CS}}$	Red-listed	10097	24386.49	-14289.49	-0.83
		Alien	7119	11058.88	-3939.88	-0.43
	NBIC$_{\text{Other}}$	Red-listed	3903	3191.55	711.45	0.20
		Alien	111	182.73	-71.73	-0.49

	NTNU	Red-listed	5	5.97	-0.97	-0.18
		Alien	3	5.06	-2.06	-0.51
	UiO$_{\text{Lichen}}$	Red-listed	2	15.78	-13.78	-1.55
	UiO$_{\text{Plant Notes}}$	Red-listed	21	38.92	-17.92	-0.60
		Alien	50	93.66	-43.66	-0.61
	UiO$_{\text{Plant Obs}}$	Red-listed	160	584.44	-424.44	-1.14
		Alien	2825	2104.98	720.02	0.29
Coniferous forest	KMN	Red-listed	9	18.04	-9.04	-0.67
		Alien	59	70.86	-11.86	-0.18
	BioFokus	Red-listed	21994	8265.05	13728.95	0.91
		Alien	2519	1808.42	710.58	0.33
	eBird	Red-listed	804	2734.62	-1930.62	-1.09
		Alien	39	71.61	-32.61	-0.59
	Jordal	Red-listed	324	1042.00	-718.00	-1.05
		Alien	140	478.04	-338.04	-1.09
	NBIC$_{\text{CS}}$	Red-listed	69319	81508.00	-12189.00	-0.16
		Alien	44651	36962.46	7688.54	0.19
	NBIC$_{\text{Other}}$	Red-listed	13206	10667.22	2538.78	0.21
		Alien	437	610.72	-173.72	-0.33
	NTNU	Red-listed	27	19.97	7.03	0.30
		Alien	43	16.91	26.09	0.87
	UiO$_{\text{Lichen}}$	Red-listed	166	52.76	113.24	1.04
	UiO$_{\text{Plant Notes}}$	Red-listed	249	130.09	118.91	0.63
		Alien	740	313.05	426.95	0.81
	UiO$_{\text{Plant Obs}}$	Red-listed	948	1953.34	-1005.34	-0.69
		Alien	5905	7035.53	-1130.53	-0.17
Deciduous forest	KMN	Red-listed	23	7.64	15.36	1.00
		Alien	54	30.01	23.99	0.57
	BioFokus	Red-listed	5306	3500.94	1805.06	0.41
		Alien	1068	766.05	301.95	0.33
	eBird	Red-listed	995	1158.35	-163.35	-0.15
		Alien	16	30.34	-14.34	-0.62

	Jordal	Red-listed	1538	441.38	1096.62	1.11
		Alien	741	202.51	538.49	1.14
	NBIC$_{\text{CS}}$	Red-listed	29165	34525.71	-5360.71	-0.17
		Alien	23683	15656.83	8026.17	0.41
	NBIC$_{\text{Other}}$	Red-listed	5845	4518.50	1326.50	0.26
		Alien	252	258.70	-6.70	-0.03
	NTNU	Red-listed	8	8.46	-0.46	-0.06
		Alien	14	7.16	6.84	0.65
	UiO$_{\text{Lichen}}$	Red-listed	21	22.35	-1.35	-0.06
	UiO$_{\text{Plant Notes}}$	Red-listed	84	55.10	28.90	0.42
		Alien	118	132.60	-14.60	-0.12
	UiO$_{\text{Plant Obs}}$	Red-listed	668	827.43	-159.43	-0.21
		Alien	2798	2980.17	-182.17	-0.06
Mixed forest	KMN	5	5	1.81	3.19	0.94
		31	31	7.10	23.90	1.25
	BioFokus	3283	3283	828.23	2454.77	1.19
		672	672	181.27	490.73	1.15
	eBird	221	221	274.04	-53.04	-0.21
		7	7	7.19	-0.19	-0.03
	Jordal	123	123	104.43	18.57	0.16
		26	26	47.93	-21.93	-0.59
	NBIC$_{\text{CS}}$	8896	8896	8168.15	727.85	0.09
		5462	5462	3704.15	1757.85	0.38
	NBIC$_{\text{Other}}$	1646	1646	1069.00	577.00	0.43
		38	38	61.21	-23.21	-0.47
	NTNU	3	3	2.00	1.00	0.40
		2	2	1.69	0.31	0.17
	UiO$_{\text{Lichen}}$	2	2	5.29	-3.29	-0.90
	UiO$_{\text{Plant Notes}}$	20	20	13.03	6.97	0.42
		40	40	31.37	8.63	0.24
	UiO$_{\text{Plant Obs}}$	263	263	195.78	67.22	0.29
		985	985	705.07	279.93	0.33

Open firm ground	KMN	Red-listed	17	36.14	-19.14	-0.72
		Alien	59	141.93	-82.93	-0.83
	BioFokus	Red-listed	3036	16556.05	-13520.05	-1.38
		Alien	1333	3622.48	-2289.48	-0.92
	eBird	Red-listed	3732	5477.82	-1745.82	-0.38
		Alien	41	143.43	-102.43	-1.11
	Jordal	Red-listed	1173	2087.25	-914.25	-0.56
		Alien	525	957.56	-432.56	-0.58
	NBIC$_{\text{CS}}$	Red-listed	64506	163271.52	-98765.52	-0.87
		Alien	22008	74040.76	-52032.76	-1.08
	NBIC$_{\text{Other}}$	Red-listed	12146	21367.86	-9221.86	-0.55
		Alien	193	1223.34	-1030.34	-1.45
	NTNU	Red-listed	49	40.00	9.00	0.20
		Alien	7	33.87	-26.87	-1.31
	UiO$_{\text{Lichen}}$	Red-listed	25	105.69	-80.69	-1.23
	UiO$_{\text{Plant Notes}}$	Red-listed	82	260.58	-178.58	-1.04
		Alien	93	627.09	-534.09	-1.48
	UiO$_{\text{Plant Obs}}$	Red-listed	6643	3912.78	2730.22	0.52
		Alien	4239	14093.09	-9854.09	-1.08
Mire	KMN	Red-listed	0	5.66	-5.66	-2.00
		Alien	3	22.24	-19.24	-1.52
	BioFokus	Red-listed	1039	2594.63	-1555.63	-0.86
		Alien	85	567.75	-482.75	-1.48
	eBird	Red-listed	351	858.48	-507.48	-0.84
		Alien	6	22.49	-16.49	-1.16
	Jordal	Red-listed	116	327.12	-211.12	-0.95
		Alien	57	150.09	-93.09	-0.90
	NBIC$_{\text{CS}}$	Red-listed	14758	25587.85	-10829.85	-0.54
		Alien	3470	11603.67	-8133.67	-1.08
	NBIC$_{\text{Other}}$	Red-listed	3117	3348.77	-231.77	-0.07
		Alien	49	191.73	-142.73	-1.19
	NTNU	Red-listed	3	6.27	-3.27	-0.71

		Alien	1	5.31	-4.31	-1.37
	UiO$_{\text{Lichen}}$	Red-listed	29	16.56	12.44	0.55
	UiO$_{\text{Plant Notes}}$	Red-listed	11	40.84	-29.84	-1.15
		Alien	21	98.27	-77.27	-1.30
	UiO$_{\text{Plant Obs}}$	Red-listed	261	613.23	-352.23	-0.81
		Alien	66	2208.68	-2142.68	-1.88
Snow/ice	KMN	Red-listed	0	0.74	-0.74	-2.00
		Alien	0	2.89	-2.89	-2.00
	BioFokus	Red-listed	2	336.98	-334.98	-1.98
		Alien	0	73.78	-73.78	-2.00
	eBird	Red-listed	15	111.51	-96.51	-1.53
		Alien	0	2.93	-2.93	-2.00
	Jordal	Red-listed	0	42.50	-42.50	-2.00
		Alien	0	19.52	-19.52	-2.00
	NBIC$_{\text{CS}}$	Red-listed	14	3323.56	-3309.56	-1.98
		Alien	0	1507.21	-1507.21	-2.00
	NBIC$_{\text{Other}}$	Red-listed	1	434.97	-433.97	-1.99
		Alien	0	24.91	-24.91	-2.00
	NTNU	Red-listed	0	0.81	-0.81	-2.00
		Alien	0	0.69	-0.69	-2.00
	UiO$_{\text{Lichen}}$	Red-listed	0	2.15	-2.15	-2.00
	UiO$_{\text{Plant Notes}}$	Red-listed	0	5.30	-5.30	-2.00
		Alien	0	12.76	-12.76	-2.00
	UiO$_{\text{Plant Obs}}$	Red-listed	0	79.68	-79.68	-2.00
		Alien	0	286.90	-286.90	-2.00
Freshwater	KMN	Red-listed	2	4.80	-2.80	-0.82
		Alien	35	18.87	16.13	0.60
	BioFokus	Red-listed	1012	2201.54	-1189.54	-0.74
		Alien	287	481.74	-194.74	-0.51
	eBird	Red-listed	1097	728.42	368.58	0.40
		Alien	81	19.09	61.91	1.24
	Jordal	Red-listed	45	277.57	-232.57	-1.44

		Alien	27	127.35	-100.35	-1.30
	NBIC$_{\text{CS}}$	Red-listed	47065	21711.30	25353.70	0.74
		Alien	6518	9845.72	-3327.72	-0.41
	NBIC$_{\text{Other}}$	Red-listed	1537	2841.43	-1304.43	-0.60
		Alien	454	162.68	291.32	0.94
	NTNU	Red-listed	1	5.32	-4.32	-1.37
		Alien	5	4.50	0.50	0.10
	UiO$_{\text{Lichen}}$	Red-listed	4	14.05	-10.05	-1.11
	UiO$_{\text{Plant Notes}}$	Red-listed	21	34.65	-13.65	-0.49
		Alien	43	83.38	-40.38	-0.64
	UiO$_{\text{Plant Obs}}$	Red-listed	207	520.33	-313.33	-0.86
		Alien	67	1874.07	-1807.07	-1.86
Ocean	KMN	Red-listed	31	8.08	22.92	1.17
		Alien	97	31.75	65.25	1.01
	BioFokus	Red-listed	340	3704.15	-3364.15	-1.66
		Alien	169	810.51	-641.51	-1.31
	eBird	Red-listed	2303	1225.58	1077.42	0.61
		Alien	49	32.10	16.90	0.42
	Jordal	Red-listed	33	467.00	-434.00	-1.74
		Alien	46	214.26	-168.26	-1.29
	NBIC$_{\text{CS}}$	Red-listed	60109	36529.70	23579.30	0.49
		Alien	4406	16565.61	-12159.61	-1.16
	NBIC$_{\text{Other}}$	Red-listed	576	4780.77	-4204.77	-1.57
		Alien	322	273.71	48.29	0.16
	NTNU	Red-listed	2	8.95	-6.95	-1.27
		Alien	1	7.58	-6.58	-1.53
	UiO$_{\text{Lichen}}$	Red-listed	2	23.65	-21.65	-1.69
	UiO$_{\text{Plant Notes}}$	Red-listed	79	58.30	20.70	0.30
		Alien	193	140.30	52.70	0.32
	UiO$_{\text{Plant Obs}}$	Red-listed	50	875.45	-825.45	-1.78
		Alien	116	3153.15	-3037.15	-1.86
	KMN	Red-listed	0	0.00	0.00	-2.00*

Not mapped		Alien	0	0.00	0.00	-2.00*
	BioFokus	Red-listed	3	0.11	2.89	1.86
		Alien	1	0.07	0.93	1.72
	eBird	Red-listed	1	0.05	0.95	1.82
		Alien	0	0.02	-0.02	-2.00*
	Jordal	Red-listed	0	0.03	-0.03	-2.00*
		Alien	0	0.03	-0.03	-2.00*
	NBIC_{CS}	Red-listed	0	1.43	-1.43	-2.00
		Alien	1	0.68	0.32	0.37
	$\text{NBIC}_{\text{Other}}$	Red-listed	19	0.20	18.80	1.96
		Alien	0	0.02	-0.02	-2.00*
	NTNU	Red-listed	0	0.00	0.00	-2.00*
		Alien	0	0.00	0.00	-2.00*
	$\text{UiO}_{\text{Lichen}}$	Red-listed	0	0.00	0.00	-2.00*
	$\text{UiO}_{\text{Plant Notes}}$	Red-listed	0	0.00	0.00	-2.00*
		Alien	0	0.00	0.00	-2.00*
	$\text{UiO}_{\text{Plant Obs}}$	Red-listed	0	0.06	-0.06	-2.00
		Alien	0	0.14	-0.14	-2.00

S.7. Effects of recorder group on species diversity estimates

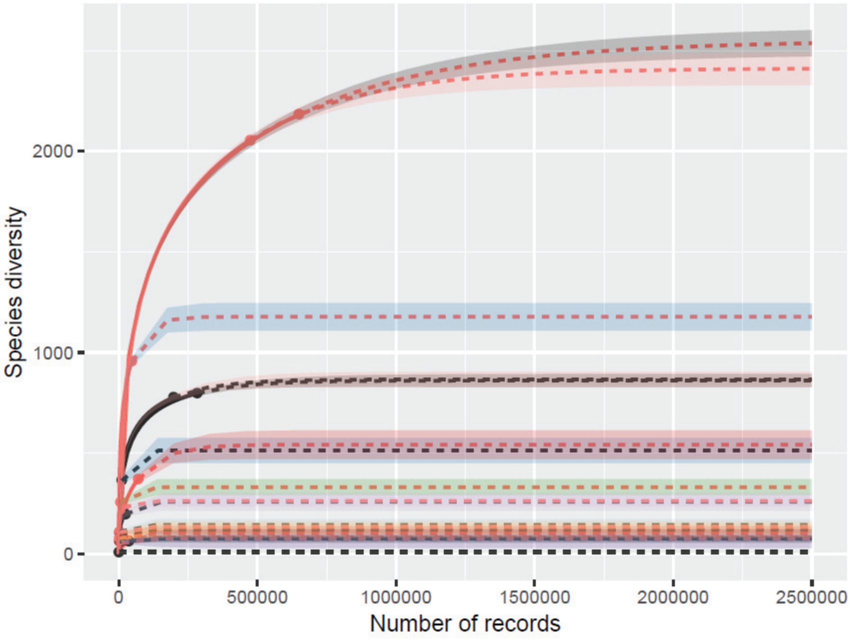

Figure S.10. Species accumulation curves based on individual based rarefaction. Conservation status is indicated by line colour, dataset is indicated by ribbon colour (see Fig. S.4 for colour legend). Solid lines reflect the interpolated species richness, dashed lines reflect the extrapolated species richness, filled circles show the observed species richness. Ribbons illustrate the 0.95 confidence interval.

Table S.7. Observed and estimated, asymptotic species richness for the four record groups, and the combined citizen science- and professional data.

Dataset	**Observed species richness**	**Estimated species richness**	**S.E.**	**Lower 0.95 CI**	**Upper 0.95 CI**
KMN, red-listed	63	76.486	8.310	67.436	104
KMN, alien	110	144.021	15.705	124.375	190.513
BioFokus, red-listed	955	1 177.722	40.849	1 110.932	1 273.121
BioFokus, alien	364	513.619	34.510	459.762	597.766
eBird, red-listed	78	78.000	0,440	78.000	79.080
eBird, alien	8	8.000	0.548	8.000	9.479
Jordal, red-listed	257	331.408	25.670	295.564	400.568
Jordal, alien	61	73.497	8.455	64.751	102.628
NBIC$_{CS}$, red-listed	2 055	2 412.084	45.691	2 333.161	2 513.104
NBIC$_{CS}$, alien	777	866.706	21.783	833.116	920.404
NBIC$_{Other}$, red-listed	372	542.664	41.081	479.183	643.744
NBIC$_{Other}$, alien	103	119.527	9.006	109.084	147.897
NTNU, red-listed	106	135.380	16.595	116.474	188.410
NTNU, alien	81	117.952	17.838	96.069	171.618
UiO$_{Lichen}$, red-listed	78	99.990	12.405	85.849	139.607
UiO$_{Plant\ Notes}$, red-listed	233	263.419	13.711	246.094	303.666
UiO$_{Plant\ Notes}$, alien	198	259.359	24.309	227.031	327.685
UiO$_{Plant\ Obs}$, red-listed	55	75.248	20.185	58.975	158.151
UiO$_{Plant\ Obs}$, alien	63	75.500	8.457	66.752	104.637
Combined, red-listed	2 182	2 550.166	46.987	2 468.978	2 654.322
Combined, alien	798	860.969	16.400	836.112	902.037

Paper II

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Urban aliens and threatened near-naturals: Land-cover affects the species richness of alien- and threatened species in an urban-rural setting

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Urbanisation has strong effects on biodiversity patterns, but impacts vary among species groups and across spatial scales. From a local biodiversity management perspective, a more general understanding of species richness across taxonomic groups is required. This study aims to investigate how fine-scale land-cover variables influence species richness patterns of locally threatened and alien species. The study was performed in Trondheim, Norway, covering a steep urbanisation gradient. Spatially correlated Generalised Linear Mixed Effects Models predicting the number of all-, threatened-and alien species by taxon, habitat, habitat heterogeneity and mean aspect within 500 m × 500 m grid cells were constructed. The habitat categories were based on detailed land-cover maps. The highest number of threatened species was found in habitats relatively less affected by humans, whereas the number of alien species were only dependent on taxonomic group and spatial correlation. It is shown that land-cover variables within an administrative border can be used to make predictions on species richness within overarching species groups. Recommendations to biodiversity management agencies are to ensure protection of natural habitats to favour locally threatened species, and closely monitor urban areas to mitigate the introduction and spread of alien species.

The majority of the world's population now live in cities, and urbanisation is predicted to increase further in the future[1,2]. Cities are frequently located in biodiversity hotspots, and increases in urban areas inevitably will happen at the cost of other habitats important for biodiversity[3–6]. This calls for studies detailing how to manage biodiversity efficiently and properly in urban areas.

Various effects of urbanisation on biodiversity have been suggested and reported, depending on the exact variables in question, and the trends differ among taxa[5,7,8]. For example, urbanisation can be a homogenising force on multiple spatial scales, impoverishing the local native species pool[7,9,10], while supplying alien species[11,12]. Thus, alpha diversity might increase, despite larger-scale beta diversity decrease[13,14]. The positive correlation between plant species richness and urbanisation can be caused by high habitat heterogeneity in urban areas, due to patches of remnant (semi-)natural habitats, allowing species with different requirements to persist[15]. Other reasons can be the introduction of alien plant species, e.g. for ornamental purposes, and a natural high productivity independent of human settlement[7,11,16].

Cadotte *et al.* (2017)[17] reported that alien species richness generally increases with urbanisation. In contrast, other studies have linked urban areas with relatively high numbers of native and/or threatened species (see e.g. Kühn and Klotz (2006)[14], Kowarik (2011)[5] and references, and Ives *et al.* (2016)[18]).

Studies of biodiversity in relation to land use, urbanisation and human disturbance have been carried out on vastly different spatial scales (meters to > 1000 km) (e.g. Blair (1996)[13], Kühn and Klotz (2006)[14], Pautasso (2007)[19], Ahrne *et al.* (2009)[20] and Bertolino *et al.* (2015)[21]). Studies on a fine spatial scale, including a broad urbanisation gradient (ranging from industrialised to natural areas) are largely lacking however (but see Turrini

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and Knop (2015)[22] and Concepción *et al.* (2016)[23])[20]. If the results of biodiversity research are to be used by local management, it is crucial that these results are obtained and delivered on a relatively small spatial scale, appropriate for potential management intervention. Hence, this study is performed on a spatial scale in close accordance with the spatial scale of urban planning and management.

For conservation purposes, focus is frequently placed on restricted groups, such as protection of native, threatened species or mitigation of alien species (see e.g. the Norwegian 'Natural diversity' law[24], the EU Habitats Directive[25], and the EU Regulation on Invasive Alien Species[26]). In particular, the similarities and differences in variables determining their distributions are of interest, e.g. alien species being favoured by urbanisation, whereas native species can be threatened by such[27,28]. Knowledge of how broad land-cover variables affect the distribution and richness of these groups could help guide decisions on city development and biodiversity management on municipality level. Threatened and alien species have rarely been investigated simultaneously (but see Deutschewitz *et al.* (2003)[29], Kühn *et al.* (2004)[16] and Matthies *et al.* (2017)[30].

The aim of this study is to investigate which general, fine-scale land-cover variables influence species richness patterns of all species, as well as specifically rare and non-native species. As a case study system, we use a northern European municipality with a strong urban to rural gradient. We predict that:

Urban areas are predicted to have higher levels of alien species richness compared to non-urban areas, as cities function as introduction sites for (plant) species associated with gardens. Similarly, key pathways for introduction of alien species are through trade and traffic, which are more prevalent in urban areas than outside[5,10,17,31,32].

Urban areas are predicted to have relatively low levels of threatened species richness due to the high level of disturbance in urban areas[7,8]. However, naturally high levels of biodiversity or suitable microhabitats within the urban matrix can potentially lead to the opposite pattern[5,16,18]. Urban areas are viewed here as areas dominated by build-up area and immediately surrounding areas.

Forests are predicted to have high levels of both threatened- and alien species richness, as approx. 48% of the Norwegian Red-listed species are generally affiliated with forests, while several alien tree species have been planted for forestry purposes throughout Norway[33–35] The associations between species richness and forest cover might depend on more fine-scale forest composition and structure, out of scope of this study.

Coastal areas are ecotones, and are thus expected to host a high number of species[36].

Open areas with sparse vegetation (or otherwise disturbed habitat) are predicted to have high levels of alien species richness, as these are able to exploit disturbed habitat[5,17,27]; e.g. alien plant species with a ruderal life strategy[37].

Habitat heterogeneity affect the richness of both groups positively, as more diverse habitat within an area provide resources for different requirements[4,29,30,36,38–41].

Topography: North-facing slopes are expected to be negatively correlated with overall species richness, as plants are negatively affected by a lack of light and lower temperatures[42].

Materials and Methods

Study area.

The study was carried out within Trondheim Municipality (Norway) administrative borders, around 63.42°N, 10.38°E (Fig. 1a,b). It is a southern-boreal[43], coastal municipality with an area of 342 km^2, a population of approximately 190,000 people[44], and annual mean temperature and precipitation are approximately 5 °C and 887 mm[45]. The municipality holds a steep urbanisation gradient; from the city centre and industrial areas, through rural areas including agricultural areas and commercial forests, and to nature reserves and areas managed for biodiversity conservation. The municipality covers highly different nature types, including both coastline, subalpine areas and limnic systems, and thus has a high potential for varied biological communities and high levels of biodiversity[44]. Trondheim municipality is fairly well-sampled with regards to species occurrence records, e.g. due to the presence and activity of the University Museum.

Data retrieval and data cleaning.

Land cover data. Land cover was based on the Norwegian AR5 maps (Land Resource map 1:5000) from NIBIO[46]. Shapefiles of the land cover maps were provided by the Trondheim Municipality in April 2018. The AR5 maps are both continually and periodically updated, and provides the most complete data on national land resources[47]. Land cover is categorised based on land cover type, tree cover type, timber productivity and soil condition, giving 66 functionally unique categories within Trondheim municipality (hereafter called "land cover types") (Supplementary Material 1, Table S.1). The map was overlaid by a 500 m × 500 m grid.

Updates of the AR5 maps are mainly done if the categorical classification of an area changes, and the responsible authorities are notified of this change[46]. Consequently, "unannounced" changes are not reflected in the data. As the land cover data was matched with GBIF records from 2013–2018, changes within this period are not taken into account.

Aspect of the terrain was retrieved from a Digital Terrain Model raster with a resolution of 25 m × 25 m. The circular aspect (unit: degrees) was transformed to a "*northness*"-measure by $Northness = cosin(Aspect(°))$, hence fitting a scale of -1 to 1 (in this definition: -1 = south-facing, 1 = north-facing). The values were rescaled to a gradient from 0 to 1 to match the scale of other included variables. All flat areas were given NA-values. For each grid cell, northness was calculated as the mean of all raster cells within the overlaid grid cell.

GBIF occurrence records. Large amounts of data on species occurrences are available from online databases, such as the Global Biodiversity Information Facility (GBIF)[48], and the Norwegian Biodiversity Information Centre[49].

All occurrence records from a bounding box around Trondheim Municipality (the exact municipality border was too detailed to include in the process) were downloaded from GBIF on 06/03-2018[50] (864,715 records in

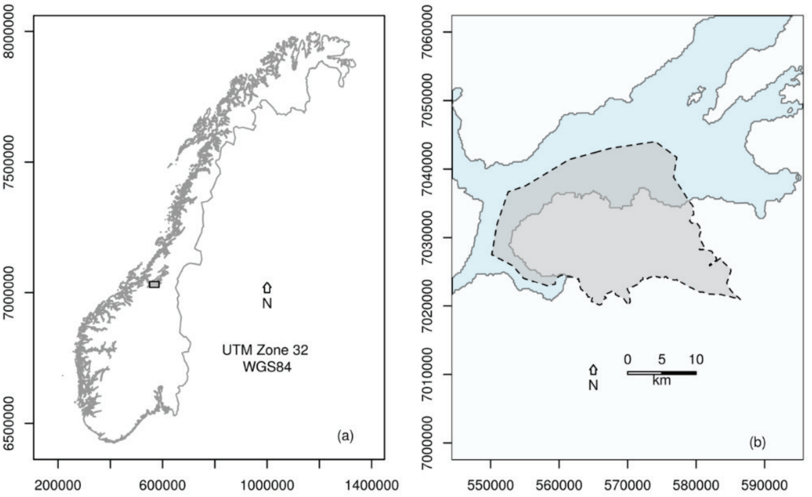

Figure 1. Location of study system. (**a**) Map of Norway, position of Trondheim Municipality indicated with a grey box, (**b**) Trondheim Municipality, municipality border indicated with dashed line and grey colour. The figure was made in R, version 3.6.1[55].

total, giving 9,117 unique species names; 48,468 records not identified to species level), and subsequently spatially filtered according to the municipality border. The data was additionally filtered according to the following criteria, reducing the number of records to 251,803 across 3,097 unique species names:

1. Records containing a full species name for comparability with the threatened- and alien species lists.
2. Coordinate uncertainty of $\leq$354 m, (1/2 length of the diagonal of 500 m × 500 m grid cells).
3. Records made between January 1st 2013 and March 6th 2018 to ensure compatibility with the used land cover maps, and a negligible amount of land cover change.

Of these records, 94.9% were within the kingdom Animalia (91.4% of the total data set were birds), 3.7% within Plantae, and 1.3% within Fungi. 0.65‰ (163 records) were from outside these kingdoms (Supplementary material 2, Table S.2). The data set was divided into threatened- and alien species (only including animals, plants and fungi).

The "threatened" status was defined based on one or more assessments of the national Norwegian Red List from 2006, 2010 and 2015, provided by The Norwegian Biodiversity Information Centre. See Supplementary material 3 for detailed description of inclusion details.

The "alien" status was based on the Alien Species List (v. 2012[51]) from The Norwegian Biodiversity Information Centre. Only species alien in mainland Norway were retained (excluding species alien only to Svalbard). All alien species were included, regardless of risk category. Discrepancies in nomenclature between GBIF records and species lists were resolved using the Taxonomic Name Resolver (function "`tnrs`" from the `taxize`-package[52]). Only terrestrial and limnic species were included in the data sets. All species classified as marine by The Norwegian Biodiversity Information Centre were manually excluded from the lists (excluding birds; all bird species in the data set were regarded as terrestrial).

32,585 records (121 unique species names) could be categorised as threatened (99.3% animals, 98.9% birds, 0.3% plants and 0.4% fungi), and 3,447 (177 species) as alien (64.6% animals, 63.4% birds, 34.3% plants and 1.1% fungi) (Supplementary material 2, Table S.2). The risk of species mis-identification is considered negligible, as the majority of records are associated with organisations deemed reliable regarding species identification (e.g. the Norwegian Ornithological Society, the Norwegian Botanical Society and the NTNU University Museum herbarium). Furthermore, as individual species are not analysed, it is unlikely that single erroneous records will affect the aggregated species pool.

The number of threatened- and alien species, and the overall species richness, registered within each grid cell was calculated, and divided into five taxonomic groups: birds, non-avian animals, plants, fungi and other taxa. "Other taxa" was excluded from further analyses due to a low amount of data.

Preparation of variables. *Land cover variables.* To reduce the number of land cover types while avoiding subjectively defining categories, hierarchical cluster analysis was used to identify grid cells with similar composition, creating a limited number of clustered land cover type categories. All grid cells within the administrative border of the Trondheim municipality were used for the cluster analysis, including cells only partially within the

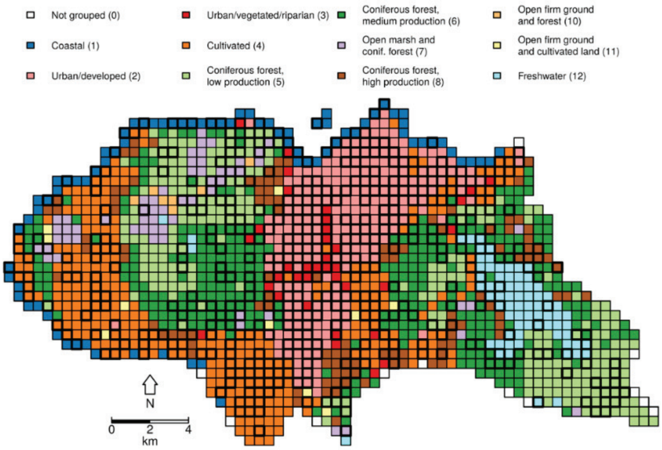

Figure 2. Trondheim Municipality coloured by habitat. Colour definitions shown in the legend. Numbers and names refer to cluster number and the given habitat name. Grid cells used for modelling are indicated with a black border. The figure was made in R, version 3.6.1[55].

municipality border, including only the within-municipality area. Marine grid cells (entirely covered by ocean) were not included, resulting in 1509 grid cells in total.

The cluster analysis was done using the function "`hclust`" on a dissimilarity matrix based on the AR5 land cover in each grid cell, using "`Complete linkage`" as the clustering method, and a Bray-Curtis dissimilarity matrix of the individual grid cells (function "`vegdist`", package `vegan`[53]). Cut-off value was set at *height*=0.99 (referring to the height of the cluster-tree, where height=1 indicates no clustering, and height=0 each individual branch (grid cell) being an autonomous cluster), resulting in 17 clusters in total, of which 6 included $\leq$3 grid cells. The clusters including $\leq$3 grid cells were mainly found on the municipality border. These were excluded from further analysis. Each cluster will hereafter be referred to as a "habitat".

The habitats were named according to the (on average) dominating land cover types within the cells (Fig. 2, Supplementary Material 1, Fig. S.1). The number of grid cells per habitat was median 76.5 (interquartile range 30-242.25, Table 1). The most frequent habitat within the municipality was *Cultivated*, followed by *Coniferous forest* and *Urban/developed areas*.

Outliers in the number of records or number of species (evaluated separately for each taxon level) were excluded based on Tukey's method (0.75 quantile + 1.5*IQR). Subsequently, the habitats *Open firm ground and forest* and *Open firm ground and cultivated land* were excluded from the analyses, as only one and two grid cells remained, respectively. 485 grid cells were included in the subsequent analyses (Fig. 2).

Habitat heterogeneity was calculated for each grid cell as the Simpson's Diversity Index. The index is calculated as 1-*D*, where *D* is $D = \sum\left(\frac{n}{N}\right)^2$, and *n* is the total area of a particular land cover type, *N* is the total area of the grid cell. The index ranges between zero (completely homogeneous land cover) and one (infinite heterogeneity in land cover; a hypothetical value). The grid cells included in the analyses ranged between 0.012 and 0.884.

Statistical analyses. Generalised Linear Mixed Effects Models (GLMM) were constructed, predicting the threatened- (Poisson error distribution), alien- (Poisson error distribution), and overall (negative binomial error distribution due to overdispersion) number of species in each grid cell by habitat, habitat heterogeneity, northness, including an interaction with taxon (birds, non-avian animals, plants, fungi and other taxa) for all variables. Total number of records within grid cells were used as offset to account for differences in sampling effort. To account for spatial autocorrelation (*Moran's I* > 1 in exploratory Generalised Linear Models), a Matérn correlation function was used as a random effect (package `spaMM`[54]). The models were fitted using Maximum Likelihood. Model selection was performed as stepwise backwards selection, based on AIC on the full models of the form: $No.\ species = habitat * taxon + habitat\ heterogeneity * taxon + northness * taxon + Matern(1 \mid longitude + latitude)$. The models were subsequently used to predict species richness across all grid cells within the Trondheim municipality, using 100 records as an offset.

All data preparation, analyses and figures were made in R, version 3.6.1[55].

Results

Different models proved to be optimal for the three species groups (all-, threatened- and alien species). For overall species richness, all predictors and interaction terms were retained, whereas threatened species richness was predicted by habitat, northness and taxon. Alien species richness was only predicted by taxon (Tables 2–4, Figs. 3–6). The spatial correlation parameters for total- (ν=0.460, ρ=0.001), threatened- (ν=2.254, ρ=0.005), and

Habitat no.	Name	No. (total)	No. (models)
0	Not grouped	12	0
1	Coastal	79	26
2	Urban/developed	249	142
3	Urban/vegetated/riparian	36	15
4	Cultivated	319	122
5	Coniferous forest, low production	240	51
6	Coniferous forest, medium production	315	68
7	Open marsh and coniferous forest	59	15
8	Coniferous forest, high production	109	28
10	Open firm ground and forest	7	0
11	Open firm ground and cultivated land	10	0
12	Freshwater	74	18
	Sum	1509	485

Table 1. Distribution of grid cells among habitats. The grid cells in the Not grouped-habitat include six clusters containing ≤ 3 grid cells. The number of grid cells used for modelling were the ones fulfilling the criteria listed in the methods. All grid cells were used for the predictions, except for habitat 10 and 11, as no grid cells from these habitats were included in the model building, thus having values undefined for the parameter.

alien (ν=0.759, ρ=0.002) species richness indicate that all model predictions are spatially correlated (Tables 2–4). Plotting the estimated correlations against distances indicate total species richness having the farthest-reaching correlations, followed by alien and threatened species richness (Supplementary material 4, Fig. S.2).

Total species richness. For overall species richness, northness had a negative effect on species richness, the magnitude varying with taxon (Table 2, Fig. 4): non-avian animals responded most strongly to northness, followed by fungi, plants and birds. The response to habitat heterogeneity varied by taxon: plants and birds responding positively to increasing levels of habitat heterogeneity, fungi and non-avian animals having a negative response (Fig. 5). Similarly, the response to habitat differed among taxa, all other variables being held constant at mean values: fewest birds are predicted in *Open marsh and coniferous forest* followed by *Coastal*, *Freshwater*, *Coniferous forest; high production* and *Urban/developed*. The highest number was predicted for *Cultivated*, followed by *Urban/vegetated/riparian*, *Coniferous forest; low production* and *–medium production*. However, 0.95 C.I. overlapped for all habitats. For non-avian animals, *Cultivated* and *Urban/developed* had lower predicted species richness compared to *Open marsh and coniferous forest*, and *Cultivated* was lower than *Coniferous forest; low production* and *–medium production* as well. All other 0.95 C.I. overlapped. The highest number of fungi species was predicted for *Open marsh and coniferous forest*, 0.95 C.I. only overlapping with *Coniferous forest; high production*. The lowest number was predicted for *Coastal*, 0.95. C.I. overlapping with *Freshwater*, *Cultivated*, *Urban/vegetated/riparian* and *Urban/developed*. The lowest number of plants was predicted for *Freshwater*, followed by *Urban/developed* (0.95 overlapping with *Urban/vegetated/riparian*, *Cultivated* and *Coniferous forest; high production*). The highest number was predicted for *Open marsh and coniferous forest*, 0.95 C.I. overlapping with *Coastal*, *Coniferous forest; medium production*, *- low production* and *Coniferous forest; high production* (Fig. 6).

Threatened species richness. For threatened species, increasing values of northness increase the predicted number of species (Table 3, Fig. 4). The highest species richness values are found for birds, followed by non-avian animals, fungi and plants. However, 0.95 C.I. overlap for all taxa except for birds and plants in *Urban/developed-* and *Cultivated* areas. The highest numbers of species are found in *Open marsh and coniferous forest*, followed by *Cultivated*, *Coastal*, *Freshwater*, *Urban/developed*, *Coniferous forest; low production*, *- high production*, *Urban/vegetated/riparian*, and *Coniferous forest*; *medium production*. However, all 0.95 C.I. overlap (Fig. 6).

Alien species richness. For alien species, only taxon was retained as a predictor; the highest number of species predicted for plants, followed by non-avian animals, fungi and birds. However, the 0.95 C.I. overlapped for all taxa except birds and plants (Table 4, Fig. 6).

Discussion

Urban areas are often found to have high levels of biodiversity, but little is known on how fine-scale land use is structuring species diversity in cities. We used species occurrence records from GBIF and official land cover classifications to determine how habitat affects total species richness, and the number of threatened and alien species. We did so by constructing spatially correlated Generalised Linear Mixed Effects Models based on habitat, habitat heterogeneity, aspect and taxonomic group within 500 m × 500 m grid cells across the Trondheim municipality, selecting the best models based on ΔAIC. The best models varied for overall-, threatened and alien

Fixed effects (family: negative binomial, shape = 0.789)			
Marginal AIC: 8014.325	**Estimate**	**Cond.SE**	**t-value**
(Intercept)	−0.979	0.347	−2.819
Urban/developed	0.198	0.288	0.689
Urban/vegetated/riparian	0.295	0.428	0.689
Cultivated	0.339	0.297	1.142
Coniferous forest, low production	0.273	0.323	0.845
Coniferous forest, medium production	0.265	0.314	0.841
Open marsh and coniferous forest	−0.172	0.433	−0.396
Coniferous forest, high production	0.192	0.367	0.525
Freshwater	0.148	0.399	0.371
Plantae	−1.998	0.503	−3.975
Animal	−1.660	0.545	−3.047
Fungi	−4.834	0.938	−5.156
Habitat heterogeneity	0.007	0.326	0.021
Northness	−0.056	0.287	−0.194
Urban/developed: Plantae	−1.418	0.402	−3.525
Urban/vegetated/riparian: Plantae	−1.378	0.612	−2.253
Cultivated: Plantae	−1.063	0.421	−2.526
Coniferous forest, low production: Plantae	−0.621	0.458	−1.355
Coniferous forest, medium production: Plantae	−0.534	0.443	−1.205
Open marsh and coniferous forest: Plantae	0.648	0.599	1.082
Coniferous forest, high production: Plantae	−0.685	0.521	−1.314
Freshwater: Plantae	−4.267	0.930	−4.589
Urban/developed: Animal	−0.956	0.434	−2.206
Urban/vegetated/riparian: Animal	−0.634	0.663	−0.956
Cultivated: Animal	−1.719	0.468	−3.677
Coniferous forest, low production: Animal	−0.551	0.501	−1.099
Coniferous forest, medium production: Animal	−0.628	0.485	−1.294
Open marsh and coniferous forest: Animal	0.612	0.654	0.935
Coniferous forest, high production: Animal	−0.860	0.581	−1.480
Freshwater: Animal	−1.281	0.655	−1.954
Urban/developed: Fungi	1.684	0.862	1.952
Urban/vegetated/riparian: Fungi	1.569	1.052	1.492
Cultivated: Fungi	1.142	0.883	1.294
Coniferous forest, low production: Fungi	2.126	0.906	2.345
Coniferous forest, medium production: Fungi	2.071	0.894	2.316
Open marsh and coniferous forest: Fungi	4.054	0.988	4.103
Coniferous forest, high production: Fungi	2.513	0.945	2.659
Freshwater: Fungi	0.215	1.160	0.185
Plantae: Habitat heterogeneity	2.002	0.481	4.165
Animal: Habitat heterogeneity	−0.022	0.528	−0.041
Fungi: Habitat heterogeneity	−0.367	0.604	−0.608
Plantae: Northness	−0.084	0.398	−0.211
Animal: Northness	−0.681	0.453	−1.503
Fungi: Northness	−0.423	0.501	−0.844
Random effects (family: Gaussian)			
Correlation parameters		Variance parameters	
ν	ρ	λ	
0.460	0.00123	0.118	

Table 2. Model output, total species richness. Model output from the spatially correlated GLMM of total species richness. The model was constructed with a negative binomial error structure. The factor levels *Coastal* and *Aves* are used as intercepts, thus categorical predictor values are relative to these.

species richness, with total species richness depending on all predictors and their interaction with taxon, whereas threatened species richness depended on habitat, aspect and taxon, and alien species richness only depended on taxon. The relationship between species richness in general are highly complex and dependent on multiple factors and interactions (Table 2, Figs. 3–6). Threatened, native species are associated with non-anthropogenic habitats (Table 3, Figs. 4 and 6), whereas alien species are mainly affected by spatial correlations on the investigated spatial

Fixed effects (family: Poisson)			
Marginal AIC: 1400.967	**Estimate**	**Cond.SE**	**t-value**
(Intercept)	−2.982	0.248	−12.022
Urban/developed	−0.420	0.195	−2.151
Urban/vegetated/riparian	−0.681	0.322	−2.114
Cultivated	0.003	0.204	0.015
Coniferous forest, low production	−0.506	0.314	−1.611
Coniferous forest, medium production	−0.753	0.272	−2.764
Open marsh and coniferous forest	0.436	0.431	1.013
Coniferous forest, high production	−0.533	0.311	−1.714
Freshwater	−0.333	0.325	−1.026
Plantae	−0.987	0.320	−3.089
Animal	−0.259	0.283	−0.912
Fungi	−0.353	0.411	−0.858
Northness	0.384	0.234	1.642
Random effects (family: Gaussian)			
Correlation parameters		Variance parameters	
ν	ρ	λ	
2.254	0.00511	0.1984	

Table 3. Model output from the spatially correlated GLMM of threatened species richness. The model was constructed with a Poisson error structure. The factor levels *Coastal* and *Aves* are used as intercepts, thus categorical predictor values are relative to these.

scale (Table 4). The key findings of this study advance our understanding of the field by confirming the association of threatened, native species with more natural habitats, and the potential for establishment of alien species across all habitats on a management-relevant spatial scale.

The retention of all predictors and interactions in the model of overall species richness illustrate the complex relationships between environmental variables and different taxonomic groups. Nevertheless, the overall negative effect of northness reflect the low species richness of north-facing slopes, compared to south-facing ones[42] (Fig. 4). The different taxa responded differently to increasing habitat heterogeneity, the only unidirectional response being for plants (positive) (Fig. 5). This supports the results of Matthies *et al.* (2017)[30] and Beninde *et al.* (2015)[56], in which respectively habitat heterogeneity and habitat richness were positively associated with species richness in urban areas. However, other studies have found a positive correlation for restricted taxonomic groups, such as arthropods[29,40], birds and mammals[30], which was not observed here.

Non-surprisingly, the different taxa responded differently to various habitats (Fig. 6). Interestingly, whereas plants, fungi and non-avian animals generally responded negatively to urban areas (differences not necessarily significantly different from other habitats however), the effect was less pronounced for birds. This could reflect their high mobility, and potential for an "urban adapter/exploiter"-status of some bird species[13]. In contrast, the habitat with the highest predicted number of both plant-, non-avian animal-, and fungi species, had the lowest predicted number of bird species.

Threatened species richness generally responded positively to increasing northness, in contrast to what would be expected (Fig. 4). This could potentially be an artefact of the habitat associations; *Coastal* areas had higher northness values (*mean* = *0.758, S.E.* = *0.022* compared to the overall *mean* = *5.35, S.E.* = *0.005*). The effect of taxon reflects the differences in the number of species within each taxonomic group being classified as threatened; (50 bird species, 26 plant species, 12 non-avian animal species, 33 fungi species included in the study). For all taxa, the lowest species numbers are predicted for all variants of coniferous forest, contrary to the initial expectations, and urban areas (Fig. 6). The negative effect of urban areas on threatened species richness mirrors the findings of Aronson *et al.* (2014)[8], and emphasises how vulnerable native species are not pre-adapted to the changed environments of the city. Contrary to expectations, the effect of the various forest habitats on threatened species is lower than for most other habitats (Table 3). The low number of threatened species in forests can be due to the lack of sampling, showing a spatial bias in the data rather than an effect. This should however be accounted for by using the number of records as an offset in the models. Rather, large parts of the forested areas in Trondheim are srongly affected by previous afforestation for timber production, where mainly coniferous species (both native and alien) were planted[33]. These forests might not provide the needed conditions for native species[57]. Plantations and secondary vegetation have been shown to harbour fewer species than primary forests[58,59]. The lack of association between forested areas and threatened species calls for a nuanced perspective on what forest types constitute suitable habitats for species of interest, as indicated by Ingram *et al.* (2015)[58] and Horák *et al.* (2019)[59]. The highest species numbers are predicted for *Open marsh and coniferous forest* and *Coastal* areas (Fig. 6); the former is likely the habitat category reflecting the lowest human impact. The high number of threatened species in coastal habitats can likely be ascribed to these habitats being ecotones, providing varied habitat conditions. Ecotones have

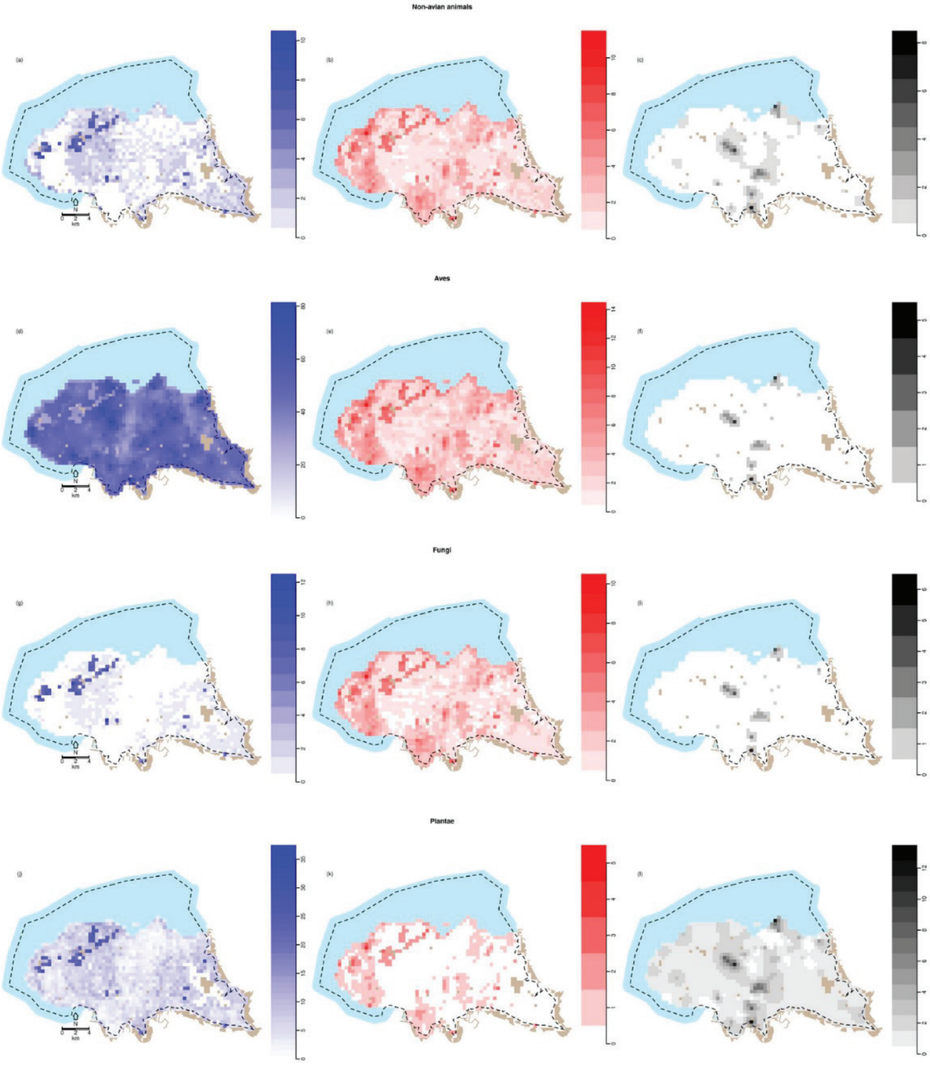

Figure 3. Maps of predicted species richness. Predicted number of species for each taxonomic- and species group given the realised habitat, habitat heterogeneity and northness. All predictions were made using 100 records (i.e. sampling events) as the offset. (**a**) Non-avian animals in total; (**b**) Threatened non-avian animals; (**c**) Alien non-avian animals; (**d**) Birds in total; (**e**) Threatened birds; (**f**) Alien birds; (**g**) Fungi in total; (**h**) Threatened fungi; (**i**) Alien fungi; (**j**) Plants in total; (**k**) Threatened plants; (**l**) Alien plants. The figure was made in R, version 3.6.1[55].

been suggested to have an increased species richness[36]. Lloyd *et al.* (2000)[38] found ecotonal species to mainly be natives, which is supported by the findings here.

Interestingly, in the model of alien species richness, only taxon was retained as a significant predictor, reflecting the differences in the number of species within each taxonomic group being classified as alien (5 bird species, 156 plant species, 10 non-avian animal species, 6 fungi species included in the study). The lack of response to either of the other investigated variables stands in stark contrast to the expectations and previous findings, but can be attributed to alien species often being generalist opportunists; the spatial scale investigated does not reflect

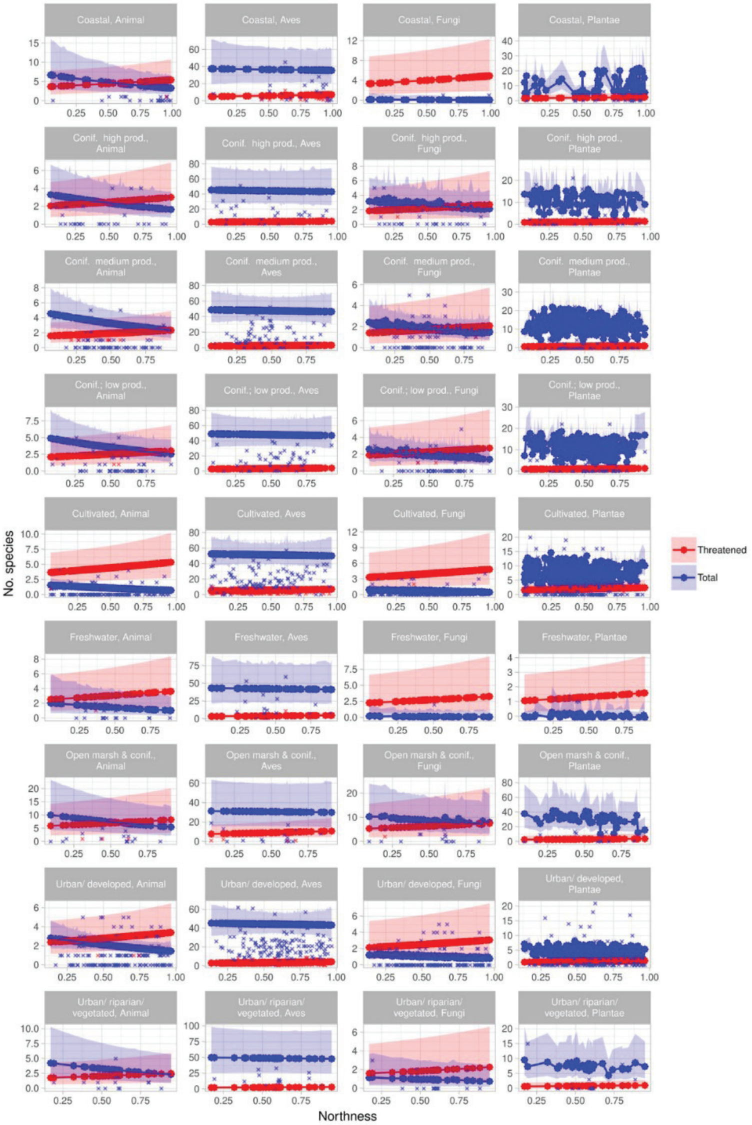

Figure 4. Effect of northness. Effect of northness on predicted species richness across taxa and within habitats. Crosses indicate observed values (incl. spatial effects and variations in all predictors), filled circles are the predictions (spatial effects removed, and all other predictors set to their mean values), and ribbons indicate 0.95 confidence intervals around the predictions. Note the different y-axes. The figure was made in R, version 3.6.1[55].

the fine-scale conditions affecting the individual species. This result highlights that on this spatial scale, all parts of the municipality are open for potential invasion by alien species. Given the spatial correlations (Supplementary material 4, Fig. S.2), it is evident that founder events and subsequent spread of alien species are of crucial importance: on the investigated scale, even more important than the configuration of environment. As many alien species are introduced through urban areas mainly due trade and traffic[12,15,31], emphasis must be put on the

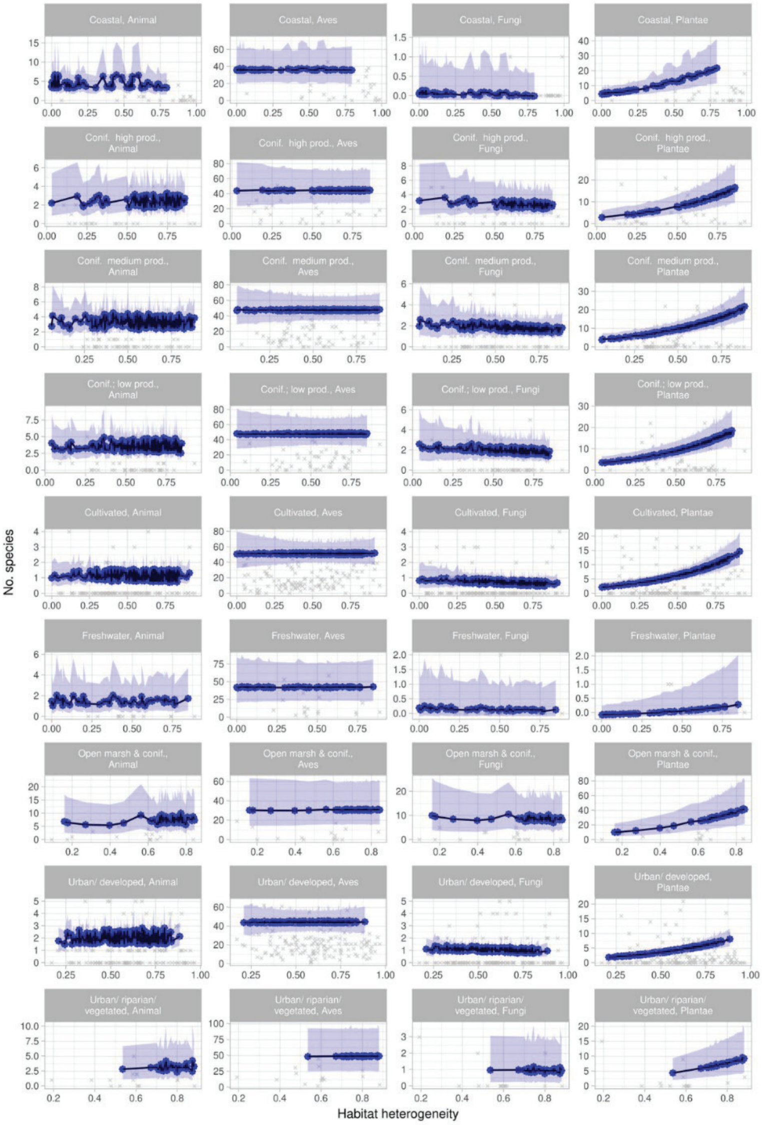

Figure 5. Effect of habitat heterogeneity. Effect of habitat heterogeneity on predicted species richness across taxa and within habitats. Crosses indicate observed values (incl. spatial effects and variations in all predictors), filled circles are the predictions (spatial effects removed, and all other predictors set to their mean values), and ribbons indicate 0.95 confidence intervals around the predictions. Note the different y-axes. The figure was made in R, version 3.6.1[55].

importance of avoiding unintentional introduction of potential invasive species. As an example, the review by Kowarik (2011)[5] found cities to be hotspots of alien plant species. In addition, port cities have been suggested as even greater hotspots of introductions, leaving Trondheim even more vulnerable[60,61].

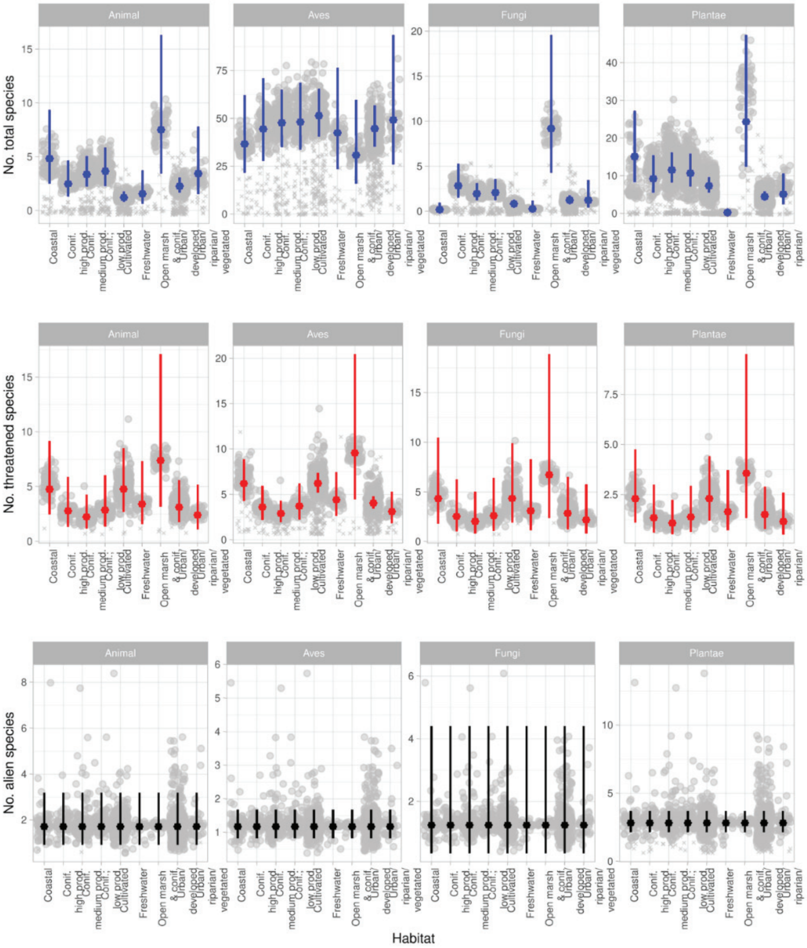

Figure 6. Effects of habitat and taxonomic group. Effect of habitat on predicted species richness across taxa and within habitats. Crosses indicate observed values (incl. spatial effects and variations in all predictors), filled grey circles are the predictions (incl. spatial effects and variations in all predictors), coloured circles indicate mean predicted values (spatial effects removed, and all other predictors set to their mean values), and lines indicate the 0.95 confidence interval of the prediction. Note the different y-axes. The figure was made in R, version 3.6.1[55].

As the explanatory variables used in these models are "indirect" (*sensu* Guisan and Zimmermann (2000)[62]), the habitats are proxies for underlying environmental (direct) drivers. Therefore, a direct extrapolation to other geographical areas should be cautious[62]. However, the general methods are highly applicable elsewhere.

Of the 1,509 grid terrestrial cells, 485 qualified for analyses; species occurrence data was sparse in the rest. Those used in the analyses were biased towards urban areas (Table 1), supporting the general trend in citizen science data; concentrated around inhabited or areas otherwise accessible to the public[63,64]. For example, areas within Trondheim municipality relatively far from human activity are under-sampled, with two habitats not being represented in the analyses at all (*Open firm ground and forest –and cultivated land*). This bias was accounted for in the models, but the differentiated sampling effort nevertheless leaves varying degrees of uncertainty for each habitat and taxon. The sample sizes differed among species groups, with many more observations of threatened than alien species. The differences thus might reflect sampling strategy rather than reality.

As the models are by nature rather crude, they inevitably lack predictor variables, which could have increased model accuracy. However, including highly detailed variables was not the aim of this study. Since

Fixed effects (family: Poisson)			
Marginal AIC: 712.727	Estimate	Cond.SE	t-value
(Intercept)	−4.441	0.80	−24.715
Plantae	0.878	0.167	5.254
Animal	0.390	0.327	1.164
Fungi	0.059	0.645	0.092
Random effects (family: Gaussian)			
Correlation parameters		Variance parameters	
ν	ρ	λ	
0.759	0.00178	0.597	

Table 4. Model output from the spatially correlated GLMM of alien species richness. The model was constructed with a Poisson error structure. The factor level *Aves* is used as intercept, thus categorical predictor values are relative to this.

the data set included a wide array of species, these will not respond in similar ways to variation in the included variables, or to missing variables[65]. The more species included in the models, the more opposing mechanisms are attempted to be fitted within a single modelling framework, giving a poorer fit, compared to models with a narrower scope.

The number of GBIF records have increased in recent years (see Speed *et al.* (2018)[64]). Of all species recorded in Trondheim, approximately 1/3 have been recorded within the municipality from year 2013 to 2018. Of the 6,020 species from the downloaded data set not included in the analyses, 33.9% (2,039) have only been recorded once, and 85.5% (5,150) have been recorded <10 times. Most of these infrequent species are insects. This taxonomic skew is likely due to this species group being poorly sampled or requiring expert knowledge to identify to species level.

Different correlations with environmental variables are expected at different spatial scales for different organisms[19,23,66]. Taxa and species with opposing responses to the included variables could mask each other, thus not revealing the underlying mechanisms[56]. Simultaneously, the mechanisms underlying species distributions vary with spatial scale, not necessarily in the same direction for different taxa[19,23,67]. As multiple different taxonomic groups were included in this study, the used spatial scale is potentially inappropriate for all taxa.

According to Pautasso (2007)[19], a negative correlation between urbanisation and species richness is expected when the study grain is smaller than 1 km, as in this study, but positive at larger scales. This is ascribed to the larger scale reflecting human settlement in productive areas, competing for space with other species, whereas the small scales reflect more detailed environmental- and land cover effects.

Our results indicate that if the Trondheim municipality is to be managed to favour biodiversity, favouring threatened species and excluding alien species, the following actions can be recommended:

Habitat heterogeneity on a relatively small spatial scale should be ensured, favouring overall species richness. This should however not be confused with fragmentation of natural habitat.

To favour threatened species, non-anthropogenic- and coastal areas should be monitored and protected, potentially expanding the actions to ecotones in general.

To limit the spread of alien species, initial introduction and establishment should be avoided. Thus, urban- and other anthropogenic areas should be closely monitored and managed[12,68].

Protection of important and heterogeneous habitat should be accounted for in unison with ensuring large habitat patches, rather than multiple smaller ones; a metastudy by Beninde *et al.* (2015)[56] showed patch area to have the largest positive effect on urban biodiversity.

Conclusions

Overall-, threatened- and alien species richness are not determined by the same land-cover variables. Total- and threatened species richness responds to both habitat and aspect, whereas alien species richness does not respond to any of the variables included in this study. The highest numbers of threatened species are associated with non-anthropogenic habitats, but in contrast to expectations, not more positively associated with forested areas than other habitats, calling for detailed investigations of the importance of forest environments for threatened species. Our finding that alien species do not respond to land-cover variables, but only spatial correlations, confirms the importance of founder events, and highlights the status of cities as gateways for alien species in general.

To mitigate the knowledge gaps from under-sampled habitats, we urge for sampling outside inhabited areas and for less investigated taxa. Using models build on administrative land cover maps and open database occurrence records can be a useful tool for local biodiversity management, by providing guidelines regarding where to aim future efforts, both regarding future conservation efforts and future investigations. Further work is however needed in dealing with the inherent biases of such databases.

In the case of Trondheim, an averaged sized Northern European city, the recommendations for biodiversity management are to ensure protection of natural habitats within a spatial resolution of 250,000 m^2, and to closely monitor and manage urban areas to mitigate the introduction and spread of alien species.

Data availability

All relevant data is available from public repository (GBIF Occurrence Download – March 6th 2018, https://doi.org/10.15468/dl.ruacxc).

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Author contributions

T.K.P., G.A., J.D.M.S. and V.G. conceived the idea and designed the methodology; T.K.P. retrieved and analysed the data; T.K.P. wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to T.K.P.

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Supplementary material

Petersen, T. K. et al. (2020). Urban aliens and threatened near-naturals : Land-cover affects the species richness of alien- and threatened species in an urban- rural setting. *Scientific Reports*, *10* (8513), 1–14.

1. Land cover characteristic of the habitats

The characteristic AR5 land cover of each habitat are evaluated based on the mean area of each land cover (m^2) within the grid cells assigned to the respective habitats. An overview of the characterising land covers can be seen in Fig. S1. The dominating land cover has been determining for the used name for each of the habitats.

The official AR5 land covers falling under the labels defined here are as shown in Table S.1 (Ahlstrøm et al. 2014)[1].

The cluster analysis was based on the land cover within the classified grid cell. The analysis was also done by incorporating the land cover within the focal grid cell and the eight first order neighbour-cells, to smooth out the categorisation. The overall patterns were similar to what was found for the “strict" analysis, however a large degree of the more fine scale variation in land cover between categories was lost. Thus, further analyses were performed using habitat categories based only on the focal grid cell.

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[1] Ahlstrøm, A. P., Bjørklund, K. and Frydenlund, J. (2014) *AR5 klassifikasjonssystem. Klassifikasjon av arealressurser.*

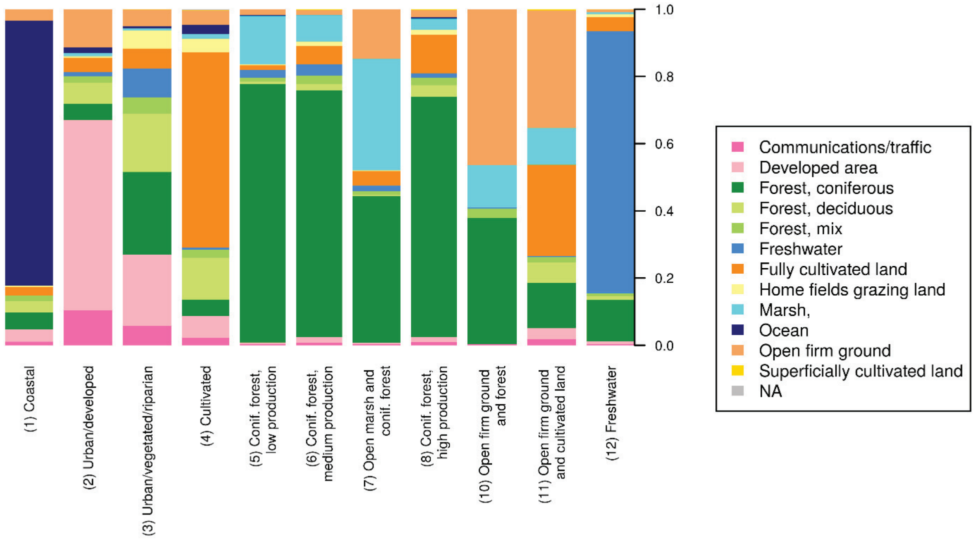

Figure S.1. Mean proportion of grid cell within each habitat covered by the respective AR5 land covers.

Table S.1 Labels of AR5 land cover types in Fig. S.1 and the included sub-classes. Only sub-classes occurring within the study area are included. Categories are translated from Ahlstrøm et al. (2014).

Label	Area type	Tree cover	Productivity	Soil condition
Communications/traffic	Communications/traffic	-	-	-
Developed areas	Developed areas	-	-	-
Forest, coniferous	Forest	Coniferous	Impediment	Bedrock
				Shallow soil
				Soil
				Organic soil

			Low	Boulder
				Shallow soil
				Soil
				Organic soil
			Medium	Shallow soil
				Soil
				Organic soil
			High	Shallow soil
				Soil
				Organic soil
			Very high	Soil
Forest, deciduous	Forest	Deciduous	Impediment	Bedrock
				Shallow soil
				Soil
				Organic soil
			Low	Soil
				Organic soil
			Medium	Shallow soil
				Soil
				Organic soil
			High	Soil
				Organic soil
Forest, mix	Forest	Mixed	Impediment	Shallow soil
				Soil
				Organic soil
			Low	Shallow soil
				Soil

				Organic soil
			Medium	Shallow soil
				Soil
				Organic soil
			High	Soil
Freshwater	Freshwater	-	-	-
Fully cultivated land	Fully cultivated land	-	-	Soil
				Organic soil
Home fields grazing land	Home fields grazing land	Deciduous	-	Soil
		-	-	Shallow soil
				Soil
				Organic soil
Marsh	Marsh	Open	Impediment	-
		Coniferous	Impediment	-
			Low	-
			Medium	-
			High	-
		Deciduous	Impediment	-
			Medium	-
		Mix	Impediment	-
			Low	-
Ocean	Ocean	-	-	-
Open firm ground	Open firm ground	-	Impediment	Artificial surface
				Bedrock
				Boulder
				Shallow soil
				Soil

			Medium	Soil
			High	Soil
Superficially cultivated land	Superficially cultivated land	-	-	Shallow soil
				Soil
NA	-	-	-	-

2. Distribution of data in taxonomic groups

Table S.2. Distribution of records between taxonomic groups. The distribution of the data from GBIF after the initial data cleaning procedure (described in the method section "*GBIF occurrence records*"), among taxonomic groups, including both number of records and number of registered species names. Capital letters indicate that subgroups are shown below in the table. Bold text indicate kingdom-level. "OTHER" indicate records/species not included in the animal-, plant- or fungi kingdom.

		All species	Threatened species	Alien species
TOTAL	Records	251,803	32,585	3,447
	Species	3,097	121	177
ANIMALIA	Records	239,038	32,351	2,226
	Species	1,353	62	15
Aves	Records	230,161	32,228	2,186
	Species	222	50	5
Mammalia	Records	729	97	7
	Species	28	4	1
Reptilia and Amphibia	Records	74	12	0
	Species	6	1	0
Arthropoda	Records	6,098	13	8

	Species	844	6	6
PLANTAE	Records	9,233	102	1,182
	Species	952	26	156
Bryophyta	Records	516	11	0
	Species	181	4	0
TRACHEOPHYTA	Records	8,481	91	1,182
	Species	702	22	156
Pinopsida	Records	357	0	124
	Species	23	0	15
Magnoliopida	Records	6,369	56	989
	Species	510	20	129
FUNGI	Records	3,369	132	39
	Species	763	33	6
OTHER	Records	163	-	-
	Species	29	-	-

3. Criteria for inclusion of threatened species

Description of the sorting of the Red List from the Norwegian Biodiversity Information Centre. The categories from 2006, 2010 and 2015 for each evaluated species evaluated were compared:

The official Norwegian Red Lists from 2006, 2010 and 2015, including the notes on the evaluations, were provided by the Norwegian Biodiversity Information Centre. The three lists provided the basis for the modified version of the Norwegian Red List used in this study. The used abbreviations are in line with the official IUCN categories: *DD* = Data Deficient, *LC* = Least Concern, *NT* = Near Threatened, *VU* = Vulnerable, *EN* = Endangered, *CR* = Critically Endangered, *RE* = Regionally Extinct, *NE* = Not Evaluated, *NA* = Not Available.

If species have not been evaluated in any year (categorised as either NA or NE), they are immediately discarded.

Similarly, if species were only evaluated as LC, or as any combination of LC and non-evaluated, they are discarded.

If species have previously been evaluated to DD (on the threatened part of the Red List), but was evaluated as LC in the latest version (2015), they were discarded.

Species listed as LC in the previous two assessments were discarded, regardless of their category in 2006.

All species evaluated to be in the threatened categories (RE, CR, EN, VU and NT) in 2015 were included in the used Red List. Species listed as DD were evaluated separately (see the further description).

All species always within the threatened categories were included in the list (incl. combinations with NA, NE and DD - thus, species never categorised as LC).

All species evaluated as data deficient in all years (DD) were included in the final version of the Red List. Similarly, all species listed as DD once, with any combination of NE and NA, were included.

All species listed as regionally extinct (RE) at any point, were included in the list.

For all species listed as LC, NA, NE or DD in the latest assessment (2015), but previously listed as any of the threatened categories (RE, CR, EN, VU, NT and DD), the notes on the reasoning for down-grading of the respective species were assessed and evaluated. Generally, species where there was great uncertainty regarding the actual current status of the species, was included in the list. Otherwise, the species was discarded.

Description/reasoning for all of the individually evaluated species can be presented upon requests.

4. Spatial correlation

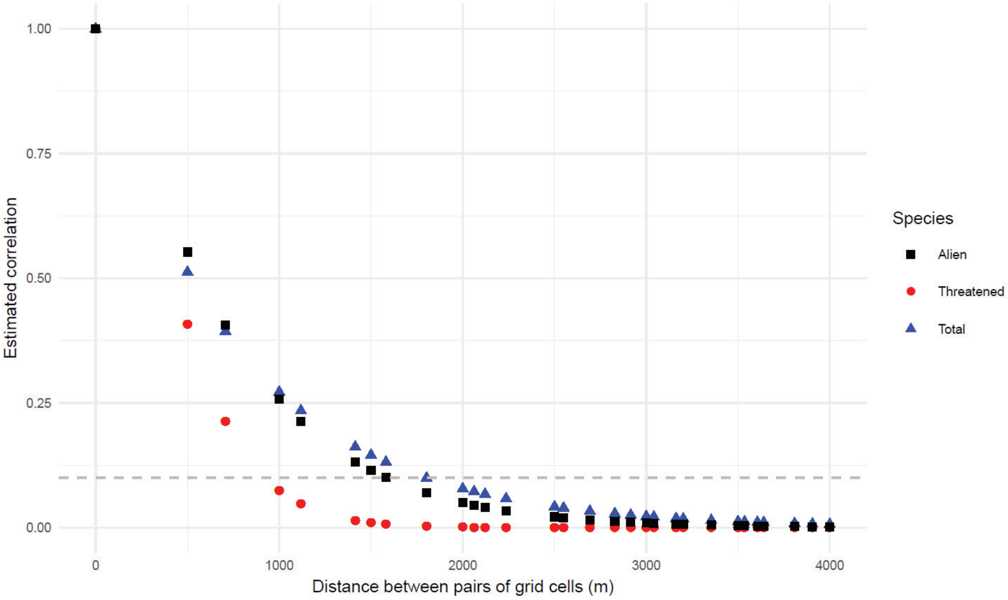

Figure S.2. Spatial correlation of models.

Estimated correlation of grid cells as a function of distance between the grid cells included in the models. Correlation- and distances are based on the spatial correlation parameters ν and ϱ, as described in the model outputs (table 2-4, main text).

Paper III

Photo: T.K. Petersen

Paper 3: Petersen, T.K., Speed, J. D. M., Grøtan, V., Austrheim, G. Competitors and ruderals go to town: Plant community composition and function along an urbanization gradient. Nordic Journal of Botany

This article is awaiting publication and is therefore not included

Paper IV

Photo: T.K. Petersen

Paper 4: Petersen, T.K., Speed, J. D. M., Grøtan, V., Frøyen, Y.K., Austrheim, G.
Urbanisation and land-cover change affect the functional turnover of bird communities but not the extent of species composition change. Submitted manuscript to Journal of Urban Ecology.

This article is awaiting publication and is therefore not included

Doctoral theses in Biology

Norwegian University of Science and Technology

Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr. philos Botany	The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook *Corvus frugilegus*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds

1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit *Parus montanus*
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988	Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988	Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure
1988	Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*)
1988	Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.)
1989	John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989	Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*
1989	Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture

1990	Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990	Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two workplaces with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams
1990	Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990	Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*
1991	Tor Kvam	Dr. scient Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway
1991	Jan Henning L'Abêe Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular
1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism
1991	Nina Jonsson	Dr. philos Zoology	Aspects of migration and spawning in salmonids
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher

1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992	Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993	Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993	Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993	Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994	Peder Fiske	Dr. scient Zoology	Sexual selection in the lekking great snipe (*Gallinago media*): Male mating success and female behaviour at the lek
1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994	Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant *Phalacrocorax carbo carbo*
1994	Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (*Rubus idaeus* L.)

1994	Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994	Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994	Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, *Vulpes vulpes*
1994	Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cockoo
1994	Solveig Bakken	Dr. scient Botany	Growth and nitrogen status in the moss *Dicranum majus* Sm. as influenced by nitrogen supply
1994	Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995	Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995	Hanne Christensen	Dr. scient Zoology	Determinants of Otter *Lutra lutra* distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink *Mustela vision*
1995	Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel *Thalassoica antarctica*; the effect of parental body size and condition
1995	Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995	Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995	Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of *Mysis relicta* and constraints on Cladoceran and Char populations
1995	Hans Haavardsholm Blom	Dr. philos Botany	A revision of the *Schistidium apocarpum* complex in Norway and Sweden
1996	Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; inpact fish-bacterial interactions on growth and survival of larvae
1996	Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996	Ingibjørg Einarsdottir	Dr. scient Zoology	Production of Atlantic salmon (*Salmo salar*) and Arctic charr (*Salvelinus alpinus*): A study of some physiological and immunological responses to rearing routines

1996	Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996	Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics
1996	Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal *Halichoerus grypus* and Harbour seal *Phoca vitulina* in the Barents sea region
1997	Gunvor Øie	Dr. scient Botany	Eevalution of rotifer *Brachionus plicatilis* quality in early first feeding of turbot *Scophtalmus maximus* L. larvae
1997	Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997	Ole Reitan	Dr. scient Zoology	Responses of birds to habitat disturbance due to damming
1997	Jon Arne Grøttum	Dr. scient Zoology	Physiological effects of reduced water quality on fish in aquaculture
1997	Per Gustav Thingstad	Dr. scient Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997	Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as
1997	Signe Nybø	Dr. scient Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway
1997	Atle Wibe	Dr. scient Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997	Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997	Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997	Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to sail bacteria by studies of natural transformation in *Acinetobacter calcoacetius*
1997	Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters

1997	Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998	Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998	Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998	Erling Johan Solberg	Dr. scient Zoology	Variation in population dynamics and life history in a Norwegian moose (*Alces alces*) population: consequences of harvesting in a variable environment
1998	Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998	Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998	Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
1999	Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999	Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999	Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North-East Atlantic

1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*
1999	Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families:
1999	Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient Zoology	Host specificity as a parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient Zoology	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient Botany	Methods for the microbial control of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000	Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway

2000	Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001	Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002	Ronny Aanes	Dr. scient Zoology	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002	Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002	Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002	Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver (*Castor fiber*)
2002	Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002	Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002	Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002	Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002	Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and the Ral GTPase from *Drosophila melanogaster*
2002	Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach

2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003	Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (*Syncerus caffer*) in Chobe National Park, Botswana
2003	Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (*Helicoverpa armigera, Helicoverpa assulta* and *Heliothis virescens*)
2003	Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
2003	Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003	Eldar Åsgard Bendiksen	Dr. scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (*Salmo salar* L.) parr and smolt
2004	Torkild Bakken	Dr. scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr. scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr. scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr. scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr. scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*)
2004	Lene Østby	Dr. scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr. scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming

2004	Lisbeth Mehli	Dr. scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr. scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr. scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr. scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr. scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	PhD Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr. scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr. scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005	Christian Westad	Dr. scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	PhD Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	PhD Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	PhD Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr. scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	PhD Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds, Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr. scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates

2006	Nils Egil Tokle	PhD Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr. philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr. scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	PhD Biology	*Acesta oophaga* and *Acesta excavata* – a study of hidden biodiversity
2006	Bjørn Henrik Hansen	PhD Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	PhD Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	PhD Biology	Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania
2006	Anna Maria Billing	PhD Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	PhD Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	PhD Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	PhD Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	PhD Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	PhD Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	PhD Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	PhD Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	PhD Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry

2007	Snorre Henriksen	PhD Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	PhD Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	PhD Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	PhD Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	PhD Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	PhD Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning
2007	Anne Skjetne Mortensen	PhD Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	PhD Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	PhD Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	PhD Biology	The ecology and behaviour of the Masai Ostrich (*Struthio camelus massaicus*) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	PhD Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, *Taeniopygia guttata*
2008	Sølvi Wehn	PhD Biology	Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	PhD Biology	The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations
2008	Katarina Mariann Jørgensen	Dr. scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	PhD Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	PhD Biology	*Arabidopsis thaliana* Responses to Aphid Infestation

2008	Jussi Evertsen	PhD Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	PhD Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	PhD Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	PhD Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	PhD Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	PhD Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009	Pål Kvello	PhD Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	PhD Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	PhD Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	PhD Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	PhD Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	PhD Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	PhD Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments - Focus on formulated diets
2010	Eli Kvingedal	PhD Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	PhD Biology	Molecular studies of genetic structuring and demography in *Arabidopsis* from Northern Europe

2010	Iddi Mihijai Mfunda	PhD Biology	Wildlife Conservation and People’s livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	PhD Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010	Anders Lyngstad	PhD Biology	Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation
2010	Hilde Færevik	PhD Biology	Impact of protective clothing on thermal and cognitive responses
2010	Ingerid Brænne Arbo	PhD Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010	Yngvild Vindenes	PhD Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010	Hans-Richard Brattbakk	PhD Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011	Geir Hysing Bolstad	PhD Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011	Karen de Jong	PhD Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby (*Gobiusculus flavescens*)
2011	Ann-Iren Kittang	PhD Biology	*Arabidopsis thaliana* L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity
2011	Aline Magdalena Lee	PhD Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011	Christopher Gravningen Sørmo	PhD Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in Arabidopsis thaliana
2011	Grethe Robertsen	PhD Biology	Relative performance of salmonid phenotypes across environments and competitive intensities
2011	Line-Kristin Larsen	PhD Biology	Life-history trait dynamics in experimental populations of guppy (*Poecilia reticulata*): the role of breeding regime and captive environment
2011	Maxim A. K. Teichert	PhD Biology	Regulation in Atlantic salmon (*Salmo salar*): The interaction between habitat and density
2011	Torunn Beate Hancke	PhD Biology	Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology

2011	Sajeda Begum	PhD Biology	Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh
2011	Kari J. K. Attramadal	PhD Biology	Water treatment as an approach to increase microbial control in the culture of cold water marine larvae
2011	Camilla Kalvatn Egset	PhD Biology	The Evolvability of Static Allometry: A Case Study
2011	AHM Raihan Sarker	PhD Biology	Conflict over the conservation of the Asian elephant (*Elephas maximus*) in Bangladesh
2011	Gro Dehli Villanger	PhD Biology	Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals
2011	Kari Bjørneraas	PhD Biology	Spatiotemporal variation in resource utilisation by a large herbivore, the moose
2011	John Odden	PhD Biology	The ecology of a conflict: Eurasian lynx depredation on domestic sheep
2011	Simen Pedersen	PhD Biology	Effects of native and introduced cervids on small mammals and birds
2011	Mohsen Falahati-Anbaran	PhD Biology	Evolutionary consequences of seed banks and seed dispersal in *Arabidopsis*
2012	Jakob Hønborg Hansen	PhD Biology	Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance
2012	Elin Noreen	PhD Biology	Consequences of diet quality and age on life-history traits in a small passerine bird
2012	Irja Ida Ratikainen	PhD Biology	Foraging in a variable world: adaptations to stochasticity
2012	Aleksander Handå	PhD Biology	Cultivation of mussels (*Mytilus edulis):* Feed requirements, storage and integration with salmon (*Salmo salar*) farming
2012	Morten Kraabøl	PhD Biology	Reproductive and migratory challenges inflicted on migrant brown trout (*Salmo trutta* L.) in a heavily modified river
2012	Jisca Huisman	PhD Biology	Gene flow and natural selection in Atlantic salmon
2012	Maria Bergvik	PhD Biology	Lipid and astaxanthin contents and biochemical post-harvest stability in *Calanus finmarchicus*
2012	Bjarte Bye Løfaldli	PhD Biology	Functional and morphological characterization of central olfactory neurons in the model insect *Heliothis virescens*.

2012	Karen Marie Hammer	PhD Biology	Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia
2012	Øystein Nordrum Wiggen	PhD Biology	Optimal performance in the cold
2012	Robert Dominikus Fyumagwa	Dr. Philos Biology	Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania
2012	Jenny Bytingsvik	PhD Biology	Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs
2012	Christer Moe Rolandsen	PhD Biology	The ecological significance of space use and movement patterns of moose in a variable environment
2012	Erlend Kjeldsberg Hovland	PhD Biology	Bio-optics and Ecology in *Emiliania huxleyi* Blooms: Field and Remote Sensing Studies in Norwegian Waters
2012	Lise Cats Myhre	PhD Biology	Effects of the social and physical environment on mating behaviour in a marine fish
2012	Tonje Aronsen	PhD Biology	Demographic, environmental and evolutionary aspects of sexual selection
2012	Bin Liu	PhD Biology	Molecular genetic investigation of cell separation and cell death regulation in *Arabidopsis thaliana*
2013	Jørgen Rosvold	PhD Biology	Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective
2013	Pankaj Barah	PhD Biology	Integrated Systems Approaches to Study Plant Stress Responses
2013	Marit Linnerud	PhD Biology	Patterns in spatial and temporal variation in population abundances of vertebrates
2013	Xinxin Wang	PhD Biology	Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (*Salmo salar*) farming
2013	Ingrid Ertshus Mathisen	PhD Biology	Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia
2013	Anders Foldvik	PhD Biology	Spatial distributions and productivity in salmonid populations
2013	Anna Marie Holand	PhD Biology	Statistical methods for estimating intra- and inter-population variation in genetic diversity
2013	Anna Solvang Båtnes	PhD Biology	Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night

2013	Sebastian Wacker	PhD Biology	The dynamics of sexual selection: effects of OSR, density and resource competition in a fish
2013	Cecilie Miljeteig	PhD Biology	Phototaxis in *Calanus finmarchicus* – light sensitivity and the influence of energy reserves and oil exposure
2013	Ane Kjersti Vie	PhD Biology	Molecular and functional characterisation of the IDA family of signalling peptides in *Arabidopsis thaliana*
2013	Marianne Nymark	PhD Biology	Light responses in the marine diatom *Phaeodactylum tricornutum*
2014	Jannik Schultner	PhD Biology	Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird
2014	Craig Ryan Jackson	PhD Biology	Factors influencing African wild dog *(Lycaon pictus*) habitat selection and ranging behaviour: conservation and management implications
2014	Aravind Venkatesan	PhD Biology	Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences
2014	Kristin Collier Valle	PhD Biology	Photoacclimation mechanisms and light responses in marine micro- and macroalgae
2014	Michael Puffer	PhD Biology	Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (*Salmo salar* L.)
2014	Gundula S. Bartzke	PhD Biology	Effects of power lines on moose *(Alces alces)* habitat selection, movements and feeding activity
2014	Eirin Marie Bjørkvoll	PhD Biology	Life-history variation and stochastic population dynamics in vertebrates
2014	Håkon Holand	PhD Biology	The parasite *Syngamus trachea* in a metapopulation of house sparrows
2014	Randi Magnus Sommerfelt	PhD Biology	Molecular mechanisms of inflammation – a central role for cytosolic phospholiphase A2
2014	Espen Lie Dahl	PhD Biology	Population demographics in white-tailed eagle at an onshore wind farm area in coastal Norway
2014	Anders Øverby	PhD Biology	Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity
2014	Kamal Prasad Acharya	PhD Biology	Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient.
2014	Ida Beathe Øverjordet	PhD Biology	Element accumulation and oxidative stress variables in Arctic pelagic food chains: *Calanus*, little auks (*Alle alle*) and black-legged kittiwakes (*Rissa tridactyla*)

2014	Kristin Møller Gabrielsen	PhD Biology	Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants
2015	Gine Roll Skjervø	Dr. philos Biology	Testing behavioral ecology models with historical individual-based human demographic data from Norway
2015	Nils Erik Gustaf Forsberg	PhD Biology	Spatial and Temporal Genetic Structure in Landrace Cereals
2015	Leila Alipanah	PhD Biology	Integrated analyses of nitrogen and phosphorus deprivation in the diatoms *Phaeodactylum tricornutum* and *Seminavis robusta*
2015	Javad Najafi	PhD Biology	Molecular investigation of signaling components in sugar sensing and defense in *Arabidopsis thaliana*
2015	Bjørnar Sporsheim	PhD Biology	Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport
2015	Magni Olsen Kyrkjeeide	PhD Biology	Genetic variation and structure in peatmosses (*Sphagnum*)
2015	Keshuai Li	PhD Biology	Phospholipids in Atlantic cod (*Gadus morhua* L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis
2015	Ingvild Fladvad Størdal	PhD Biology	The role of the copepod *Calanus finmarchicus* in affecting the fate of marine oil spills
2016	Thomas Kvalnes	PhD Biology	Evolution by natural selection in age-structured populations in fluctuating environments
2016	Øystein Leiknes	PhD Biology	The effect of nutrition on important life-history traits in the marine copepod *Calanus finmarchicus*
2016	Johan Henrik Hårdensson Berntsen	PhD Biology	Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird
2016	Marianne Opsahl Olufsen	PhD Biology	Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish
2016	Rebekka Varne	PhD Biology	Tracing the fate of escaped cod (*Gadus morhua* L.) in a Norwegian fjord system
2016	Anette Antonsen Fenstad	PhD Biology	Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (*Somateria mollissima*)
2016	Wilfred Njama Marealle	PhD Biology	Ecology, Behaviour and Conservation Status of Masai Giraffe (*Giraffa camelopardalis tippelskirchi*) in Tanzania

2016	Ingunn Nilssen	PhD Biology	Integrated Enviromental Mapping and Monitoring: A Methodological approach for end users.
2017	Konika Chawla	PhD Biology	Discovering, analysing and taking care of knowledge.
2017	Øystein Hjorthol Opedal	PhD Biology	The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability.
2017	Ane Marlene Myhre	PhD Biology	Effective size of density dependent populations in fluctuating environments
2017	Emmanuel Hosiana Masenga	PhD Biology	Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (*Lycaon pictus*) Packs in the Serengeti Ecosystem, Tanzania
2017	Xiaolong Lin	PhD Biology	Systematics and evolutionary history of *Tanytarsus* van der Wulp, 1874 (Diptera: Chironomidae)
2017	Emmanuel Clamsen Mmassy	PhD Biology	Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park
2017	Richard Daniel Lyamuya	PhD Biology	Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania
2017	Katrin Hoydal	PhD Biology	Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands
2017	Berit Glomstad	PhD Biology	Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism
2017	Øystein Nordeide Kielland	PhD Biology	Sources of variation in metabolism of an aquatic ectotherm
2017	Narjes Yousefi	PhD Biology	Genetic divergence and speciation in northern peatmosses (*Sphagnum*)
2018	Signe Christensen-Dalgaard	PhD Biology	Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway
2018	Janos Urbancsok	PhD Biology	Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on *Arabidopsis thaliana*
2018	Alice Mühlroth	PhD Biology	The influence of phosphate depletion on lipid metabolism of microalgae
2018	Franco Peniel Mbise	PhD Biology	Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania
2018	Stine Svalheim Markussen	PhD Biology	Causes and consequences of intersexual life history variation in a harvested herbivore population

2018	Mia Vedel Sørensen	PhD Biology	Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems
2018	Hanna Maria Kauko	PhD Biology	Light response and acclimation of microalgae in a changing Arctic
2018	Erlend I. F. Fossen	PhD Biology	Trait evolvability: effects of thermal plasticity and genetic correlations among traits
2019	Peter Sjolte Ranke	PhD Biology	Demographic and genetic and consequences of dispersal in house sparrows
2019	Mathilde Le Moullec	PhD Biology	Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony
2019	Endre Grüner Ofstad	PhD Biology	Causes and consequences of variation in resource use and social structure in ungulates
2019	Yang Jin	PhD Biology	Development of lipid metabolism in early life stage of Atlantic salmon (*Salmo salar*)
2019	Elena Albertsen	PhD Biology	Evolution of floral traits: from ecological contex to functional integration
2019	Mominul Islam Nahid	PhD Biology	Interaction between two Asian cuckoos and their hosts in Bangladesh
2019	Knut Jørgen Egelie	Phd Biology	Management of intellectual property in university-industry collaborations – public access to and control of knowledge
2019	Thomas Ray Haaland	Phd Biology	Adaptive responses to environmental stochasticity on different evolutionary time-scales
2019	Kwaslema Malle Hariohay	Phd Biology	Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania
2019	Mari Engvig Løseth	Phd Biology	Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (*Haliaeetis albicilla*) nestlings
2019	Joseph Mbyati Mukeka	Phd Biology	Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates
2019	Helene Løvstrand Svarva	Phd Biology	Dendroclimatology in southern Norway: tree rings, demography and climate
2019	Nathalie Briels	Phd Biology	Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies
2019	Anders L.Kolstad	Phd Biology	Moose browsing effects on boreal production forests – implications for ecosystems and human society

2019	Bart Peeters	Phd Biology	Population dynamics under climate change ad harvesting: Results from the high Arctic Svalbard reindeer
2019	Alex Kojo Datsomor	Phd Biology	The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (*Salmo salar L*): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes
2020	Ingun Næve	Phd Biology	Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (*Salmo salar*) production and reproduction
2020	Rachael Morgan	Phd Biology	Physiological plasticity and evolution of thermal performance in zebrafish
2020	Mahsa Jalili	Phd Biology	Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (*Salmo salar L.):* possible nutriomics approaches
2020	Haiqing Wang	Phd Biology	Utilization of the polychaete *Hediste diversicolor* (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for value adding applications'
2020	Louis Hunninck	Phd Biology	Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems
2020	Kate Layton-Matthews	Phd Biology	Demographic consequences of rapid climate change and density dependence in migratory Arctic geese
2020	Amit Kumar Sharma	Phd Biology	Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis
2020	Lars Rød-Eriksen	Phd Biology	Drivers of change in meso-carnivore distributions in a northern ecosystem
2020	Lone Sunniva Jevne	Phd Biology	Development and dispersal of salmon lice (*Lepeophtheirus salmonis Krøyer*, 1837) in commercial salmon farming localities
2020	Sindre Håvarstein Eldøy	Phd Biology	The influence of physiology, life history and environmental conditions on the marine migration patterns of sea trout
2020	Vasundra Touré	Phd Biology	Improving the FAIRness of causal interactions in systems biology: data curation and standardisation to support systems modelling applications
2020	Silje Forbord	Phd Biology	Cultivation of *Saccharina latissima* (Phaeophyceae) in temperate marine waters; nitrogen uptake kinetics, growth characteristics and chemical composition

2020	Jørn Olav Løkken	Phd Biology	Change in vegetation composition and growth in the forest-tundra ecotone – effects of climate warming and herbivory
2020	Kristin Odden Nystuen	Phd Biology	Drivers of plant recruitment in alpine vegetation
2021	Sam Perrin	Phd Biology	Freshwater Fish Community Responses to Climate Change and Invasive Species
2021	Lara Veylit	Phd Biology	Causes and consequences of body growth variation in hunted wild boar populations
2021	Semona Issa	Phd Biology	Combined effects of environmental variation and pollution on zooplankton life history and population dynamics
2021	Monica Shilereyo	Phd Biology	Small Mammal Population Ecology and Ectoparasite Load: Assessing Impacts of Land Use and Rainfall Seasonality in the Serengeti Ecosystem, Tanzania
2021	Vanessa Bieker	Phd Biology	Using historical herbarium specimens to elucidate the evolutionary genomics of plant invasion
2021	Håkon Austad Langberg	Phd Biology	Fate and transport of forever chemicals in the aquatic environment: Partitioning and biotransformation of mixtures of Per- and Polyfluoroalkyl Substances (PFAS) from different point sources and resulting concentrations in biota

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