Plant occurrence in space and time: the importance of land use, habitat structure, and pollination mode

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Contents

Chapter 1

General introduction

Kaixuan Pan

Global biodiversity decline

Biodiversity can be defined as life on earth, which ranges from different kinds of animals, plants, fungi, and microorganisms to habitats, ecosystems and whole biomes (The convention on biological diversity, 1992). Sustaining biodiversity is very important as it keeps ecosystems stable, supplies humans with basic needs (food, fuel, shelter, medicine and some other goods), provides regulating services (e.g. pollination, seed dispersal, climate regulation, and control of agricultural pests), delivers supporting services (e.g. water purification and nutrient cycling) and maintains cultural values such as spiritual or religious service (Balvanera et al., 2014; Mi et al., 2021). However, many wild species are in decline and many are on the brink of extinction due to Anthropogenic causes. The present epoch, the Anthropocene, is often referred to as the sixth mass extinction in Earth's history (Barnosky et al., 2011; Ceballos et al., 2015; Isbell et al., 2017; Johnson et al., 2017). According to the Living Planet Report (Living Planet Report, 2020) the world has seen a 68% drop in mammal, bird, fish, reptile, and amphibian populations since 1970. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services(IPBES) also reported that up to one million plant and animal species are facing extinction, and many within the next decades (IPBES, 2019, 2020). We are exhausting biodiversity on the planet at a far greater rate than it can replenish itself (Rockström et al., 2009), and it has been commonly acknowledged that humanity is ultimately responsible for biodiversity loss, which causes the decrease of ecosystem services provided by nature and threatens sustainable human development (Johnson et al., 2017; IPBES, 2019, 2020).

Biotic and abiotic factors driving plant diversity dynamics

Plant communities are the prime members and among the most important structural components of terrestrial ecosystems (Giam et al., 2010; Antonelli et al., 2019; Living Planet Report, 2020). They control numerous ecological processes and provide fundamental support for a wide variety of organisms on Earth. Therefore, the threats faced by a plant community affects in turn the entire ecosystem. Given the importance of plant species in our ecosystems, we should focus attention on their recognition, monitoring and protection. However, plant species' status and temporal trends remain poorly understood compared to studies focusing on vertebrates (Betts et al., 2017). For example, approximately 50% of the world's plant species are lacking distribution data, while the distribution of most vertebrates is known (Pelletier et al., 2018; IUCN, 2020).

It is estimated that nowadays ~300.000 vascular plant species exist on Earth. However, only 10% of species' status and trends have been assessed by the International Union for Conservation of Nature (IUCN) (Bachman et al., 2019), which makes it difficult to take effective actions to conserve the remaining 90% of species. Of the 10% of assessed species, almost 22% are threatened with extinction (Brummitt et al., 2015). According to another report released by Kew Gardens in 2020, the percentage of plants that are threatened with extinction is 39.4%, which is higher than the rate estimated in 2016 (State of the World's Plants and Fungi, 2016, 2020). The number of plant species already extinct is twice the sum of extinct mammals, birds and amphibians (Humphreys et al., 2019).

The loss and fragmentation of natural habitats, climate change and nitrogen deposition are identified as three of the most important drivers of global environment change, and they are predicted to cause more effects on plant biodiversity in this century (Sala et al., 2000). These factors act additively or synergistically to affect biodiversity (Brook et al., 2008;

Cusack et al., 2016; Schulte To Bühne et al., 2021) and lead to changes in species abundances (Bowler et al., 2017; Northrup et al., 2019), species richness and diversity (Simkin et al., 2016; Hof et al., 2018; Di Marco et al., 2019; Peters et al., 2019), geographical distribution (Root et al., 2003; Chen et al., 2011; Barbet-Massin et al., 2012) and species occurrence (Wamelink et al., 2020).

Among the multiple drivers of contemporary extinctions, natural habitat loss is considered to be the most important (Sala et al., 2000). A large body of work exists detailing how biodiversity changes in response to changes in natural land cover and degradation of the environment. For example, the amount of natural land cover positively correlates with pollinator richness and abundance (Cusser et al., 2016), plant richness (Blaser et al., 2018), as well as mammals and birds (Mendenhall et al., 2016). Other studies show a unimodal relationship with highest species richness in areas with intermediate cover of natural habitats (birds: Desrochers et al., 2011 and plants: Bascompte and Rodriguez, 2001). All of these studies show that a relatively high natural land cover is important for sustaining biodiversity. However, the importance of natural land cover for plant diversity remains unclear.

Another biotic factor that affects plant species richness are structural aspects of the vegetation structure itself (e.g. canopy density in a forest) but few studies take this into consideration when quantifying the effect of land-use on plant diversity. Recent studies show that vegetation structure might be an important environmental factor driving plant occurrence by interacting with the other factors. For example, forest canopy interception of nitrogen compounds mitigates its negative effect on under-forest ecosystems (Liu et al., 2020). Another example is that vegetation structure modulates the microclimate under the canopy and influences the impact of climate change on plants (Frenne et al., 2013). However, how and to what extent vegetation structure mitigates the effect of other environmental factors requires more cross-site assessments at local scales.

Plants are well-connected in ecological networks. They regularly establish relationships with fungi and their dispersal and pollination often depends on animals. One of the most critical relationships of plants is the plant-pollinator interaction (Potts et al., 2016). Pollinator dependent plants consist of most of the plant biodiversity of the world and provide humans with over 35% of the most critical crops (Ollerton et al., 2011; Huang et al., 2021; Tscharntke, 2021; Dicks et al., 2021; Wei et al., 2021). However, some studies have reported an alarming decline in pollinators at either national and regional scales (Biesmeijer et al., 2006; Hallmann et al., 2021; Warren et al., 2021). This has raised our concern for insect-plant interactions and insect-pollinated plant conservation. However, it remains unknown whether and to what extent insect-pollinated species have declined in our ecosystems at the community level. Understanding how and how quickly natural communities change is an important task in ecology. Accurate baseline knowledge is needed to take appropriate action to mitigate future changes.

Plant species conservations

Many efforts have been made to deal with the crisis of biodiversity loss. One of the greatest efforts has been to establish protected areas, which aim at conserving species *in situ*. Increasingly, protected areas are expected to protect biodiversity and secure ecosystem services (Watson et al., 2014; Xu et al., 2017). Protected areas are described as ‘clearly defined areas that are recognized, dedicated and managed to achieve long-term conservation of nature' (Dudley, 2008). Several studies show that well-managed protected areas reduce rates of habitat loss (the chief threat to biodiversity) in both terrestrial (Joppa and Pfaff, 2010; Geldmann et al., 2013) and marine (Micheli and Niccolini, 2013; Edgar et al., 2014) environments. Some strong evidence also indicates that protected areas maintain species' population levels (including threatened species) better than other management approaches (Geldmann et al., 2013; Sheehan et al., 2013; Sciberras et al., 2013. At present, the proportion of protected areas accounts for 15% of the global terrestrial surface (Stokstad, 2020). To stop and even reverse biodiversity loss, more ambitious targets have been set, including proposals for post-2020 protected area targets of 30% of the planet by 2030 (Dinerstein et al., 2019) and calls for protection of half the terrestrial biosphere by 2050 (Locke, 2013; Dinerstein et al., 2017; Watson and Venter, 2017). However, with ongoing global threats like climate change, increases in N deposition and conflict between habitat conservation, food provision and other land uses (Leclère et al., 2020), it is questionable whether and to what extent such protection management regimes sufficiently protect species and whether we are on the right track for adequate species conservation. There is an urgent need to assess the conservation effectiveness of PA management for biodiversity conservation.

In view of the biodiversity crisis and the limited opportunities for expanding protected areas (Mendenhall et al., 2016), efforts to secure biodiversity and ecosystem services in human-dominated landscapes are expanding. The question then becomes: what is the potential of different habitats for biodiversity conservation in the Anthropocene? In broad terms, the focus can be on biodiversity conservation in natural, urban and rural areas (agricultural areas). Nature is often considered to be the most important habitat for species. Most protected areas are located in natural areas or even intact wilderness. However, wild areas only account for 44% of terrestrial surfaces and only 18% of plants are endemic to these areas (Mittermeier et al., 2003). Species conservation only depending on these areas is insufficient to halt biodiversity loss.

Agricultural areas are also considered to be an important habitat to sustain biodiversity. Although the expansion of agriculture ranks as one of the main drivers of biodiversity loss (IPBES, 2019, 2020), agricultural habitats can also host important biodiversity. Agricultural areas can be habitats for many species (Prugh et al., 2008; Karp et al., 2012; Chaudhary et al., 2015; Martins and Pereira, 2017), and a significant number of wild species have adapted or even become dependent on farmland habitats (Li et al., 2020). For example, European farmlands are valuable habitats for many species, such as *Alopecurus myosuroides* (Doxa et al., 2010; Cormont et al., 2016). Farmlands provide important food resources for many mammals (Magioli et al., 2019). Additionally, agricultural areas support some plant species not found in other habitat types (Mendenhall et al., 2016).

Nowadays, urban areas are considered the fastest growing land cover type (Fuller et al., 2007), and continue to expand quickly (Angel et al., 2011; Seto et al., 2012; Shi and Yu, 2014). Rapid city sprawl leads to the loss of natural habitats and decreases in biodiversity (Gong et al., 2013; Shaw et al., 2017), especially in biodiversity hotspots. However, it also provides us a chance to conserve species in urban environments. Urban green spaces can be the most important 'semi-natural' ecosystems in high density urban areas, particularly if they are potential habitats for some plant species, such as *Agrostemma githago* (Kowarik, 2011; Kümmerling and Müller, 2012; Torres et al., 2016). Ives et al. (2016) even found that urban areas can sustain a great deal of threatened species. However, assessment about the potential of different habitats (nature, rural and urban area) for plant species conservation is still largely lacking.

Research aims and questions

In this thesis I explore the changes in the occurrence of plant species across space and time. I examine whether these changes are dependent on the type and status of a plant species. I address these aims via a series of sub-questions in the following four chapters (Figure 1):

1) Whether and to what extent is natural land cover important for plant species' conservation, and whether the importance differs among different plant groups? (Chapter 2)

2) If the coverage of (semi-)natural habitat explains the distribution of plant species, what are the impacts of different (semi-)habitat types and 3D vegetation structure on plant species occurrence, and does this depend on their pollination modes (i.e. insect, wind and self-pollination)? (Chapter 3)

3) Furthermore, given the alarming reports of insect decline over time, whether and to what extent has the occurrences of plants pollinated by different modes (i.e. insect, wind and self-pollination) changed over time? (Chapter 4)

4) Given the importance and continuous decline of insect-pollinated plants and red list species, are current conservation strategies (i.e. establishing protected areas & conserving species in nature, rural and urban areas) sufficient to conserve these species and how can we improve conservation strategies? (Chapter 5)

Plant diversity in the Netherlands

The Netherlands has a long history of observing the occurrence of flora across the whole country. For ages volunteers have been actively observing plants in the country. From 1901, a citizen science project started with identifying and mapping the distributions of plant species across the Netherlands. Every year, around 800-1000 km2 of the country is monitored by professional volunteers, with 250 volunteers working on the project regularly and 1500 incidentally (https://www.floron.nl/about-us). These observation data almost cover the whole country (Fig. 1), they are validated based on knowledge rules and expert assessments. With such great work on species monitors, it’s possible to assess the dynamics of different species and the overall effectiveness of species conservations in the Netherlands.

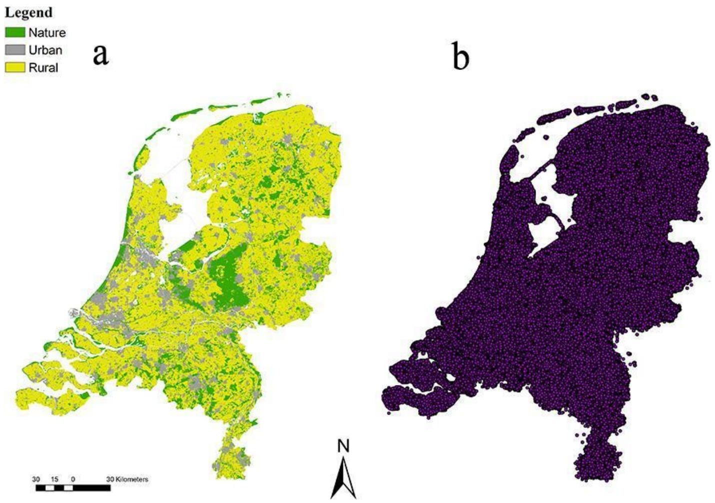

Fig.1 The distribution of land-use types and species observations in the Netherlands.

The Netherlands has experienced major conversions from natural habitats to agricultural or urban use in its history and currently has one of the most intensively managed landscapes in the world with agriculture accounting for approximately 63% and urban areas accounting for 15% of the country. Over the past century, the country has experienced a major decline in plant diversity, with about 4% of the vascular plants disappeared entirely from the Netherlands (Fig. 2; Notenboom et al., 2006), due to a variety of human activities, which has been documented in many literatures (Tamis et al., 2005; Snoo et al., 2012; Carvalheiro et al., 2013; EZ, 2015). Evidence includes declines in insect-pollinated plants, and plants that are vulnerable to rich nutrients (Tamis et al., 2005). Other evidence shows that plants on arable fields have declined by 35 percent since 1900. Although the decline rate is slowing down, it can’t hide the truth that biodiversity loss persists despite all attempts. Currently, there are still nearly 40% of vascular plants in the Red list under threat (https://www.clo.nl/en/indicators/en1052-number-of-threatened-species).

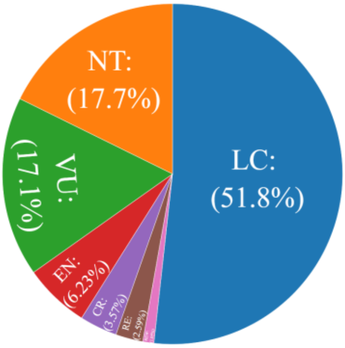

Fig. 2 Percentages of species regarding each IUCN category. RE (Extinct): 3%, REW (Extinct in the Wild): 1%, CR (Critically Endangered): 4%, EN (Endangered): 6%, VU (Vulnerable): 17%, NT (Near Threatened): 18%, and LC (Least Concern): 52%. Source: Rode Lijst Vaatplanten 2012 (Sparrius & Beringen, 2014).

Threats including the loss and fragmentation of natural habitats, climate change and nitrogen deposition are identified as three most important drivers of terrestrial biodiversity loss in the Netherlands, with land use as the most serious threat. Continuous convention from natural areas to agricultural use and intensive management of land use have an ongoing negative impact on plant diversity (Notenboom et al., 2006). Although people have realised the importance of (semi-)natural habitats and increased natural area and improved spatial connectivity, it is still not enough to halt species decline. In addition, the critical load for nitrogen deposition is still a big problem (Notenboom et al., 2006). Despite the fact that nitrogen deposition has dropped as a result of environmental actions to minimise pressures, nitrogen deposition has and is still threatening plant species across the country. Climate change including temperature increase and increasing desiccation is estimated to reduce 40% of its plant species (Wamelink and Kurvers, 2022).

The Netherlands has adapted various conservation actions in the country to stem the tide of biodiversity loss. The Netherlands Nature Network and Natura (NNN) 2000 are on-going. Natura 2000 in the Netherlands is part of the European network of protected nature areas aiming at protecting certain species and habitats, while the NNN includes all existing and planned nature areas, which will be finished by 2027. However, to what extent the effectiveness of these actions can protect species still needs to be assessed.

In this thesis, we take the Netherlands as the study areas and explore the series of questions that I proposed above.

Thesis outline

Chapter 2: Importance of natural land cover for plant species' conservation: A nationwide study in The Netherlands

This chapter aims to figure out exactly whether and to which extent (semi-)natural habitat cover affects plant species. Land-cover change by humans, particularly (semi-)natural area loss, is reducing biodiversity on Earth. Understanding the effect of (semi-)natural habitat cover on species can provide ecological insight and convincing evidence for developing biodiversity conservation strategies. However, few empirical studies indicate the importance of natural land cover to plant species' presence. To find out the importance of natural land cover to plant species, this chapter includes 32 native and 412 exotic plant species across all landscapes nationwide and analyses the dynamics in species occurrences across landscapes with different coverage of semi-natural habitats.

Chapter 3: The distributions of insect, wind and self-pollination of plants in the Netherlands in relation to habitat types and 3D vegetation structure

As (semi-)natural land cover is important to plant species, this chapter zooms in on semi-natural habitats, and explores whether the distribution of plants pollinated by different pollination modes is related to environmental conditions, e.g. habitat types and vegetation structure. To understand this is important since pollination is one of the most critical events of reproduction of plants, with insect, wind and self as the most common pollination modes. Here, I use distribution records of Dutch plant species to map the composition of pollination modes of different plant groups (woody species, herbs and grasses) across (semi-)natural habitats and assess whether spatial distributions of different pollination modes are correlated with the 3D vegetation structure.

Chapter 4: Dutch landscapes are losing insect-pollinated plants

Pollinator dependent plants consist of most of the plant biodiversity of the world and constitute over 80% of the most critical crops. Given the strong decline in insect species and the importance of pollinators to plant species, this chapter assesses whether and to what extent the occurrences of plants in semi-natural habitats have changed over time at the community level, and whether this change depends on pollination groups (i.e. insect, wind and self-pollination)? The assessment is conducted based on plants recorded in 625,247 Dutch vegetation plots from 1930 to 2017.

Chapter 5: Where, what habitats and how much area of the habitats do we need for conserving different species?

In this chapter, I attempt to provide conservation suggestions to mitigate the decline of species by assessing current conservation efforts. Specifically, I assessed the plant diversity (alpha, beta and gamma diversity) of different plant groups in different land-use types (nature, rural and urban areas) and conservation levels (Natura 2000 vs non-Natura 2000), and try to assess whether current conservation efforts are going in the right direction for conserving plant species and how to conserve different species more efficiently.

Chapter 6: General discussion

In this chapter, I discuss the results and implications of this research project. More specifically, I discuss the methods of measuring plant diversity. Furthermore, I will discuss the importance of natural land cover and pollinators to plant species. Finally, I discuss the conservation effectiveness of different land-use types and protection levels on different species groups and how to improve the conservation of plant species.

References

Angel, S., Parent, J., Civco, D.L., Blei, A., Potere, D., 2011. The dimensions of global urban expansion: Estimates and projections for all countries, 2000–2050. Progress in Planning 75, 53–107.

Antonelli, A., Smith, R.J., Simmonds, M.S.J., 2019. Unlocking the properties of plants and fungi for sustainable development. Nat Plants 5, 1100–1102. https://www.nature.com/articles/s41477-019-0554-1.

Bachman, S.P., Field, R., Reader, T., Raimondo, D., Donaldson, J., Schatz, G.E., Lughadha, E.N., 2019. Progress, challenges and opportunities for Red Listing. Biol Conserv 234, 45–55. https://www.sciencedirect.com/science/article/pii/s000632071831557x.

Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., Byrnes, J., O'Connor, M.I., Hungate, B.A., Griffin, J.N., 2014. Linking Biodiversity and Ecosystem Services: Current Uncertainties and the Necessary Next Steps. BioScience 64, 49–57.

Barbet-Massin, M., Thuiller, W., Jiguet, F., 2012. The fate of E uropean breeding birds under climate, land-use and dispersal scenarios. Glob Change Biol 18, 881–890. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2486.2011.02552.x.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57. https://www.nature.com/articles/nature09678.

Bascompte, J., Rodriguez, M.A., 2001. Habitat patchiness and plant species richness. Ecol Lett 4, 417–420.

Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A., Butchart, S.H.M., Levi, T., 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. Nature 547, 441–444. https://www.nature.com/articles/nature23285.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science (New York, N.Y.) 313, 351–354.

Blaser, W.J., Oppong, J., Hart, S.P., Landolt, J., Yeboah, E., Six, J., 2018. Climate-smart sustainable agriculture in low-to-intermediate shade agroforests. Nat Sustain 1, 234–239. https://www.nature.com/articles/s41893-018-0062-8.

Bowler, D.E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R., Baert, L., Bauer, H.-G., Blick, T., Brooker, R.W., Dekoninck, W., Domisch, S., Eckmann, R., Hendrickx, F., Hickler, T., Klotz, S., Kraberg, A., Kühn, I., Matesanz, S., Meschede, A., Neumann, H., O'Hara, R., Russell, D.J., Sell, A.F., Sonnewald, M., Stoll, S., Sundermann, A., Tackenberg, O., Türkay, M., Valladares, F., van Herk, K., van

Klink, R., Vermeulen, R., Voigtländer, K., Wagner, R., Welk, E., Wiemers, M., Wiltshire, K.H., Böhning-Gaese, K., 2017. Cross-realm assessment of climate change impacts on species' abundance trends. Nat Ecol Evol 1, 67. https://www.nature.com/articles/s41559-016-0067.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. Trends Ecol Evol 23, 453–460. https://www.sciencedirect.com/science/article/pii/s016953470800195x.

Brummitt, N.A., Bachman, S.P., Griffiths-Lee, J., Lutz, M., Moat, J.F., Farjon, A., Donaldson, J.S., Hilton-Taylor, C., Meagher, T.R., Albuquerque, S., Aletrari, E., Andrews, A.K., Atchison, G., Baloch, E., Barlozzini, B., Brunazzi, A., Carretero, J., Celesti, M., Chadburn, H., Cianfoni, E., Cockel, C., Coldwell, V., Concetti, B., Contu, S., Crook, V., Dyson, P., Gardiner, L., Ghanim, N., Greene, H., Groom, A., Harker, R., Della Hopkins, Khela, S., Lakeman-Fraser, P., Lindon, H., Lockwood, H., Loftus, C., Lombrici, D., Lopez-Poveda, L., Lyon, J., Malcolm-Tompkins, P., McGregor, K., Moreno, L., Murray, L., Nazar, K., Power, E., Quiton Tuijtelaars, M., Salter, R., Segrott, R., Thacker, H., Thomas, L.J., Tingvoll, S., Watkinson, G., Wojtaszekova, K., Nic Lughadha, E.M., 2015. Green Plants in the Red: A Baseline Global Assessment for the IUCN Sampled Red List Index for Plants. PLOS ONE 10, e0135152. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0135152.

Carvalheiro, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R., Groom, Q., Hennekens, S., van Landuyt, W., Maes, D., van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.P.M., Schaminée, J., WallisDeVries, M.F., Biesmeijer, J.C., 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. Ecol Lett 16, 870–878.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Sci Adv 1, e1400253.

Chaudhary, A., Verones, F., Baan, L. de, Hellweg, S., 2015. Quantifying Land Use Impacts on Biodiversity: Combining Species-Area Models and Vulnerability Indicators. Environ Sci Technol 49, 9987–9995.

Chen, I.-C., Hill, J.K., Shiu, H.-J., Holloway, J.D., Benedick, S., Chey, V.K., Barlow, H.S., Thomas, C.D., 2011. Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. Glob Ecol Biogeogr 20, 34–45.

Cormont, A., Siepel, H., Clement, J., Melman, T., WallisDeVries, M.F., van Turnhout, C., Sparrius, L.B., Reemer, M., Biesmeijer, J.C., Berendse, F., Snoo, G.R. de, 2016. Landscape complexity and farmland biodiversity: Evaluating the CAP target on natural elements. J Nat Conserv 30, 19–26. https://www.sciencedirect.com/science/article/pii/s1617138115300388.

Cusack, D.F., Karpman, J., Ashdown, D., Cao, Q., Ciochina, M., Halterman, S., Lydon, S., Neupane, A., 2016. Global change effects on humid tropical forests: Evidence for biogeochemical and biodiversity shifts at an ecosystem scale. Rev Geophys 54, 523–610.

Cusser, S., Neff, J.L., Jha, S., 2016. Natural land cover drives pollinator abundance and richness, leading to reductions in pollen limitation in cotton agroecosystems. Agric Ecosyst Environ 226, 33–42. https://www.sciencedirect.com/science/article/pii/s0167880916302237.

Desrochers, R.E., Kerr, J.T., Currie, D.J., 2011. How, and how much, natural cover loss increases species richness. Glob Ecol Biogeogr 20, 857–867.

Di Marco, M., Harwood, T.D., Hoskins, A.J., Ware, C., Hill, S.L.L., Ferrier, S., 2019. Projecting impacts of global climate and land-use scenarios on plant biodiversity using compositional-turnover modelling. Glob Chang Biol 25, 2763–2778.

Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J., Potts, S.G., 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. Nat Ecol Evol 5, 1453–1461. https://www.nature.com/articles/s41559-021-01534-9.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., Souza, N. de, Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. BioScience 67, 534–545.

Dinerstein, E., Vynne, C., Sala, E., Joshi, A.R., Fernando, S., Lovejoy, T.E., Mayorga, J., Olson, D., Asner, G.P., Baillie, J.E.M., Burgess, N.D., Burkart, K., Noss, R.F., Zhang, Y.P., Baccini, A., Birch, T., Hahn, N., Joppa, L.N., Wikramanayake, E., 2019. A Global Deal For Nature: Guiding principles, milestones, and targets. Sci Adv 5, eaaw2869.

Doxa, A., Bas, Y., Paracchini, M.L., Pointereau, P., Terres, J.-M., Jiguet, F., 2010. Low-intensity agriculture increases farmland bird abundances in France. J Appl Ecol 47, 1348–1356. https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2664.2010.01869.x.

Dudley, N., 2008. Guidelines for applying protected area management categories. IUCN, Gland Switzerland.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Försterra, G., Galván, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220. https://www.nature.com/articles/nature13022.

EZ, 2015. Besluit van de Staatssecretaris van Economische Zaken van 15 oktober 2015, DGAN-PDJNG / 15129301, houdende vaststelling van geactualiseerde Rode lijsten flora en fauna. Staatscourant 36471.

Frenne, P. de, Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petrík, P., Schultz, J., Sonnier, G., van Calster, H., Waller, D.M., Walther, G.-R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. Proc. Natl. Acad. Sci. U.S.A. 110, 18561–18565.

Fuller, R.A., Irvine, K.N., Devine-Wright, P., Warren, P.H., Gaston, K.J., 2007. Psychological benefits of greenspace increase with biodiversity. Biol Lett 3, 390–394.

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., Burgess, N.D., 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biol Conserv 161, 230–238. https://www.sciencedirect.com/science/article/pii/s0006320713000670.

Giam, X., Bradshaw, C.J., Tan, H.T., Sodhi, N.S., 2010. Future habitat loss and the conservation of plant biodiversity. Biol Conserv 143, 1594–1602. https://www.sciencedirect.com/science/article/pii/S0006320710001631.

Gong, C., Chen, J., Yu, S., 2013. Biotic homogenization and differentiation of the flora in artificial and near-natural habitats across urban green spaces. Landsc Urban Plan 120, 158–169.

Hallmann, C.A., Ssymank, A., Sorg, M., Kroon, H. de, Jongejans, E., 2021. Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. Proc. Natl. Acad. Sci. U.S.A. 118.

Hof, C., Voskamp, A., Biber, M.F., Böhning-Gaese, K., Engelhardt, E.K., Niamir, A., Willis, S.G., Hickler, T., 2018. Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. Proc. Natl. Acad. Sci. U.S.A. 115, 13294–13299.

Huang, H., Tu, C., D’Odorico, P., 2021. Ecosystem complexity enhances the resilience of plant-pollinator systems. One Earth 4, 1286–1296. https://www.sciencedirect.com/science/article/pii/s2590332221004668.

Humphreys, A.M., Govaerts, R., Ficinski, S.Z., Nic Lughadha, E., Vorontsova, M.S., 2019. Global dataset shows geography and life form predict modern plant extinction and rediscovery. Nat Ecol Evol 3, 1043–1047. https://www.nature.com/articles/s41559-019-0906-2.

IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on biodiversity and ecosystem services.

IPBES, 2020. Summary for policymakers of the global assessment report on biodiversity and ecosystem services.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A., O’Connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L., Larigauderie, A., 2017. Linking the influence and dependence of people on biodiversity across scales. Nature 546, 65–72. https://www.nature.com/articles/nature22899.

IUCN, 2020. The IUCN Red List of Threatened Species. Version 2020-2. IUCN. (2020). The IUCN Red List of Threatened Species. Version 2020-2.

Ives, C.D., Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., Garrard, G.E., Bekessy, S.A., Fuller, R.A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L.E., Kendal, D., 2016. Cities are hotspots for threatened species. Glob Ecol Biogeogr 25, 117–126.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science (New York, N.Y.) 356, 270–275.

Joppa, L., Pfaff, A., 2010. Reassessing the forest impacts of protection: the challenge of nonrandom location and a corrective method. Ann N Y Acad Sci 1185, 135–149.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R., Daily, G.C., 2012. Intensive agriculture erodes β-diversity at large scales. Ecol Lett 15, 963–970.

Kowarik, I., 2011. Novel urban ecosystems, biodiversity, and conservation. Environ Pollut (Barking, Essex : 1987) 159, 1974–1983.

Kümmerling, M., Müller, N., 2012. The relationship between landscape design style and the conservation value of parks: A case study of a historical park in Weimar, Germany. Landsc Urban Plan 107, 111–117.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., Palma, A. de, DeClerck, F.A.J., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Humpenöder, F., Jennings, N., Krisztin, T., Mace, G.M., Ohashi, H., Popp, A., Purvis, A., Schipper, A.M., Tabeau, A., Valin, H., van Meijl, H., van Zeist, W.-J., Visconti, P., Alkemade, R., Almond, R., Bunting, G., Burgess, N.D., Cornell, S.E., Di Fulvio, F., Ferrier, S., Fritz, S., Fujimori, S., Grooten, M., Harwood, T., Havlík, P., Herrero, M., Hoskins, A.J., Jung, M., Kram, T., Lotze-Campen, H., Matsui, T., Meyer, C., Nel, D., Newbold, T., Schmidt-Traub, G., Stehfest, E., Strassburg, B.B.N., van Vuuren, D.P., Ware, C., Watson, J.E.M., Wu, W., Young, L., 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. Nature 585, 551-556.

Li, L., Hu, R., Huang, J., Bürgi, M., Zhu, Z., Zhong, J., Lü, Z., 2020. A farmland biodiversity strategy is needed for China. Nat Ecol Evol 4, 772–774. https://www.nature.com/articles/s41559-020-1161-2.

Liu, T., Mao, P., Shi, L., Eisenhauer, N., Liu, S., Wang, X., He, X., Wang, Z., Zhang, W., Liu, Z., Zhou, L., Shao, Y., Fu, S., 2020. Forest canopy maintains the soil community composition under elevated nitrogen deposition. Soil Biol Biochem 143, 107733. https://www.sciencedirect.com/science/article/pii/s0038071720300304.

Living Planet Report, 2020. Living Planet Report. Living Planet Report 2020-Bending the curve of biodiversity loss.

Locke, H., 2013. Nature needs half: A necessary and hopeful new agenda for protected areas. PARKS 19 (2): 13–22. 10.2305/IUCN . CH. 2013. Parks 19, 13–22. javascript:

Magioli, M., Moreira, M.Z., Fonseca, R.C.B., Ribeiro, M.C., Rodrigues, M.G., Ferraz, K.M.P.M.d.B., 2019. Human-modified landscapes alter mammal resource and habitat use and trophic structure. Proc. Natl. Acad. Sci. U.S.A. 116, 18466–18472.

Martins, I.S., Pereira, H.M., 2017. Improving extinction projections across scales and habitats using the countryside species-area relationship. Sci Rep 7, 12899. https://www.nature.com/articles/s41598-017-13059-y.

Mendenhall, C.D., Shields-Estrada, A., Krishnaswami, A.J., Daily, G.C., 2016. Quantifying and sustaining biodiversity in tropical agricultural landscapes. Proc. Natl. Acad. Sci. U.S.A. 113, 14544–14551.

Mi, X., Feng, G., Hu, Y., Zhang, J., Chen, L., Corlett, R.T., Hughes, A.C., Pimm, S., Schmid, B., Shi, S., Svenning, J.-C., Ma, K., 2021. The global significance of biodiversity science in China: an overview. Natl Sci Rev 8, nwab032.

Micheli, F., Niccolini, F., 2013. Achieving Success under Pressure in the Conservation of Intensely Used Coastal Areas. Ecol Soc 18.

Mittermeier, R.A., Mittermeier, C.G., Brooks, T.M., Pilgrim, J.D., Konstant, W.R., Da Fonseca, G.A.B., Kormos, C., 2003. Wilderness and biodiversity conservation. Proc. Natl. Acad. Sci. U.S.A. 100, 10309–10313.

Northrup, J.M., Rivers, J.W., Yang, Z., Betts, M.G., 2019. Synergistic effects of climate and land-use change influence broad-scale avian population declines. Glob Chang Biol 25, 1561–1575.

Notenboom, J., MP van Veen, LG Wesselink, 2006. Halting the loss of biodiversity in the Netherlands.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326.

Pelletier, T.A., Carstens, B.C., Tank, D.C., Sullivan, J., Espíndola, A., 2018. Predicting plant conservation priorities on a global scale. Proc. Natl. Acad. Sci. U.S.A. 115, 13027–13032.

Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Gerschlauer, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Kühnel, A., Mayr, A.V., Mwangomo, E., Ngereza, C., Njovu, H.K., Otte, I., Pabst, H., Renner, M., Röder, J., Rutten, G., Schellenberger Costa, D., Sierra-Cornejo, N., Vollstädt, M.G.R., Dulle, H.I., Eardley, C.D., Howell, K.M., Keller, A., Peters, R.S., Ssymank, A., Kakengi, V., Zhang, J., Bogner, C., Böhning-Gaese, K., Brandl, R., Hertel, D., Huwe, B., Kiese, R., Kleyer, M., Kuzyakov, Y., Nauss, T., Schleuning, M., Tschapka, M., Fischer, M., Steffan-Dewenter, I., 2019. Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568, 88–92. https://www.nature.com/articles/%20s41586-019-1048-z.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. Nature 540, 220–229. https://www.nature.com/articles/nature20588.

Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., Brashares, J.S., 2008. Effect of habitat area and isolation on fragmented animal populations. PNAS 105, 20770–20775.

Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin, F.S., Lambin, E.F., Lenton, T.M., Scheffer, M., Folke, C., Schellnhuber, H.J., Nykvist, B., Wit, C.A. de, Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P.K., Costanza, R., Svedin, U., Falkenmark, M., Karlberg, L., Corell, R.W., Fabry, V.J., Hansen, J., Walker, B., Liverman, D., Richardson, K., Crutzen, P., Foley, J.A., 2009. A safe operating space for humanity. Nature 461, 472–475. https://www.nature.com/articles/461472a;

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60. https://www.nature.com/articles/nature01333.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science (New York, N.Y.) 287, 1770–1774.

Schulte To Bühne, H., Tobias, J.A., Durant, S.M., Pettorelli, N., 2021. Improving Predictions of Climate Change-Land Use Change Interactions. Trends Ecol Evol 36, 29–38. https://www.sciencedirect.com/science/article/pii/s0169534720302494.

Sciberras, M., Jenkins, S.R., Kaiser, M.J., Hawkins, S.J., Pullin, A.S., 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. Environ Evid 2, 4.

Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proc. Natl Acad Sci U.S.A. 109, 16083–16088.

Shaw, A., Miller, K., Wescott, G., 2017. Australian native gardens: Is there scope for a community shift? Landsc Urban Plan 157, 322–330.

Sheehan, E.V., Stevens, T.F., Gall, S.C., Cousens, S.L., Attrill, M.J., 2013. Recovery of a temperate reef assemblage in a marine protected area following the exclusion of towed demersal fishing. PLOS ONE 8, e83883.

Shi, P., Yu, D., 2014. Assessing urban environmental resources and services of Shenzhen, China: A landscape-based approach for urban planning and sustainability. Landsc Urban Plan 125, 290–297.

Simkin, S.M., Allen, E.B., Bowman, W.D., Clark, C.M., Belnap, J., Brooks, M.L., Cade, B.S., Collins, S.L., Geiser, L.H., Gilliam, F.S., Jovan, S.E., Pardo, L.H., Schulz, B.K., Stevens, C.J., Suding, K.N., Throop, H.L., Waller, D.M., 2016. Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. Proc Natl Acad Sci U.S.A. 113, 4086–4091.

Snoo, G.R. de, Naus, N., Verhulst, J., van Ruijven, J., Schaffers, A.P., 2012. Long-term changes in plant diversity of grasslands under agricultural and conservation management. Appl Veg Sci 15, 299–306. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1654-109X.2011.01181.x?casa_token=_DMlR1jRtscAAAAA%3ACVihdvuS7xypmhSfKBLJuY8HcUq3jtwDqwaAKUjuSNTDYy8zMCYZ2YKfTE6TcfHvTq9wcowh0tKIWZX4.

State of the World’s Plants and Fungi, 2016. State of the World’s Plants and Fungi 2020. https://www.kew.org/sites/default/files/2020-09/Kew%20State%20of%20the%20Worlds%20Plants%20and%20Fungi.pdf.

State of the World’s Plants and Fungi, 2020. State of the World’s Plants and Fungi 2020. https://www.kew.org/sites/default/files/2020-09/Kew%20State%20of%20the%20Worlds%20Plants%20and%20Fungi.pdf.

Stokstad, E., 2020. Global efforts to protect biodiversity fall short. Science (New York, N.Y.) 369, 1418.

Tamis, W., van’t Zelfde, M., van der Meijden, R., Groen, C., Udo de Haes, H.A., 2005. Ecological interpretation of changes in the dutch flora in the 20th century. Biol Conserv 125, 211–224.

The convention on biological diversity, 1992. The convention on biological diversity.

Torres, A., Jaeger, J.A.G., Alonso, J.C., 2016. Multi-scale mismatches between urban sprawl and landscape fragmentation create windows of opportunity for conservation development. Landsc Ecol 31, 2291–2305. https://link.springer.com/article/10.1007/s10980-016-0400-z.

Tscharntke, T., 2021. Disrupting plant-pollinator systems endangers food security. One Earth 4, 1217–1219. https://www.sciencedirect.com/science/article/pii/s2590332221004802.

Wamelink, G.W.W., Mol-Dijkstra, J.P., Reinds, G.J., Voogd, J.C., Bonten, L.T.C., Posch, M., Hennekens, S.M., Vries, W. de, 2020. Prediction of plant species occurrence as affected by nitrogen deposition and climate change on a European scale. Environ Pollut (Barking, Essex : 1987) 266, 115257. https://www.sciencedirect.com/science/article/pii/s0269749119334086.

Wamelink, G. W. Wieger; Kurvers, Katrien (2022): The Netherlands may lose up to 40% of its plant species due to climate change.

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D., Ellis, S., 2021. The decline of butterflies in Europe: Problems, significance, and possible solutions. Proc Natl Acad Sci U.S.A. 118.

Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515, 67–73. https://www.nature.com/articles/nature13947.

Watson, J.E.M., Venter, O., 2017. Ecology: A global plan for nature conservation. Nature 550, 48–49. https://www.nature.com/articles/nature24144.

Wei, N., Kaczorowski, R.L., Arceo-Gómez, G., O'Neill, E.M., Hayes, R.A., Ashman, T.-L., 2021. Pollinators contribute to the maintenance of flowering plant diversity. Nature 597, 688–692. https://www.nature.com/articles/s41586-021-03890-9.

Xu, W., Xiao, Y., Zhang, J., Yang, W., Zhang, L., Hull, V., Wang, Z., Zheng, H., Liu, J., Polasky, S., Jiang, L., Xiao, Y., Shi, X., Rao, E., Lu, F., Wang, X., Daily, G.C., Ouyang, Z., 2017. Strengthening protected areas for biodiversity and ecosystem services in China. Proc Natl Acad Sci U.S.A. 114, 1601–1606.

Chapter 2

Importance of natural land cover for plant species' conservation: a nationwide study in The Netherlands

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Abstract

While shifts to high-intensity land cover have caused overwhelming biodiversity loss, it remains unclear how important natural land cover is to the occurrence, and thus the conservation, of different species groups. We used over 4 million plant species' observations to evaluate the conservation importance of natural land cover by its association with the occurrence probability of 1 122 native and 403 exotic plant species at 1 km resolution by species distribution models. We found that 74.9% of native species, 83.9% of the threatened species and 77.1% rare species preferred landscapes with over 50% natural land cover, while these landscapes only accounted for 15.6% of all grids. Most species preferred natural areas with a mixture of forest and open areas rather than areas with completely open or forested nature. Compared to native species, exotic species preferred areas with lower natural land cover and the cover of natural open area, but they both preferred extremely high and low cover of natural forest area. Threatened and rare species preferred higher natural land cover, either cover of natural forest area or cover of natural open area than not threatened and common species, but rare species were also more likely to occur in landscapes with 0-25% cover of natural open area. Although more natural land cover in a landscape will not automatically result in more native species, because there is often a non-linear increase in species occurrence probability when going from 0% to 100% natural land cover, for conserving purposes, over 80% natural land cover should be kept in landscapes for conserving threatened and very rare species, and 60% natural land cover is the best for conserving common native species. Our results stress the importance of natural areas for plant species' conservation. It also informs improvements to species conservation by increasing habitat diversity.

Introduction

Global biodiversity is declining at an unprecedented rate and around one million plant and animal species are facing extinction (Bridgewater et al., 2019; Tollefson, 2019). The transformation of natural habitat into agriculture, infrastructure and urban areas is considered as one of the main drivers of these declines (Sala et al., 2000; van Klink et al., 2020). Currently, approximate three-quarters of the terrestrial biosphere has been altered by human activities (Ellis and Ramankutty, 2008) and the impact of these alterations on biodiversity is expected to increase this century (Visconti et al., 2016). Natural (e.g. natural forest, wetland and dunes, *etc*.) and semi-natural habitats (e.g. production forest, extensive pastures) are recognized as the stronghold for the majority of species on Earth (Di Marco et al., 2019; Mokany et al., 2020), although some species can use human modified ecosystems (Magioli et al., 2019; Galán-Acedo et al., 2019). In fact, many threatened species only occur in natural habitats, making the loss of natural habitat a more severe problem for those species (Dudley, 2013). Consequently, the extent of (semi)natural land cover (NLC) is a key determinant of species conservation status in a given landscape.

However, the different relations between NLC and biodiversity are a contentious issue in the debate surrounding the importance of and need for natural areas to conserve biodiversity. For example, studies on plant richness come to different conclusions, with some showing a linear increase with natural habitat cover (Blaser et al., 2018), others a quadratic relationship with the highest species richness in areas with intermediate cover of natural habitats (Bascompte and Rodriguez, 2001), and yet others a lack of correlation between plant species richness and natural habitat cover (Cormont et al., 2016). This is presumably because the importance of NLC likely varies between species and possibly groups of species, for example, threatened vs non-threatened (Berg et al., 1994) or native vs exotic species. A better understanding of the importance of NLC to different species and species groups is urgently needed to improve biodiversity conservation in the Anthropocene.

Natural areas may include different ecosystems and habitat types, from forests to shrublands and open grasslands to wetlands. The abiotic conditions vary substantially between these ecosystems ranging from shady, moist forests to sunlit, warm and dry open habitats, and thus provide very different living conditions for species (Frenne et al., 2013; Arx et al., 2013). While an increased amount of forest cover may result in high plant species richness in general (Mendenhall et al., 2016), not all species prefer habitats with high forest cover (Casado et al., 2004). Richness of some shade-intolerant plant species decreases with forest cover (Benchimol et al., 2017), as those species prefer more open habitats. Consequently, to assess the importance of natural habitats for species conservation, it may be important to discriminate between natural areas consisting of natural forest areas (NLC-F) or of natural open areas (NLC-O).

In this study, we assess the importance of NLC to the conservation of plant species in the Netherlands. We aim at evaluating the importance of habitat with different extent of NLC for the occurrence, rather than fitness or richness, of certain species. This method will provide us with novel insight into the occurrence probability of almost all species along the proportion of NLC across the landscapes (Laughlin et al., 2020). We address the following sub-questions: (1) does the extent of NLC associate with native plant species' occurrence? (2) do different types of natural areas (forests versus open habitats) affect the conservation status (presence) of native plants? (3) given the importance of natural areas to conservation-relevant species, we ask whether there is a correlation between the status of the plant species (native/exotic, threatened/not threatened and rare/common) and the preferred amount of natural area (or forest or open) in the landscape? (4) Does more NLC make landscapes suitable to more species of conservation-relevance?

Method

Study area

Our study area is the Netherlands, for which long-term and detailed monitoring data of biodiversity exist. Most of the country consists of human-dominated landscapes with agriculture (about 62%) and urban and industrial areas (about 15%), while few (semi-)natural landscapes remain (about 23%).

Land cover

Compared to non-natural habitats, which can also be potential habitats for plants, NLC in this paper includes all natural or semi-natural habitats (S1 Table) receiving little human disturbance and management. To derive a complete national dataset from which NLC could be obtained, we combined data from three national sources on land use and land cover: *Informatiemodel natuurbeheer* (Inter Provinciaal Overleg, 2016), *basisregistratie gewaspercelen* (Ministerie van Economische Zaken (EZK), 2015), and *bestand bodemgebruik* (Centraal Bureau voor de Statistiek (CBS), 2012) using ESRI ArcGIS Desktop 10.2 (https://desktop.arcgis.com/en/). These three datasets included 175 land cover classes at the country scale. Marshall (Marshall, 2018) aggregated these 175 classes into 16 land cover classes at a resolution of 10x10 m. We further re-classified these 16 classes into '(semi-)natural land cover' and 'non-natural land cover' (S1 Table). Since this study focuses on the terrestrial ecosystems and wetland ecosystems, we excluded the land cover class of 'open water' (large bodies of surface waters, whether fresh or brackish).

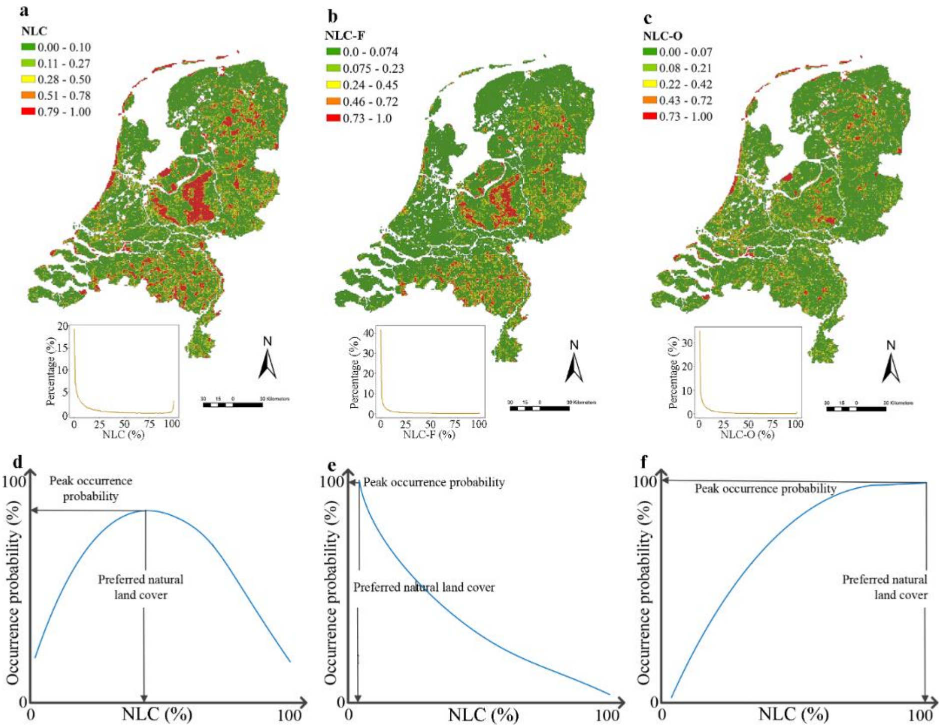


Fig 1. Land cover map and illustration of plant species responding to NLC. a, the distribution of NLC across the Netherlands. b, the distribution of the NLC-F across the Netherlands. c, the distribution of the NLC-O across the Netherlands. d-f, Illustration of three types of hypothetical curves indicating plant species responding to NLC (or NLC-F or NLC-O).

Next, we calculated the proportion of NLC within each 1 x 1 km cell in the Netherlands. The NLC-F and proportion of NLC types except for natural forest, further referred to as the NLC-O, were also calculated in order to compare the preferences of plant species for natural forest and natural open habitats (S1 Table, Fig 1a-c). Based on calculated proportions of NLC, NLC-F and NLC-O in each grid, the proportion (F_i) of grids in the Netherlands with different NLC (or NLC-F or NLC-O) equalling i was calculated by

$$F_i = N_i / N \qquad \text{Equation 1.}$$

where N_i is the number of grids with NLC (or NLC-F or NLC-O) equalling i and N is the total number of grids. To avoid artefacts relating to the species-area relationship from affecting our results, only cells where open water was <10% (equalling a land surface proportion of =>90% in each cell) were included in our analysis (see S1 text for a sensitivity analysis, S1 Fig).

Plant species data

We used presence-only records for vascular plants, which include seed plants, conifers, ferns and clubmosses, in the Netherlands from the Dutch National Database of Flora and Fauna (NDFF, www.ndff.nl) collected between the period 2010-2017. Our analysis used species-level taxonomy, so we excluded observations at genus and family level, as well as nomina dubia (e.g. '*Geranium dissectum* / *molle / pusillum*'). Species with an 'extinct' or 'disappeared' status (Sparrius et al., 2014) were also excluded. Included observations were either point observations or polygons with areas smaller than 3 ha, and the latter indicated the presence of a species within a given area. All polygons were converted to points by taking the centroid of the polygon. Next, each observation was attributed to a 1 x 1 km cell. This left us with 4 773 313 observations (S2 Fig), including 1 128 native and 416 exotic species (S2 Table). All of these species are accepted in the Netherlands, and their corresponding names in the World Flora Online were also included in S2 Table for comparison. Exotic species, which include many cultivated species, were included in this study to compare with native species. Although many exotic species are cultivated, they have been a real part of the environment after introduction to the Netherlands. Finally, duplicate species records were removed to leave a single presence value for each species in each 1 x 1 km cell in the dataset.

Species distribution modelling

To gain insight in the response of plant species to NLC, NLC-F and NLC-O, we developed species distribution models (SDMs), which have been validated to be an effective method to link environmental variables to species distributions (Laughlin et al., 2020). By using SDMs, we assessed the species occurrence probability rather than fitness or richness and found out which extent of NLC is the best habitat for certain species. In addition to the three variables of interest (NLC, NLC-F and NLC-O), we also included bioclimatic data and soil types. We extracted 19 bioclimatic variables (bio1-bio19) from the WorldClim 2.1 database with resolution 30 seconds (Fick and Hijmans, 2017). Due to multi-collinearity between these bioclimatic variables, we used principal components analysis (PCA) to convert 19 bioclimatic variables into 5 linearly uncorrelated variables (Kriticos et al., 2014), which capture 93% of the variability in the full suite of 19 bioclimatic variables (S3 Table). A national layer of soil types (10 classes produced in 2006) was obtained from https://www.wur.nl/nl/show/Grondsoortenkaart.htm. This was used to generate a rasterized coverage of 10 soil types at 1 km resolution using ESRI ArcGIS Desktop 10.6.1 (https://desktop.arcgis.com/en/). Due to strong correlations between NLC and NLC-F, as well as NLC and NLC-O (S4 Table), we included either NLC or NLC-F and NLC-O in two separate SDMs (i.e. SDM1 includes NLC, five bioclimatic variables and ten soil types; SDM2 includes NLC-F, NLC-O, five bioclimatic variables and ten soil types).

We employed maximum entropy modelling (Phillips et al., 2006) (MaxEnt), which can robustly deal with a variety of presence-only data (Phillips et al., 2006; Phillips and Dudík, 2008; González-Irusta et al., 2015) and has outperformed most other SDM modelling applications in dealing with small samples and preventing overfitting (Hernandez et al., 2006; Aguirre-Gutiérrez et al., 2013). MaxEnt models were developed using the function *maxent* from the R package dismo (Hijmans et al.., 2017) in R version 3.5.1 (R Core Team, 2018). For each species, two separate SDMs were run as mentioned above. For each variable included in the model, we calculated the response of species occurrence probability to this variable, which will be used in further analysis. We used the permutation importance for evaluating the importance of different variables (NLC, etc.) (Zhang et al., 2018). The validation of the robustness of species distribution prediction was carried out with AUC generated by SDMs (Manel et al., 2002). However, AUC values indicating SDM accuracy based on presence-background data are flawed. Hence, we tested the validity of MaxEnt models for each species by comparing the AUC value to a null model (Raes and ter Steege, 2007). To generate the null model for a species, we constructed 100 MaxEnt models with the same parameterization and structure of the corresponding empirical model, but now using an equal number of randomly drawn occurrence records (Enriquez-Urzelai et al., 2019). We then computed the 95% C.I. AUC value based on yielded 100 AUC values from each null model and assessed whether AUC values of empirical MaxEnt models were higher than their corresponding 95% C.I. AUC values of the fitted null models (Raes and ter Steege, 2007). Those species for which the AUC values of SDMs were not significantly higher than null models were excluded from further analyses due to the species occurrence not significantly explained by the predictors included in the SDM.

Response of species to NLC and preferred NLC

Of each species for which the occurrence was significantly explained by the SDM, the shape of the response to NLC (or NLCF or NLCO) was determined, by classifying the curve into 'Increase' (positive linear model), 'Decrease' (negative linear model), 'Unimodal' (quadratic model), 'U-shaped' and 'None' (a response curve with no relationship with either NLC, NLC-F or NLC-O). To get the shape of the response of each species, we assessed the corresponding NLC (or NLC-F or NLC-O) values to the peak and lowest occurrence probability values, using the following criteria: (i) we assigned an increasing response curve if the NLC (or NLC-F or NLC-O) value at peak occurrence probability value equalled 100% and the NLC value at the lowest occurrence probability value equalled 0%; (ii) we assigned a decreasing response curve if the NLC value at peak occurrence probability value equalled 0% and the NLC value at the lowest occurrence probability value equalled 100%; (iii) we assigned a u-shaped response curve if the NLC value at the lowest occurrence probability value ranged between 1% and 99%; (iv) we assigned a unimodal response curve if the NLC value at peak occurrence probability value ranged between 1% and 99%; (v) we assigned a flat response curve ('None') if the NLC value at peak occurrence probability value equalled the NLC value at the lowest occurrence probability value. Response curves of 1 525 species with either decreasing, unimodal or increasing shapes were presented in S3 Fig. 10. No species performed u-shaped response curves and species with a neutral (without a relationship, named 'None') response were omitted as not preferring any NLC. Secondly, for each species with a decreasing, increasing or unimodal relationship with natural cover, we determined their preference for nature (or natural forest or open). This 'preferred natural land cover' (preferred NLC, NLC-F or NLC-O) represents the percentage of NLC (or, NLC-F or NLC-O) at the predicted peak occurrence probability (Fig 1d-f). For those species with decreasing or increasing relations with NLC (or NLC-F or NLC-O), their preferred NLCs (preferred NLC-Fs or NLC-Os) are always '0%' or '100%', respectively. For species with unimodal shapes, their preferred NLCs (preferred NLC-Fs or NLC-Os) are the NLCs (NLC-Fs or NLC-Os) corresponding to the peak occurrence probability of the predicted response curve. Plant species with unimodal response curves differed substantially in preferred NLC (and in preferred NLC-Fs or NLC-Os). For illustrative purposes and to facilitate comparisons between plant responses, we divide them in four classes: (i) unimodal0-25%, with peak of unimodal curve at (0%, 25%) NLC (or NLC-F or NLC-O); (ii) unimodal25-50%, with peak at [25%, 50%) NLC; (iii) unimodal50-75%, with peak at [50%, 75%) NLC; and (iv) unimodal75-100%, with peak at [75%, 100%) NLC. In the comparisons, we distinguished six groups (Increasing curve, decreasing curve and the four unimodal groups) based on preferred NLC, NLC-F or NLC-O.

Species occurrence in landscape cells (1x1km) relative to the distribution of NLC in those cells nationwide

To assess whether the occurrence of species followed the distribution of NLC in the Netherlands or not, the proportion of observations of species within group k (one of six groups described above) occurring in grid cells with NLC equalling i (F_{ik}) was calculated by

$$F_{ik}=N_{ik}/N_k \qquad \text{Equation 2.}$$

where N_{ik} is the number of observations of species within group k and occurring in grids with NLC equalling i. N_k is the number of all observations of species within group k.

Finally, the representativeness of the occurrence of a species group along NLC, describes the difference between the proportion of occurrences of grid cells with different NLC in the Netherlands and the relative occurrence of each species group along NLC. The difference in representativeness (R_{ik}), was calculated by

$$R_{ik} = F_{ik} - F_i \qquad \text{Equation 3.}$$

Association between species category and preferred NLC, NLC-F and NLC-O

To assess whether different species groups differ in their response to natural cover, we classified all species based on their (1) origin (native and exotic); (2) threatened status (threatened and not threatened); (3) rarity (rare and common); (4) growth form (woody and herbaceous). Data on threatened status, rarity and species origin were obtained from the Red List of Vascular Plants of the Netherlands (Sparrius et al., 2014). Ninety-three percent of the data about growth form were extracted from online existing databases (Kleyer et al., 2008; Engemann et al., 2016; Taseski et al., 2019) and 7% were manually assigned using images on Google Image (https://images.google.com/) and Wikipedia (https://www.wikipedia.org/). Since we were interested in differences between main categories, for the threatened status of species, we omitted Data Deficient (DD), and reclassified Least Concern (LC) and Near Threatened (NT) as ‘not threatened’ and Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) as ‘threatened’.

We then compared how these three broad species categories are related to four groups of preferred NLC, NLC-F and NLC-O (0-25%, 25-50%, 50-75% and 75-100%). We used Contingency Analyses (Pearson’s) to assess differences between levels within each category. All analyses and visualisations were conducted in R version 3.5.1 (R Core Team, 2018).

Average occurrence probability increase

The increase in occurrence probability per plant group was calculated by

$$OP_i = \sum_{j=1}^{j=n}(OP_{ij} - OP_{0j})/n \qquad \text{Equation 4.}$$

where OP_i is the averaged occurrence probability increase by increasing NLC from 0% to i%, OP_{ij} is the occurrence probability of species j at NLC i%, OP_{0j} is the occurrence probability of species j at NLC 0%. n is the total number of species in a certain group (e.g. threatened species).

Results

NLC, NLC-F and NLC-O patterns across the Netherlands

To explore the relationships between NLC and species' presence, we first quantified the NLC, NLC-F and NLC-O across space and mapped their frequency distributions (Fig 1a-c). Both NLC-F and NLC-O showed a sharply decreasing pattern. Although NLC showed a 'U-shaped' pattern, the proportion of grid cells with 100% NLC was still much lower than that with 0% NLC. Taken together, the frequency distribution of NLC, NLC-F and NLC-O at the 1x1 km scale revealed that 90% of the landscapes in the Netherlands have less than 73% NLC, less than 39% NLC-F and less than 29% NLC-O.

NLC correlates to plant species occurrence

We analysed the relationships between native plant species occurrence and NLC. Out of 1 128 native plant species, SDMs for 1 122 species were significantly better than the null model and those species showed either a decreasing, unimodal or increasing relationship with NLC (Fig 2a). Results of all 1 122 species are in S2 Table and response curves of these species are in S3 Fig. Based on permutation importance value, NLC was, on average, a more important variable for explaining species occurrence than other variables (Table 1). Of the 1 122 native plant species, 20 times more species showed a linear increase with NLC (21.4%, 240 spp.) than a linear decrease (1%, 11 spp.) with NLC (Fig 2a-b, d). The majority of species (77.6%, 871 spp.) showed a unimodal response curve (Fig 2a, c) with NLC.

Table 1. Comparison of permutation importance among variables. Higher values indicate a higher importance and thus more explanatory power in the models.

		All spp.	Native spp.	Exotic spp.
	Summary	Mean	Mean	Mean
	NLC	19.58	22.79	10.90
	bioclim1	10.34	11.20	8.01

Model1 (with NLC)	bioclim2	13.18	14.31	10.14
	bioclim3	3.37	2.72	5.11
	bioclim4	3.69	3.36	4.60
	bioclim5	2.47	2.39	2.71
	built_upon_area	8.76	7.25	12.86
	heavy_clay	2.90	2.44	4.15
	heavy_sabulous_clay	2.97	2.42	4.44
	light_clay	5.93	5.34	7.54
	light_sabulous_clay	2.64	1.95	4.53
	loam	1.46	1.24	2.07
	peat	5.72	5.25	6.99
	sand	14.43	15.43	11.71
	swampy_on_sand	1.96	1.47	3.27
	water	0.58	0.44	0.96
Model2 (with NLCF+NLCO)		All spp.	Native spp.	Exotic spp.
	Summary	Mean	Mean	Mean
	NLC-F	7.42	7.61	6.89
	NLC-O	12.80	15.01	6.75
	bioclim1	10.06	10.92	7.71
	bioclim2	13.44	14.53	10.47
	bioclim3	3.58	2.97	5.27
	bioclim4	3.63	3.32	4.47
	bioclim5	2.47	2.34	2.80
	built_upon_area	8.83	7.59	12.22
	heavy_clay	2.96	2.56	4.04
	heavy_sabulous_clay	3.05	2.61	4.25
	light_clay	5.82	5.34	7.14
	light_sabulous_clay	2.80	2.10	4.70
	loam	1.48	1.25	2.11
	peat	5.73	5.32	6.84

	sand	13.58	14.72	10.46
	swampy_on_sand	1.88	1.42	3.14
	water	0.48	0.39	0.74

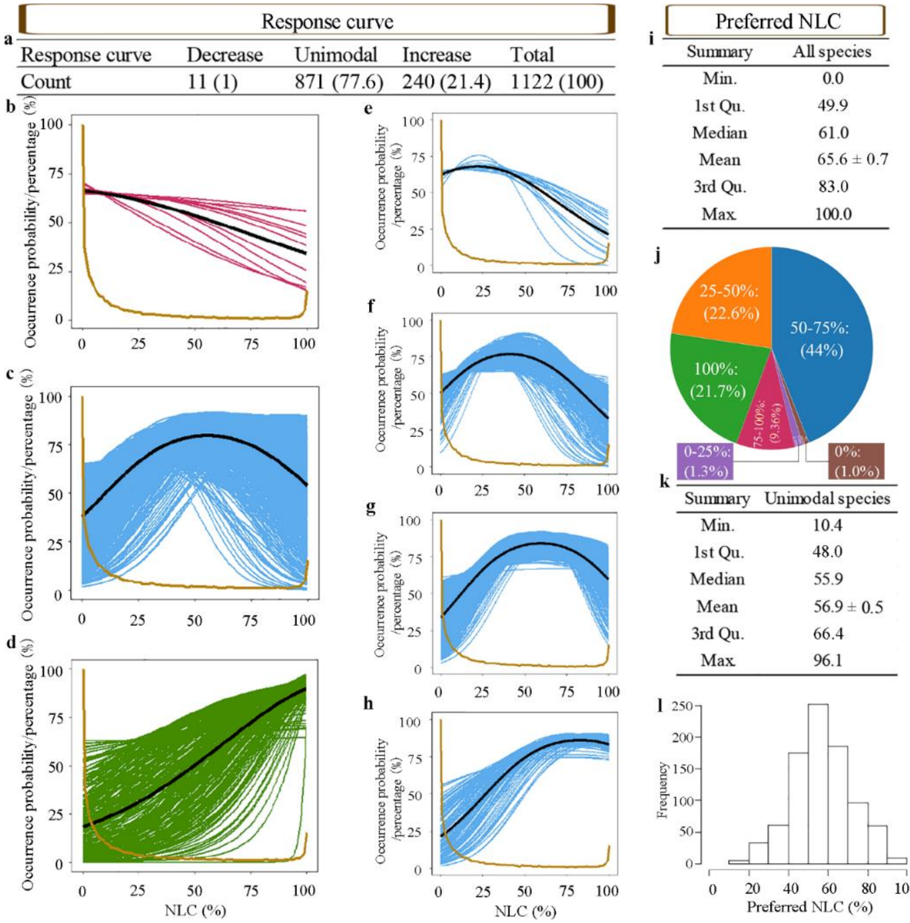


Fig 2. Response to NLC for 1 122 native plant species with significant null models. 3 species with a neutral (without a relationship, named 'None') response were omitted as not preferring any NLC. a-h, Response curves of plant species to NLC. i-l, Summary statistics of preferred NLCs. a, Summary of all 1 122 native plants responding to NLC (with percentages in parentheses). b-d, Response curves of species with decreasing (each magenta line indicates one species) (b), unimodal (each blue line indicates one species) (c) and increasing (each green line indicates one species) (d) relations with NLC. The dark black line is the average response curve of each species group. The yellow line indicates the standardized proportion of grids with different NLC in the Netherlands. Both the occurrence probability and the standardized proportion (percentage) range from 0% to 100%

and are indicated by the y axis. e-h, Species with unimodal shapes were split into four groups based on their preferred NLCs (e, species with preferred NLCs ranging from 0-25%; f, species with preferred NLCs ranging from 25-50%; g, species with preferred NLCs ranging from 50-75%; h, species with preferred NLCs ranging from 75-100%). i-j, Statistics of preferred NLCs of all 1 122 native plant species (i, summary of 1 122 plant species' preferred NLCs; j, percentage of species (in brackets) in different preferred NLC range groups, i.e. 0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%). k-l, Statistics of preferred NLCs of species with unimodal shapes (k, summary of plant species' preferred NLCs; l, histogram of preferred NLCs of plant species with unimodal relations with NLC). All mean values are means ± SE.

Moreover, the steepness of the response curves varied widely between different species (Fig 2), even between species with the same response curve shape (either increase, unimodal or decrease). For example, both *Carex extensa* and *Carex distans* had unimodal relationships with NLC, but the curve of *Carex extensa* was much steeper than that of the *Carex distans* (S3 Fig).

We further calculated the preferred NLC, i.e. the NLC corresponding to the peak occurrence probability in the response curve, to portray where these native plant species are most likely to occur. The median and mean of preferred NLC of the 1 122 species were 61.0% and 65.6%, respectively (Fig 2i). In total, 840 of 1 122 species (accounting for 74.9%) preferred NLC above 50%, with 346 of those preferring NLC above 75% (Fig 2j). What's more, threatened and rare species particularly preferred landscapes with high NLC. Of the threatened species, 193 of 230 (accounting for 83.9%) preferred NLC higher than 50%, with 120 of those species preferring NLC higher than 75% (Fig 3, S4 Fig). Of the rare species, 388 of 503 (accounting for 77.1%) preferred NLC higher than 50%, with 233 of those species preferring NLC higher than 75% (Fig 3). However, when assessing the proportion of grid cells with different NLC in the Netherlands (Figs 1, the yellow line in 2, and 3), grid cells with NLC above 50% only account for 15.6% of all grid cells in the Netherlands, while these concurred with the preferred NLC of 74.9% native species, 83.9% threatened species and 77.1% rare species. In short, there is a strong mismatch between the NLC available in the Netherlands and the preference for landscapes with higher NLC of the majority of native plant species (Fig 3).

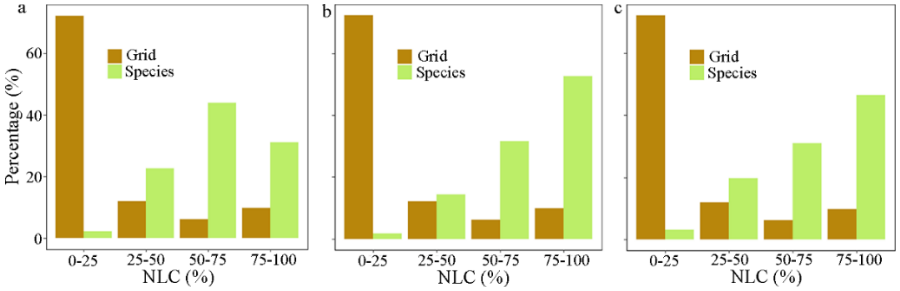


Fig 3. Percentage of grids with different NLC and species with different preferred NLC in the Netherlands. a, 1 122 native species. b, 230 threatened species. **c**, 503 rare species. The brown colour means the distribution of grid cells with different NLC and the green colour means the distribution of species with different preferred NLC.

Since most species showed unimodal shapes, but their preferences for NLC varied widely (ranging from 10.4% to 96.1%, Fig 2k), we divided them into four groups based on NLC preference of 0-25%, 25-50%, 50-75% and 75-100% (Fig 2e-h). The percentages of species in the four groups were 1.3%, 22.6%, 44.0% and 9.4% respectively (the sum is not 100% as species with decreasing and increasing response curves were excluded) (Fig 2j). Overall, the frequency distribution of preferred natural cover of species with unimodal responses followed a normal distribution, with a median of 55.9% (Fig 2k-l). Over 69.1% of these species were more likely to occur in landscapes with NLC more than 50%.

Next, we compared the relative occurrence of each species group (increase, decrease, unimodal0-25%, unimodal25-50%, unimodal50-75% and unimodal75-100%) to the presence distribution of NLC in the landscapes of the Netherlands. In this way, we can show the extent to which different species groups overuse or underuse grid cells with different NLC. Species groups with increasing response curves and unimodal curves with preferred NLC 75-100% were under-represented in areas with low NLC but over-represented in areas with high NLC (Fig 4). The species group with decreasing response curves and preferred NLC 0-25% were a bit over-represented in areas with low NLC and under-represented in areas with high NLC. Finally, the group with preferred NLC 25-50% was under-represented in low NLC and high NLC but over-represented in moderate NLC, while the group with preferred NLC 50-75% was only under-represented in areas with low NLC. In general, most species were over-represented in areas with high NLC but under-represented in low NLC cells.

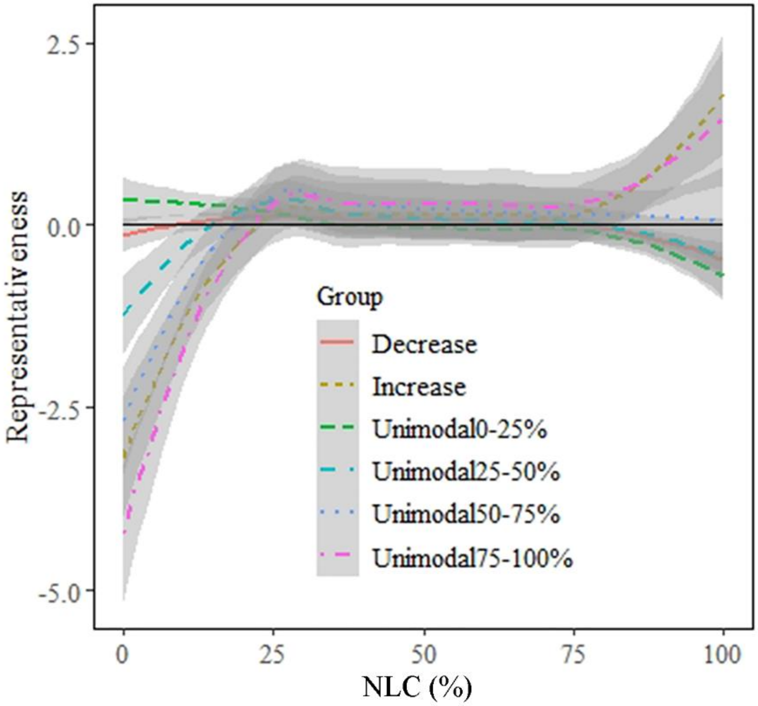


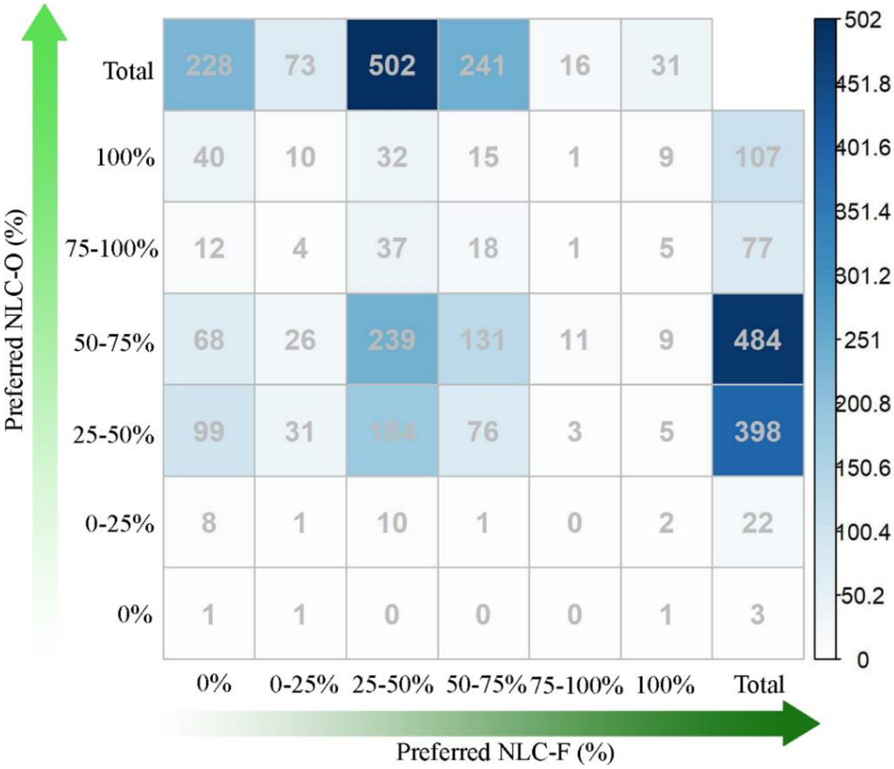
Fig 4. The representativeness, i.e. relative occurrence of a species group in relation to the NLC availability in the Netherlands. It describes the difference between the proportion of occurrence of grid cells with different NLC in the Netherlands and the relative occurrence of each species group along NLC. Species were classified into decrease, increase, preferred NLCs of 0-25% (unimodal0-25%), 25-50% (unimodal25-50%), 50-75% (unimodal50-75%) and 75-100% (unimodal75-100%), respectively. Lines represent the best-fit regressions and the grey bands represent the regression 95% confidence interval. The black horizontal line indicated 0.

Differences in preferences of plant species for NLC-F or NLC-O

For 1 091 and 1 121 species, of 1 122 native species, the SDM showed meaningful response curves (i.e. SDM models were better than null models) with NLC-F and NLC-O, respectively (S5 and S6 Figs, S2 Table). Average permutation importance showed that these two variables ranked first and fifth respectively (Table 1). According to the response curves of species to NLC-F and NLC-O, we obtained the shapes and preferred NLC-F and NLC-O for each species. We found that most species (76.3%) showed a unimodal response to NLC-F. The mean and median of preferred NLC-F of 1 091 species were 35.9% and 39.9% (S5 Fig); Most species (88.8%) also showed a unimodal response to NLC-O. The mean and median of preferred NLC-O of 1 121 species were 57.6% and 55.0% (S6 Fig).

We compared the preferences for NLC-F and NLC-O of each native species and found that most species preferred areas with 25-75% NLC-F and NLC-O (Fig 5). Threatened and rare species also preferred moderate NLC-F and NLC-O (S7 and S8 Figs).

In other words, a minority of native species prefers landscapes with a very high (>75%) NLC-F (47spp., 4.3%) or NLC-O (184spp., 16.9%). Only 9 species (0.8%) showed increasing occurrence probabilities with both NLC-F and NLC-O increase. In this case, these species prefer high NLC, but natural types don't matter for these species. One species (0.1%) showed decreasing occurrence probabilities with both NLC-F and NLC-O increase. Forty species (3.7 %) showed increasing relationships with NLC-O but decreased relationships with NLC-F. These species prefer natural open areas but not natural forest areas. In contrast, only one species (0.1%) preferred natural forest areas but not natural open areas.



	0%	0-25%	25-50%	50-75%	75-100%	100%	Total
Total	228	73	502	241	16	31	
100%	40	10	32	15	1	9	107
75-100%	12	4	37	18	1	5	77
50-75%	68	26	239	131	11	9	484
25-50%	99	31	184	76	3	5	398
0-25%	8	1	10	1	0	2	22
0%	1	1	0	0	0	1	3

Fig 5. Preferred NLC-F and preferred NLC-O of native plant species. Preferred NLC-F and NLC-O were classified into six groups, corresponding to species with decreasing shapes (preferred NLC-F or NLC-O equalling 0%), species with increasing shapes (preferred NLC-F or NLC-O equalling 100%), species with preferred NLC-F or NLC-O between 0% and 25%, species with preferred NLC-F or NLC-O ranging from 25% to 50%, species with preferred NLC-F or NLC-O ranging from 50% to 75%, species with preferred NLC-F or NLC-O ranging from 75% to 100%. The number of species (in each grid) increases with the blue colour in each grid getting dark.

Importance of nature to plant species varies between threatened and unthreatened as well as between native and exotic species

Finally, we explored whether the preference for NLC, NLC-F and NLC-O varies between species categories. Contingency Analysis revealed that threatened and rare species were more likely to occur in landscapes with NLC, NLC-F and NLC-O more than 75% compared to not threatened and common species (Fig 6a-f, S9 Fig). Rare species were also more likely to occur in landscapes with NLC-O between 0% and 25% compared to common species.

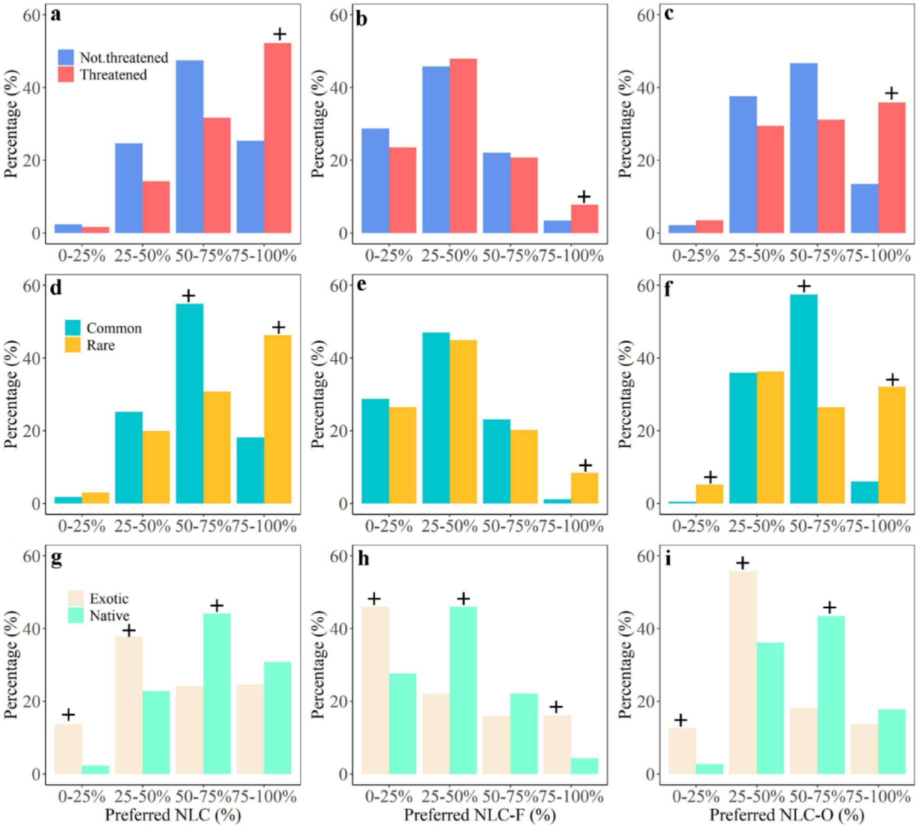


Fig 6. Percentage distribution of species along the preferred NLC, preferred NLC-F and preferred NLC-O within each species category (threatened status, rarity and origin of species). a-c, Percentage distribution of threatened and not threatened species along preferred NLC (a), NLC-F (b) and NLC-O (c). d-f, Percentage distribution of common and rare species along preferred NLC (d), NLC-F (e) and NLC-O (f). h-i, Percentage distribution of native and exotic species along preferred NLC (g), NLC-F (h) and NLC-O (i). '+' indicates values that are above expectation according to our Contingency Analysis (see supplementary analysis for detailed results).

Most exotic plant species in the Netherlands showed unimodal relationships with NLC, with a peak in the response curve between 25%-50% NLC (S10 Fig). Contingency Analysis indicated that exotic species were more likely to occur in landscapes with NLC and NLC-O lower than 50% compared to native species (Fig 6g-i, S9 Fig). In contrast, native species were more likely to occur in landscapes with a relatively high NLC and NLC-O (50-75%). Exotic species also preferred landscapes with 0-25% and above 75% NLC-F, but native species preferred landscapes with 25-50% NLC.

Discussion

The importance of NLC to plant species' presence

Almost all native plant species in the Netherlands had an association with NLC and more species preferred landscapes with high NLC than low NLC. This nationwide study confirms the importance of NLC to plant species, and it supports the need of protecting natural habitats for species conservation (Watson and Venter, 2017). Of the 1 122 native species, 74.9% (840 species) preferred NLC above 50%. This strongly contrasts with the 15.6% of Dutch landscapes that have NLC higher than 50%. It suggests that most species in the Netherlands lack sufficient suitable landscapes, and this is particularly true for threatened species. The overrepresentation of most species in high NLC landscapes and their underrepresentation in low NLC landscapes further exemplifies the imbalance between current landscapes and species' needs in the Netherlands. It also indicates that any increase in NLC in low NLC landscapes might mitigate species decline and promote species occurrence. This is consistent with the marginal occurrence probability increase, which is high in areas with low NLC (S11 Fig). Although a correlative study such as ours cannot definitely assign causality, the findings from controlled experimental studies at small scale suggest NLC alters plant biodiversity and increase NLC can increase species (Bascompte and Rodriguez, 2001; Blaser et al., 2018).

Although most species preferred NLC above 50%, more species preferred NLC 50-75% than 75-100%. There were also more species preferring NLC 25-50% than 0-25%. This broad hump-shape trend is consistent with the intermediate disturbance hypothesis (Connell, 1978), which stipulates that natural areas with intermediate levels of land cover change may provide more heterogeneous habitats (higher habitat diversity) harbouring more species than completely natural areas, e.g. continuous deciduous forests, salt marshes. This is also found by another study at large scale, which shows that unimodal relationships exist between Canadian avian species and NLC (Rachelle et al., 2011). However, this relationship is mainly explained by the amount of NLC per se and not by increased habitat diversity. These patterns are in line with the 'habitat amount hypothesis' which states that species respond primarily to the total habitat amount at the landscape level and that there is little additional effect of the habitat configuration on species (Fahrig, 2013). Threatened plant species were even more prevalent in landscapes with 75-100% NLC than other native plants, which concurs with the findings of Berg et al (Berg et al., 1994). These findings reveal that landscapes with very high NLC are particularly valuable for the protection of threatened species.

Unsurprisingly, individual plant species showed very different relations with NLC and the most common response was a preference for landscapes with 50-75% NLC. Following on from this, we assume that species richness is also the highest in landscapes with 50-75% NLC. Indeed, the relationship of species richness with NLC based on observations was quadratic, which is consistent with the predicted richness-NLC relationships based on species-level responses (Supplementary Method, S12 Fig). Although our study does not give any insight into whether and how individual species affect the response of community species richness to NLC, some findings about the traits of individual species and their assemblage dictating the responding of the community to the environment (e.g., climate) have been observed before (Aguirre-Gutiérrez et al., 2019).

Given the relatively long red lists of threatened species/rare species and the sparsity of natural habitats in the Netherlands, governmental and private conservation initiatives to strengthen the conservation of plant species should strive to increase the cover of natural habitats and the presence of natural elements in degraded landscapes and sustain currently protected areas. This is because landscapes with NLC always harbour more species than landscapes without NLC (Fig 7). However, more NLC in a landscape will not automatically result in more native species because there is often a non-linear increase in species occurrence probability when going from 0% to 100% NLC. The optimum NLC lies between 64-100%, being generally higher for threatened species (with optimum at 80% NLC) and rare species (with optimum at 70% NLC), particularly very rare species (with optimum at 100% NLC), than for not threatened and common species (Fig 7 b-d). Exotic species show a different pattern with the highest occurrence in landscapes with lower NLC than that of native species (Fig 7 a). Thus, increasing NLC in totally disturbed landscapes (0% NLC) to 64% or even more is likely to increase species richness overall, but different species groups require different restoration strategies.

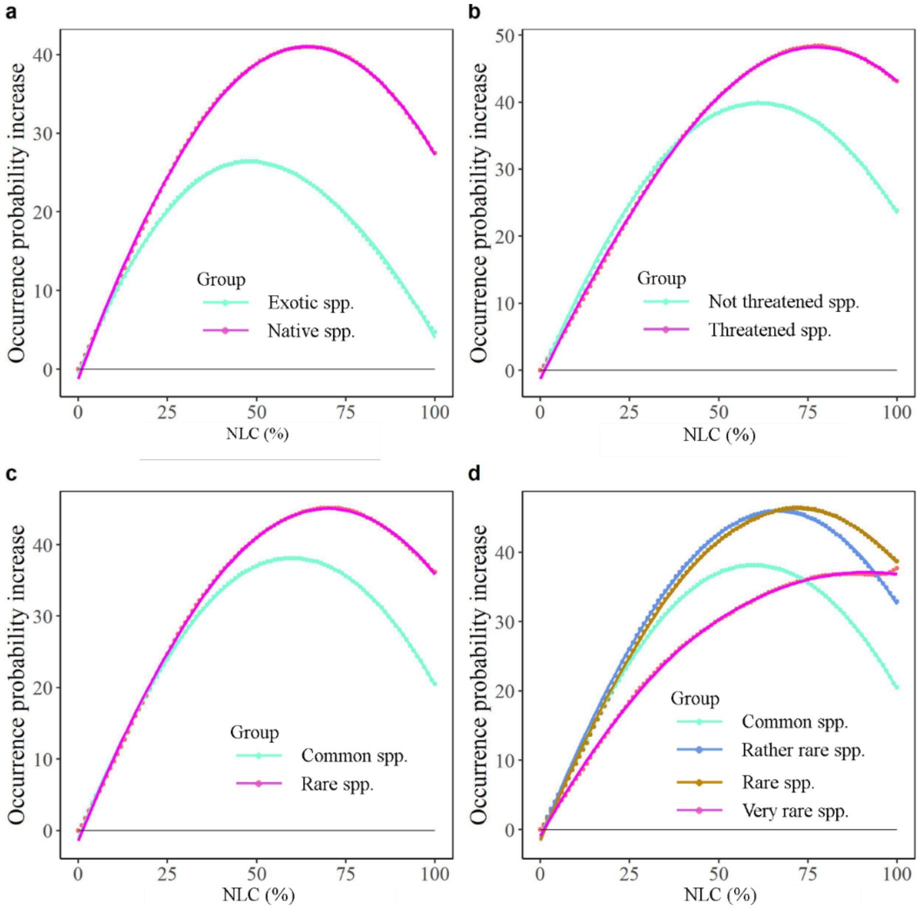


Fig 7. The average occurrence probability change (average occurrence probability change from 0% NLC to others, e.g. NLC at 1x1 km resolution increases from 0% to 11%) of different species groups. a, All native species vs exotic species. b, Threatened species vs not threatened species. c, Rare species vs common species. d, Rare species vs common species, but rare species are classified into three categories (i.e. very rare, rare, rather rare) according to the Red List of Vascular Plants of the Netherlands (Sparrius, L. B., Odé, B., & Beringen, R, 2014). Lines represent the best-fit regressions.

Effect of open or forested natural landscapes on species conservation

Natural habitats and landscapes range from open grasslands and wetlands, through mixed landscapes to closed forests. Since abiotic conditions vary widely between these landscapes (Frenne et al., 2013; Arx et al., 2013), we analysed the preference of plant species for more open natural areas (higher NLC-O) or forested natural areas (higher NLC-F). As expected, native plant species have different preferences for one or the other (e.g. *Alisma gramineum* preferred 0% NLC-F but 65% NLC-O). However, most plant species preferred moderately open or closed natural areas rather than areas with completely open or forested nature. Our findings are consistent with ecological theory (Connell, 1978; Connor and McCoy, 1979; Kallimanis et al., 2008), as well as empirical results of light preference indicated by, for example Ellenberg's Indicator (Hill et al., 1999), where most species have moderate light preference values. This result means that a mixture of forest and open cover suits more species than a high forest cover or completely open cover. Clearly, from an individual species' perspective, conclusions may be different, but our study disproves the often heard argument that creating more forests as part of the climate adaptation agenda is beneficial to biodiversity conservation at large, which has also been criticized by the scientific community elsewhere (Karen et al., 2020). Similarly, it disproves the statement that biodiversity at large needs agriculture as the vast majority of the Dutch plant species prefers landscapes with substantial, i.e. >50%, natural habitats. This fits with the recent opinion that the EU should integrate mosaics of diverse ecosystems to realize the biodiversity strategy rather than massive tree planting (Gómez-González et al., 2020). However, compared to totally disturbed landscapes (0% NLC-F or NLC-O), plants occurring in forested natural landscapes show a slightly different relationship than plants occurring in open natural landscapes (Figs 8 and 9). Landscapes with NLC-O show similar occurrence patterns as NLC, namely they always harbour more native species than landscapes without NLC-O (Fig 8). However, landscapes with 100% forest harbour fewer native species than completely disturbed landscapes (Fig 9). Landscapes with 100% forest or open harbour fewer exotic species than completely disturbed landscapes.

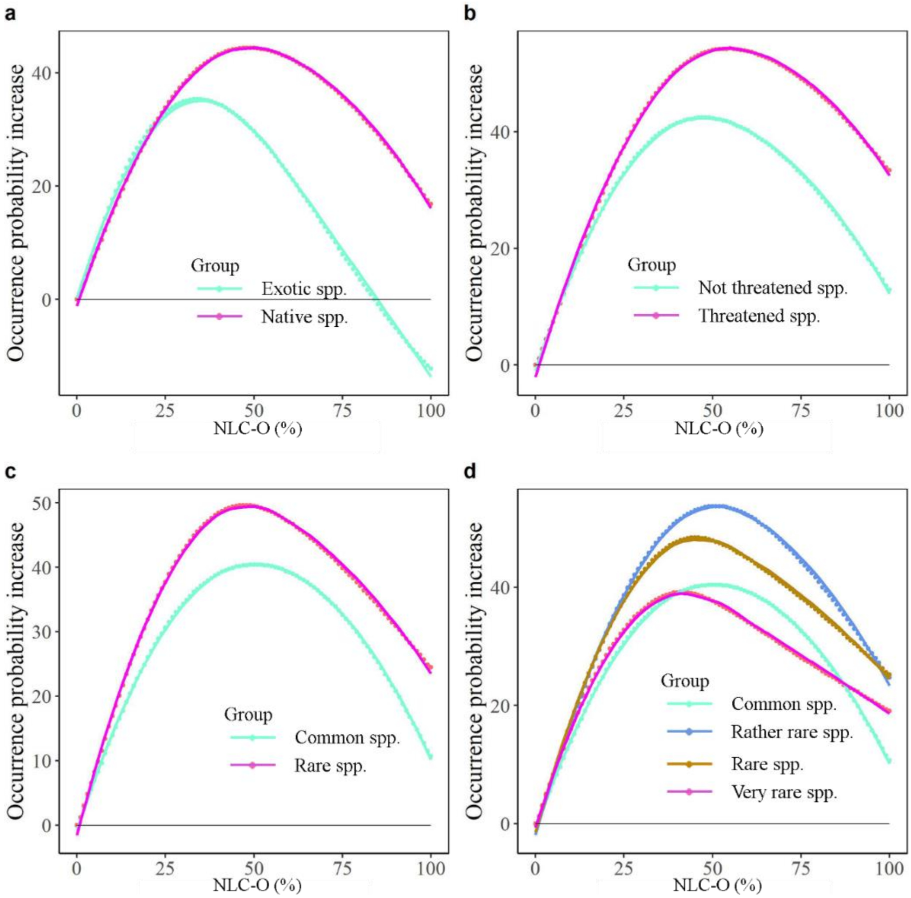


Fig 8. The average occurrence probability change (average occurrence probability change from 0% NLC-O to others, e.g. the NLC-O at 1x1 km resolution increases from 0% to 11%) of different species groups. a, all native species vs exotic species. b, threatened species vs not threatened species. c, rare species vs common species. d, Rare species vs common species, but rare species are classified into three categories (i.e. very rare, rare, rather rare) according to the Red List of Vascular Plants of the Netherlands (Sparrius, L. B., Odé, B., & Beringen, R, 2014). Lines represent the best-fit regressions.

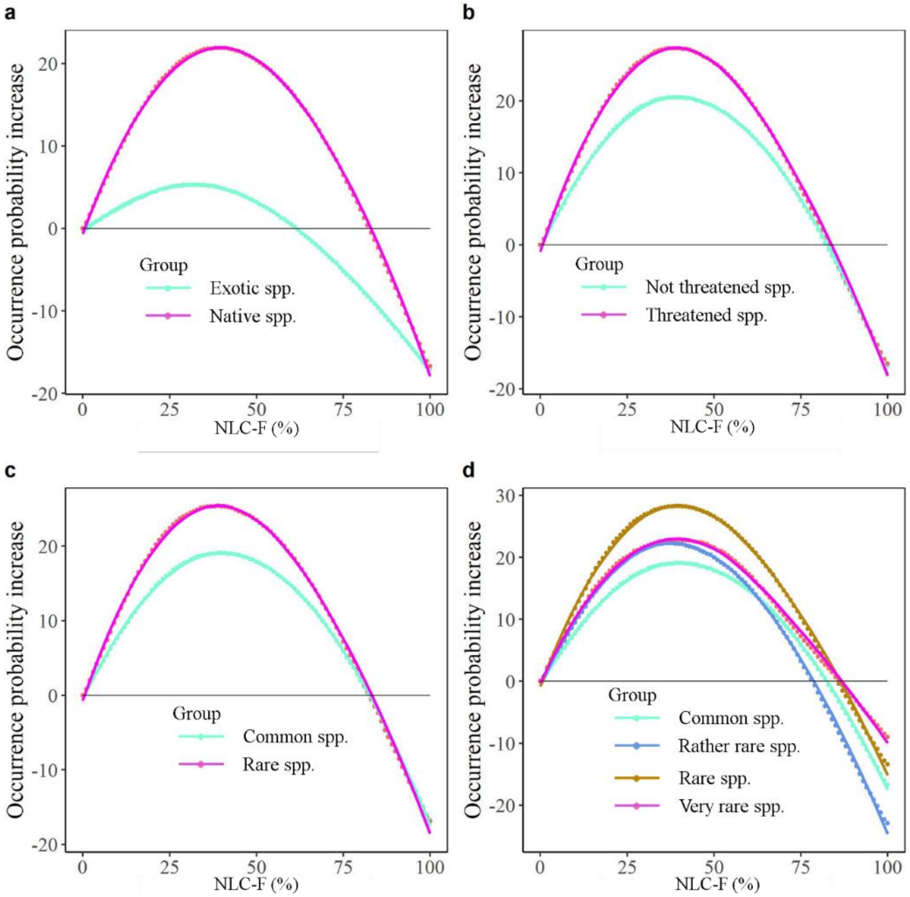


Fig 9. The average occurrence probability change (average occurrence probability change from 0% NLC-F to others, e.g. the NLC-F increases from 0% to 11%) of different species groups. a, all native species vs exotic species. b, threatened species vs not threatened species. c, rare species vs common species. d, Rare species vs common species, but rare species are classified into three categories (i.e. very rare, rare, rather rare) according to the Red List of Vascular Plants of the Netherlands (Sparrius, L. B., Odé, B., & Beringen, R, 2014). Lines represent the best-fit regressions.

Preference of threatened, rare and exotic species for natural landscapes

Much of the effort in nature conservation is aimed at rare or threatened species (Levin et al., 1996), e.g. those on the EU Natura 2000 lists. Our results support this investment, as threatened and rare species are more dependent on natural landscapes than other species. This is probably because threatened and rare species have more specific abiotic preferences or are more susceptible to disturbances and interspecific competition (Levin et al., 1996; Gurevitch and Padilla, 2004), and conditions may be met more often in high NLC areas (e.g. protected areas (Jackson et al., 2009)). However, some natural open renimants in human dominated areas can also be refuge of some rare species (Mckinney, 2002; Lundholm and Richardson, 2010).

Exotic species are less likely to occur in landscapes with relatively high NLC and NLC-O. One possible reason is that they are more capable of invading disturbed habitats (Maskell et al., 2006) but less so in high NLC areas with more native species (Levine, 2000; Kennedy et al., 2002; Ruijven et al., 2003; Fargione and Tilman, 2005; Oakley and Knox, 2013), where interspecific competition may be stronger (Corbin and D'Antonio, 2004). Exotic woody species also had a higher occurrence probability in highly forested areas. This may be an artifact from the overrepresentation of woody species in the Dutch exotic flora (S13 Fig).

Comparing the effect of NLC to soil types and bioclimate

Although we focus on species conservation by exploring the relationships between land cover and plant species, we also compared the effect of land cover factors to other factors (ten soil types and five bioclimatic variables), the importance of which have been indicated by many studies (e.g. (Titeux et al., 2009)). Our results indicate that NLC is often the most important factor to plant species presence, although the importance decreases when we consider NLC-F and NLC-O separately. One reason for NLC to be so important, may be its close relation to local microclimate (Yates et al., 2000; Foley et al., 2005; Luskin and Potts, 2011), in combination with the relatively similar macroclimatic conditions across the Netherlands. In general, NLC modulates macroclimatic conditions (i.e. WorldClim-derived data) and thus affects plant species presence (Frenne et al., 2013; Harwood et al., 2014) in addition to climate. Interestingly, NLC was much more important than soil and bioclimatic factors for the presence of native species, while the opposite was true for exotic species (Table 1).

Conclusion and management implications

In conclusion, this nationwide study assessing an unprecedented number of species has shown that NLC is strongly related to plant species' presence. Interestingly, particularly in the light of ongoing loss of NLC, this study is the first to quantify these relationships. Most species, particularly species of conservation concern, prefer landscapes with higher than 50% NLC (e.g. natural wetland, grassland, heathland or forest). This is a strong contrast to the current landscapes in the Netherlands, i.e. few landscapes have NLC higher than 50%. Thus, protecting natural landscapes, particularly landscapes with substantial NLC, is greatly beneficial to species conservation and should be the priority goal. On this basis, increasing the area of natural elements in landscapes will increase the occurrence probability of most species, with the highest marginal increase in strongly disturbed landscapes. Moreover, most species prefer natural areas with a mixture of forest and open areas. Thus, a landscape with a mixture of different natural types is better for plant biodiversity in general, and also for threatened species, than an area with one type of natural cover (natural forest or open area). Following mixed landscapes, areas with natural open cover should have the higher priority of conservation than with natural forest cover since threatened and rare species are more likely to occur in landscapes with high NLC-O but low NLC-F. Finally, conservation initiatives should aim to increase NLC, by the combination of maintaining current natural cover and restoring disturbed landscapes.

While landscapes with approx. 60% will conserve common native species, high levels (>80%) will best aid very rare and threatened species. We hope that this work will help government and conservation agencies to improve conservation guidelines, focus their efforts on natural areas and increasing natural elements and natural habitat types in artificial areas and in this way stand a better chance to realize their national and regional biodiversity strategy targets. Our method can also be used in other regions to help local governments identify species of particular concern from the stressor of natural areas decrease and identify landscapes with which extent of NLC does species prefer.

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References

Aguirre-Gutiérrez, J., Carvalheiro, L.G., Polce, C., van Loon, E.E., Raes, N., Reemer, M., Biesmeijer, J.C., 2013. Fit-for-purpose: species distribution model performance depends on evaluation criteria - Dutch Hoverflies as a case study. PloS one 8, e63708.

Aguirre-Gutiérrez, J., Oliveras, I., Rifai, S., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T.R., Feldpausch, T.R., Gvozdevaite, A., Hubau, W., Kraft, N.J.B., Lewis, S.L., Moore, S., Niinemets, Ü., Peprah, T., Phillips, O.L., Ziemińska, K., Enquist, B., Malhi, Y., 2019. Drier tropical forests are susceptible to functional changes in response to a long-term drought. Ecol Lett 22, 855–865.

Arx, G. von, Graf Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. J Ecol 101, 1201–1213.

Bascompte, J., Rodriguez, M.A., 2001. Habitat patchiness and plant species richness. Ecol Lett 4, 417–420.

Benchimol, M., Mariano-Neto, E., Faria, D., Rocha-Santos, L., Souza Pessoa, M. de, Gomes, F.S., Talora, D.C., Cazetta, E., 2017. Translating plant community responses to habitat loss into conservation practices: Forest cover matters. Biol Conserv 209, 499–507.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., Weslien, J., 1994. Threatened Plant, Animal, and Fungus Species in Swedish Forests: Distribution and Habitat Associations. Conserv Biol 8, 718–731.

Blaser, W.J., Oppong, J., Hart, S.P., Landolt, J., Yeboah, E., Six, J., 2018. Climate-smart sustainable agriculture in low-to-intermediate shade agroforests. Nat Sustain 1, 234–239.

Bridgewater, P., Loyau, A., Schmeller, D.S., 2019. The seventh plenary of the intergovernmental platform for biodiversity and ecosystem services (IPBES-7): a global assessment and a reshaping of IPBES. Biodivers Conserv 28, 2457–2461.

Casado, M.A., Castro, I., Ramírez-Sanz, L., Costa-Tenorio, M., Miguel, J.M. de, Pineda, F.D., 2004. Herbaceous plant richness and vegetation cover in Mediterranean grasslands and shrublands. Plant Ecol 170, 83–91.

Centraal Bureau voor de Statistiek (CBS), 2012. Bestand Bodemgebruik Productbeschrijving.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science (New York, N.Y.) 199, 1302–1310.

Connor, E.F., McCoy, E.D., 1979. The Statistics and Biology of the Species-Area Relationship. Am Nat 113, 791–833.

Corbin, J.D., D'Antonio, C.M., 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85, 1273–1283.

Cormont, A., Siepel, H., Clement, J., Melman, T., WallisDeVries, M.F., van Turnhout, C., Sparrius, L.B., Reemer, M., Biesmeijer, J.C., Berendse, F., Snoo, G.R. de, 2016. Landscape complexity and farmland biodiversity: Evaluating the CAP target on natural elements. J Nat Conserv 30, 19–26.

Di Marco, M., Ferrier, S., Harwood, T.D., Hoskins, A.J., Watson, J.E.M., 2019. Wilderness areas halve the extinction risk of terrestrial biodiversity. Nature 573, 582–585.

Dudley, N. (Ed.), 2013. Guidelines for applying protected area management categories including IUCN WCPA best practice guidance on recognising protected areas and assigning management categories and governance types. IUCN, Gland.

Ellis, E.C., Ramankutty, N., 2008. Putting people in the map: anthropogenic biomes of the world. Front Ecol Environ 6, 439–447.

Engemann, K., Sandel, B., Boyle, B., ENQUIST, B.J., Jørgensen, P.M., KATTGE, J., McGill, B.J., Morueta-Holme, N., Peet, R.K., Spencer, N.J., VIOLLE, C., Wiser, S.K., Svenning, J.-C., 2016. A plant growth form dataset for the New World. Ecology 97, 3243.

Enriquez-Urzelai, U., Kearney, M.R., Nicieza, A.G., Tingley, R., 2019. Integrating mechanistic and correlative niche models to unravel range-limiting processes in a temperate amphibian. Glob Chang Biol 25, 2633–2647.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. J. Biogeogr. 40, 1649–1663.

Fargione, J.E., Tilman, D., 2005. Diversity decreases invasion via both sampling and complementarity effects. Ecol Lett 8, 604–611.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol 37, 4302–4315.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science (New York, N.Y.) 309, 570–574.

Frenne, P. de, Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petrík, P., Schultz, J., Sonnier, G., van Calster, H., Waller, D.M., Walther, G.-R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. Proc. Natl. Acad. Sci. U.S.A. 110, 18561–18565.

Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E., Verde Arregoitia, L., Vega, E., Peres, C.A., Ewers, R.M., 2019. The conservation value of human-modified landscapes for the world’s primates. Nat Commun 10, 152.

Gómez-González, S., Ochoa-Hueso, R., Pausas, J.G., 2020. Afforestation falls short as a biodiversity strategy. Science (New York, N.Y.) 368, 1439.

González-Irusta, J.M., González-Porto, M., Sarralde, R., Arrese, B., Almón, B., Martín-Sosa, P., 2015. Comparing species distribution models: a case study of four deep sea urchin species. Hydrobiologia 745, 43–57.

Gurevitch, J., Padilla, D.K., 2004. Are invasive species a major cause of extinctions? Trends Ecol Evol 19, 470–474.

Harwood, T.D., Mokany, K., Paini, D.R., 2014. Microclimate is integral to the modeling of plant responses to macroclimate. Proc. Natl. Acad. Sci. U.S.A. 111, E1164-5.

Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29, 773–785.

Hijmans, R. J., Phillips, S., Leathwick, J., Elith, J., 2017. Package 'dismo'. dismo: Species distribution modeling. R package version 1.1-4, Retrieved from https://CRAN.R-project.org/package=dismo.

Hill, M.O., Mountford, J.O., Roy, D.B., 1999. Ellenberg's indicator values for British plants. ECOFACT volume 2: technical annex. Institute of Terrestrial Ecology.

Inter Provinciaal Overleg, 2016. Informatiemodel natuurbeheer (IMNAB): Index Natuur en Landschap.

Jackson, S.F., Walker, K., Gaston, K.J., 2009. Relationship between distributions of threatened plants and protected areas in Britain. Biol Conserv 142, 1515–1522.

Kallimanis, A.S., Mazaris, A.D., Tzanopoulos, J., Halley, J.M., Pantis, J.D., Sgardelis, S.P., 2008. How does habitat diversity affect the species–area relationship. Glob Ecol Biogeogr 17, 532–538.

Karen, D. H., Brancalion, P. H., 2020. Tree planting is not a simple solution. Science 368, 580–581. https://science.sciencemag.org/content/368/6491/580.full.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D., Reich, P., 2002. Biodiversity as a barrier to ecological invasion. Nature 417, 636–638.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J., Eriksson, O., Garnier, E., Peco, B., 2008. The Leda Traitbase: a database of life-history traits of the Northwest European flora. J Ecol 96(6), 1266-1274.

Kriticos, D.J., Jarošik, V., Ota, N., 2014. Extending the suite of bioclim variables: a proposed registry system and case study using principal components analysis. Methods Ecol Evol 5, 956–960.

Laughlin, D.C., Gremer, J.R., Adler, P.B., Mitchell, R.M., Moore, M.M., 2020. The Net Effect of Functional Traits on Fitness. Trends Ecol Evol 35, 1037–1047.

Levin, D.A., Francisco-Ortega, J., Jansen, R.K., 1996. Hybridization and the Extinction of Rare Plant Species. Conserv Biol 10(1), 10-16.

Levine, J.M., 2000. Species diversity and biological invasions: relating local process to community pattern. Science (New York, N.Y.) 288, 852–854.

Lundholm, J.T., Richardson, P.J., 2010. MINI-REVIEW: Habitat analogues for reconciliation ecology in urban and industrial environments. J Appl Ecol 47, 966–975.

Luskin, M.S., Potts, M.D., 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle. Basic Appl Ecol 12, 540–551.

Magioli, M., Moreira, M.Z., Fonseca, R.C.B., Ribeiro, M.C., Rodrigues, M.G., Ferraz, K.M.P.M.d.B., 2019. Human-modified landscapes alter mammal resource and habitat use and trophic structure. Proc. Natl. Acad. Sci. U.S.A. 116, 18466–18472.

Manel, S., Williams, H.C., Ormerod, S.J., 2002. Evaluating presence-absence models in ecology: the need to account for prevalence. J Appl Ecol, 38(5), 921-931.

Marshall, L., 2018. Wild bee diversity across space and time: the role of land use/land cover and climate, Presses universitaires de Namur.

Maskell, L.C., Bullock, J.M., Smart, S.M., Thompson, K., Hulme, P.E., 2006. The distribution and habitat associations of non-native plant species in urban riparian habitats. J Veg Sci 17, 499–508.

Mckinney, M.L., 2002. Urbanization, Biodiversity, and Conservation. BioScience 52, 883.

Mendenhall, C.D., Shields-Estrada, A., Krishnaswami, A.J., Daily, G.C., 2016. Quantifying and sustaining biodiversity in tropical agricultural landscapes. Proc. Natl. Acad. Sci. U.S.A. 113, 14544–14551.

Ministerie van Economische Zaken (EZK), 2015. Basisregistratie Gewaspercelen (BRP).

Mokany, K., Ferrier, S., Harwood, T.D., Ware, C., Di Marco, M., Grantham, H.S., Venter, O., Hoskins, A.J., Watson, J.E.M., 2020. Reconciling global priorities for conserving biodiversity habitat. Proc. Natl. Acad. Sci. U.S.A. 117, 9906–9911.

Oakley, C.A., Knox, J.S., 2013. Plant species richness increases resistance to invasion by non-resident plant species during grassland restoration. Appl Veg Sci 16, 21–28.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol Model 190(3-4), 231-259.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

R Core Team, 2018. R: A language and environment for statistical computing.

Rachelle E. Desrochers, Jeremy T. Kerr, David J. Currie, 2011. How, and how much, natural cover loss increases species richness. Glob Ecol Biogeogr 20, 857–867. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1466-8238.2011.00658.x.

Raes, N., ter Steege, H., 2007. A null-model for significance testing of presence-only species distribution models. Ecography 30, 727–736.

Ruijven, J., Deyn, G.B. de, Berendse, F., 2003. Diversity reduces invasibility in experimental plant communities: the role of plant species. Ecol Lett 6, 910–918.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science (New York, N.Y.) 287, 1770–1774.

Sparrius, L. B., Odé, B., & Beringen, R, 2014. Basisrapport Rode Lijst Vaatplanten 2012 volgens Nederlandse en IUCN-criteria. Floron Rapport 57.

Taseski, G.M., Beloe, C.J., Gallagher, R.V., Chan, J.Y., Dalrymple, R.L., Cornwell, W.K., 2019. A global growth-form database for 143,616 vascular plant species. Ecology 100, e02614.

Titeux, N., Maes, D., Marmion, M., Luoto, M., Heikkinen, R.K., 2009. Inclusion of soil data improves the performance of bioclimatic envelope models for insect species distributions in temperate Europe. J. Biogeogr. 36, 1459–1473.

Tollefson, J., 2019. Humans are driving one million species to extinction. Nature 569, 171.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science (New York, N.Y.) 368, 417–420.

Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S.H.M., Joppa, L., Alkemade, R., Di Marco, M., Santini, L., Hoffmann, M., Maiorano, L., Pressey, R.L., Arponen, A., Boitani, L., Reside, A.E., van Vuuren, D.P., Rondinini, C., 2016. Projecting Global Biodiversity Indicators under Future Development Scenarios. Conserv Lett 9, 5–13.

Watson, J.E.M., Venter, O., 2017. Ecology: A global plan for nature conservation. Nature 550, 48–49.

Yates, C.J., Norton, D.A., Hobbs, R.J., 2000. Grazing effects on plant cover, soil and microclimate in fragmented woodlands in south-western Australia: implications for restoration. Austral Ecol 25, 36–47.
Zhang, K., Yao, L., Meng, J., Tao, J., 2018. Maxent modeling for predicting the potential geographical distribution of two peony species under climate change. Sci Total Environ 634, 1326–1334. http://www.sciencedirect.com/science/article/pii/S0048969718312774.

Supporting information

Sensitivity analysis for removing grids with more than 10% open water

Since the land cover of open water does not support vascular plants, including cells with large amounts of open water may introduce a bias due to the species-area relationship. We therefore omitted cells with more than 10% open water, following as did (Rachelle et al., 2011; Clark et al., 2019). We further used 850 species to check the effect of this omission on the occurrence frequency of species, which represents the occurrence probability of species to some extent, based on grid cells with land cover more than 90% and land cover equalling 100% (Equation 1-2). Results were shown in S1 Fig. Our sensitivity analysis showed that the average occurrence frequency from grid cells with land cover more than 90% are almost highly 1:1 linearly correlated to occurrence probability from grid cells with land cover equalling 100%. Based on sensitivity analysis and references above, we decided grid cells with more than 90% land cover are acceptable.

The average occurrence frequency of each species (AOF_{ij}) either based on either grid cells with land cover more than 90% or land cover equalling 100% was calculated by

$$OF_{ij} = N_{ij}/N_i \qquad \text{Equation 1.}$$

$$AOF_{ij} = \sum_{i=0}^{i=n<=100} OF_{ij}/n \qquad \text{Equation 2.}$$

Where, N_{ij} is the number of grids with natural land cover (NLC) equalling i and occupied by species j and N_i is the number of grids with NLC equalling i. OF_{ij} is the occurrence frequency of species j in all grids with NLC equalling i.

Calculation of plant species richness responding to NLC

Predicted richness~NLC relationships. Based on the response curve, we predicted the richness~NLC relationship. First, for each NLC, we calculated the number of species with occurrence probability above 80% and took it as the richness corresponding to the NLC. Further, we gave four different fitting models (null, linear, quadratic, exponential) and used AIC to choose the best fitting model with a significant *p*-value. Finally, the quadratic model was the best fitting model with a significant *p*-value.

Richness~NLC relationships based on real observations. First, we overlaid species occurrence data with grid cells with different NLCs. Then, we calculated the number of species occurring in each grid and analysed the relationships between richness and NLC.

3. Average marginal occurrence probability increase

The average marginal occurrence probability change of all plant species with 1% NLC increase was calculated by

$$OP_i = \sum_{j=1}^{j=n}(OP_{ij} - OP_{(i-1)j})/n \qquad \text{Equation 3.}$$

where OP_i is the average marginal occurrence probability change, OP_{ij} is the occurrence probability of species *j* at NLC *i*%, $OP_{(i-1)j}$ is the occurrence probability of species *j* at NLC (*i*-1)%. *n* is the number of species.

S1 Table. Land cover types in this research.

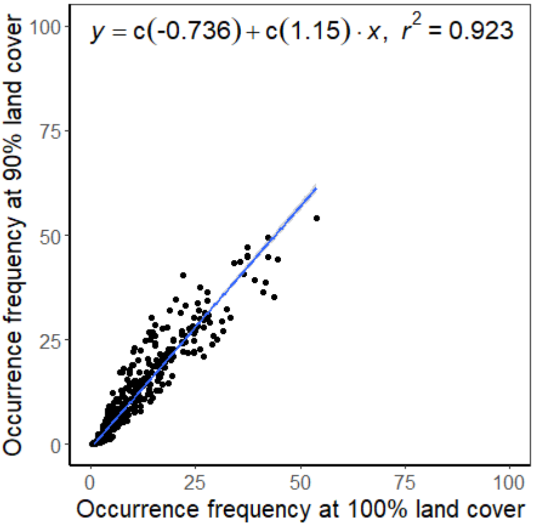
Rank	Classes in Marshall (2018)	Merged classes in our study	
		Natural/non-natural area	Natural forest/open
1	Heather	Natural area	Natural open
2	Urban green	Natural area	Natural open
3	Semi-natural forest	Natural area	Natural forest
4	Production forest	Natural area	Natural forest
5	Swamp peat	Natural area	Natural open
6	Semi-natural grassland	Natural area	Natural open
7	Dune	Natural area	Natural open
8	River swamp	Natural area	Natural open
9	Crop	Non-natural area	
10	Fruit	Non-natural area	
11	Pasture	Non-natural area	
12	Urban grey	Non-natural area	
13	Greenhouse horticulture	Non-natural area	
14	Other agricultural uses	Non-natural area	
15	Fresh water	exclude	
16	Brackish water	exclude	

S2 Table. Full table of results.xlsx (https://doi.org/10.1371/journal.pone.0259255.s003)

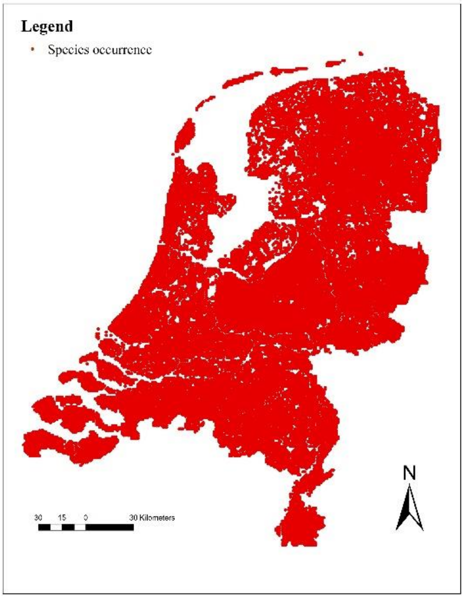
S3 Table. PCA for 19 bioclimatic variables. The first five principal components explained more than 90% of the variability in the full suite of 19 bioclimatic variables.

	Variance	% of var.	Cumulative % of var.
Dim.1	8	42.1	42.1
Dim.2	5.3	28.1	70.1
Dim.3	2.4	12.9	83
Dim.4	1.2	6.4	89.4
Dim.5	0.7	3.9	93.3
Dim.6	0.4	2	95.3
Dim.7	0.3	1.7	97
Dim.8	0.2	1	98
Dim.9	0.1	0.7	98.7
Dim.10	0.1	0.5	99.2
Dim.11	0.1	0.3	99.5
Dim.12	0	0.1	99.7
Dim.13	0	0.1	99.8
Dim.14	0	0.1	99.9
Dim.15	0	0	99.9
Dim.16	0	0	100
Dim.17	0	0	100
Dim.18	0	0	100
Dim.19	0	0	100

S4 Table. Spearman's test for all 18 variables included in this research.xlsx
(https://doi.org/10.1371/journal.pone.0259255.s005)

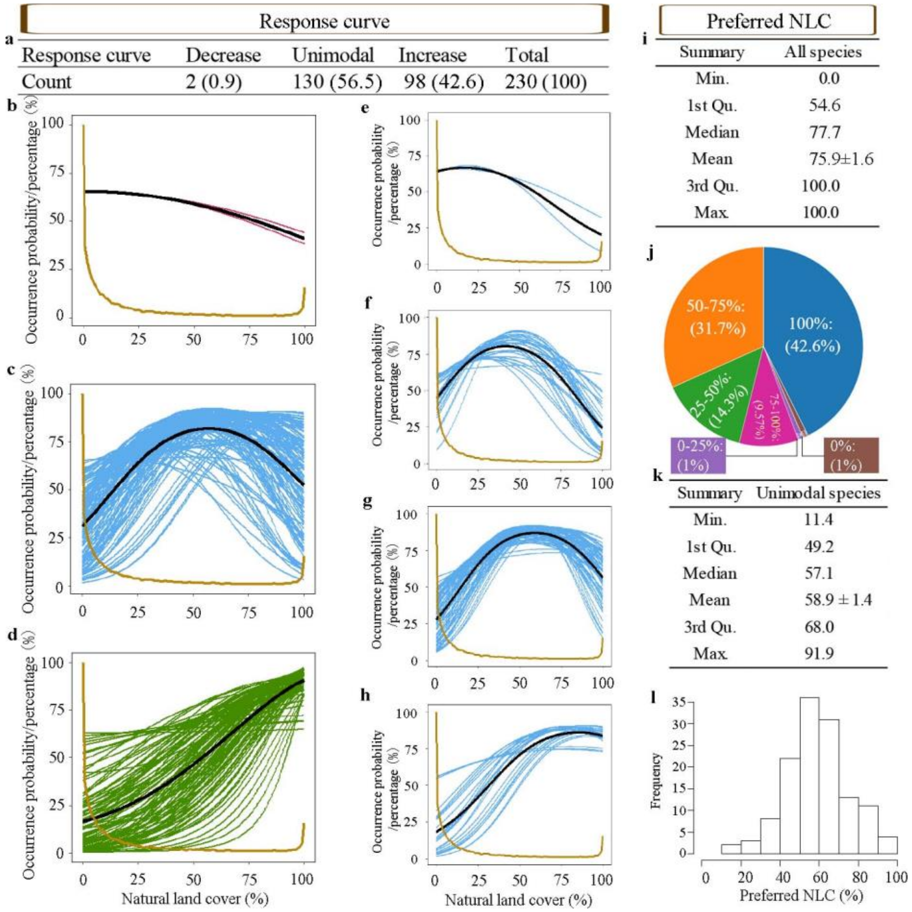


S1 Fig. The average occurrence frequency based on grid cells with more than 90% land cover vs grid cells with 100% land cover. Each point indicates one plant species. The x axis means the average occurrence frequency based on all grid cells with 100% land cover. The y axis means the average occurrence frequency based on all grid cells with more than 90% land cover.

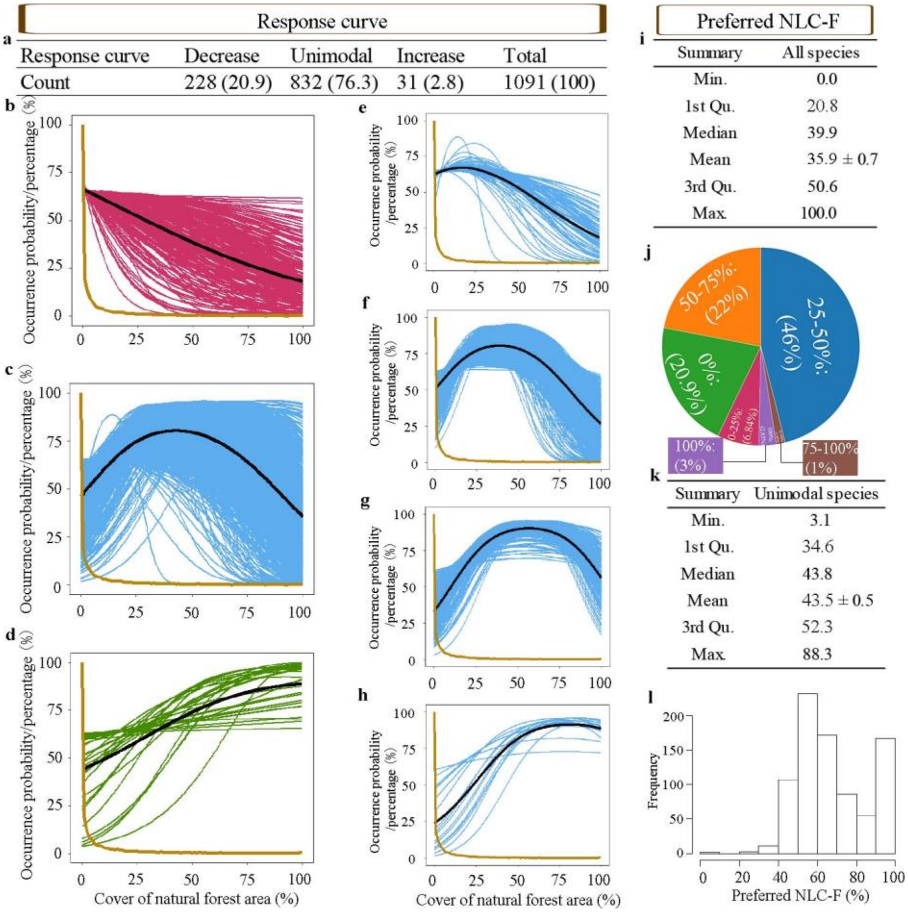


S2 Fig. 4 773 313 observations of plant species.

S3 Fig. Response curves of 1 525 plant species (both native and exotic species) to natural land cover.pdf (https://doi.org/10.1371/journal.pone.0259255.s008)



S4 Fig. 230 threatened plant species responding to natural land cover (NLC). 2 species with a significantly neutral (without a relationship, named 'None') response were omitted as not preferring any NLC. **a-h**, Response curves of plant species to NLC. **k-l**, Summary statistics of preferred NLCs. **a**, Summary of all 230 threatened plants responding to NLC (with percentages in parentheses). **b-d**, Response curves of species with increasing (each red line indicates one species) (**b**), unimodal (each blue line indicates one species) (**c**) and decreasing (each green line indicates one species) (**d**) relations with NLC. The dark black line is the average response curve of each species group. The yellow line indicates the standardized proportion of grids with different NLCs in the Netherlands. Both the occurrence probability and the standardized proportion (percentage) range from 0% to 100% and are indicated by the y axis. **e-h**, Species with unimodal shapes are split into four categories based on their preferred NLCs (**e**, species with preferred NLCs ranging from 0-25%; **f**, species with preferred NLCs ranging from 25-50%; **g**, species with preferred NLCs ranging from 50-75%; **h**, species with preferred NLCs ranging from 75-100%). **i-j**, Statistics of preferred NLCs of all 230 threatened plant species (**i**, summary of 230 plant species' preferred NLCs; **j**, percentage of species in different categories, including 0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%). **k-l**, Statistics of preferred NLCs of species with unimodal shapes (**k**, summary of plant species' preferred NLCs; **l**, histogram of preferred NLCs of plant species with unimodal relations with NLC). All mean values are means ± SE.



Response curve

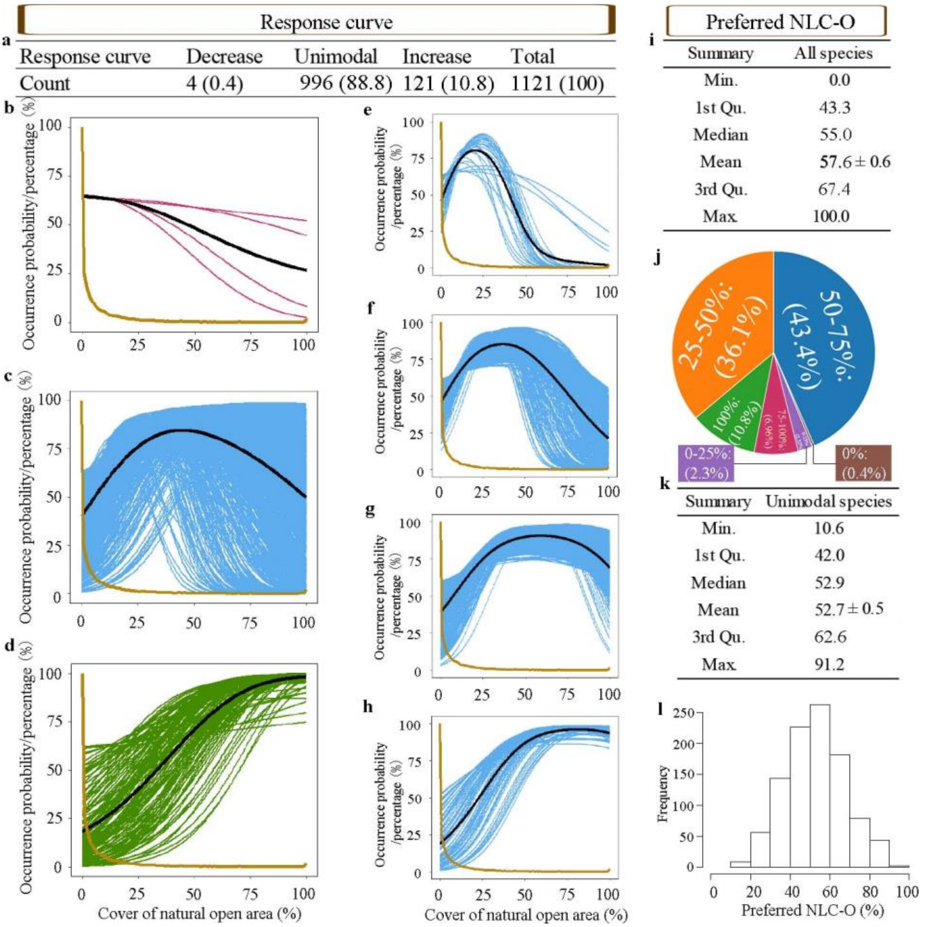
Response curve	Decrease	Unimodal	Increase	Total
Count	228 (20.9)	832 (76.3)	31 (2.8)	1091 (100)

Preferred NLC-F

Summary	All species
Min.	0.0
1st Qu.	20.8
Median	39.9
Mean	35.9 ± 0.7
3rd Qu.	50.6
Max.	100.0

Summary	Unimodal species
Min.	3.1
1st Qu.	34.6
Median	43.8
Mean	43.5 ± 0.5
3rd Qu.	52.3
Max.	88.3

S5 Fig. 1 091 native plant species responding to the cover of natural forest area (NLC-F). 24 species with 'U-shaped' responses were omitted as not ecologically realistic, and 6 species with a significantly neutral (without a relationship, named 'None') response were omitted as not preferring any NLC-F. **a-h**, Response curves of plant species to NLC-F. **k-l**, Summary statistics of preferred NLC-Fs. **a**, Summary of all 1 091 native plants responding to NLC-F (with percentages in parentheses). **b-d**, Response curves of species with decreasing (each red line indicates one species) (**b**), unimodal (each blue line indicates one species) (**c**) and increasing (each green line indicates one species) (**d**) relations with NLC-F. The dark black line is the average response curve of each species group. The yellow line indicates the standardized proportion of grids with different NLC-Fs in the Netherlands. Both the occurrence probability and the standardized proportion (percentage) range from 0% to 100% and are indicated by the y axis. **e-h**, Species with unimodal shapes are split into four categories based on their preferred NLC-Fs (**e**, species with preferred NLC-Fs ranging from 0-25%; **f**, species with preferred NLC-Fs ranging from 25-50%; **g**, species with preferred NLC-Fs ranging from 50-75%; **h**, species with preferred NLC-Fs ranging from 75-100%). **i-j**, Statistics of preferred NLC-Fs of all 1 091 native plant species (**i**, summary of 1 091 plant species' preferred NLC-Fs; **j**, percentage of species in different categories, including 0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%). **k-l**, Statistics of preferred NLC-Fs of species with unimodal shapes (**k**, summary of plant species' preferred NLC-Fs; **l**, histogram of preferred NLC-Fs of plant species with unimodal relations with NLC-Fs). All mean values are means ± SE.

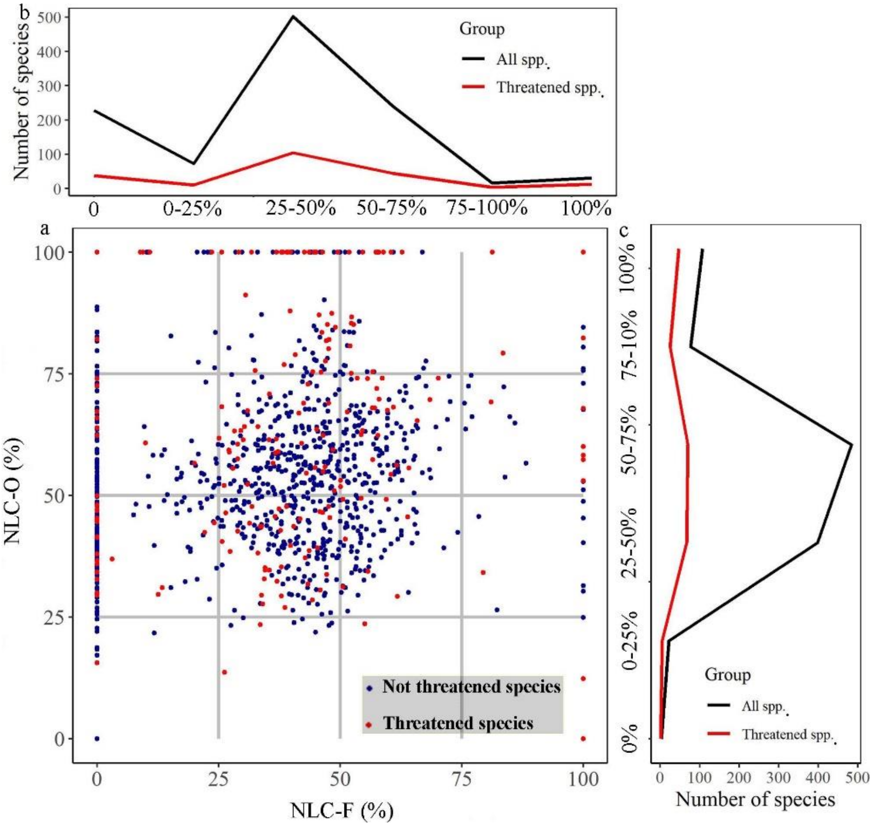


Response curve	Decrease	Unimodal	Increase	Total
Count	4 (0.4)	996 (88.8)	121 (10.8)	1121 (100)

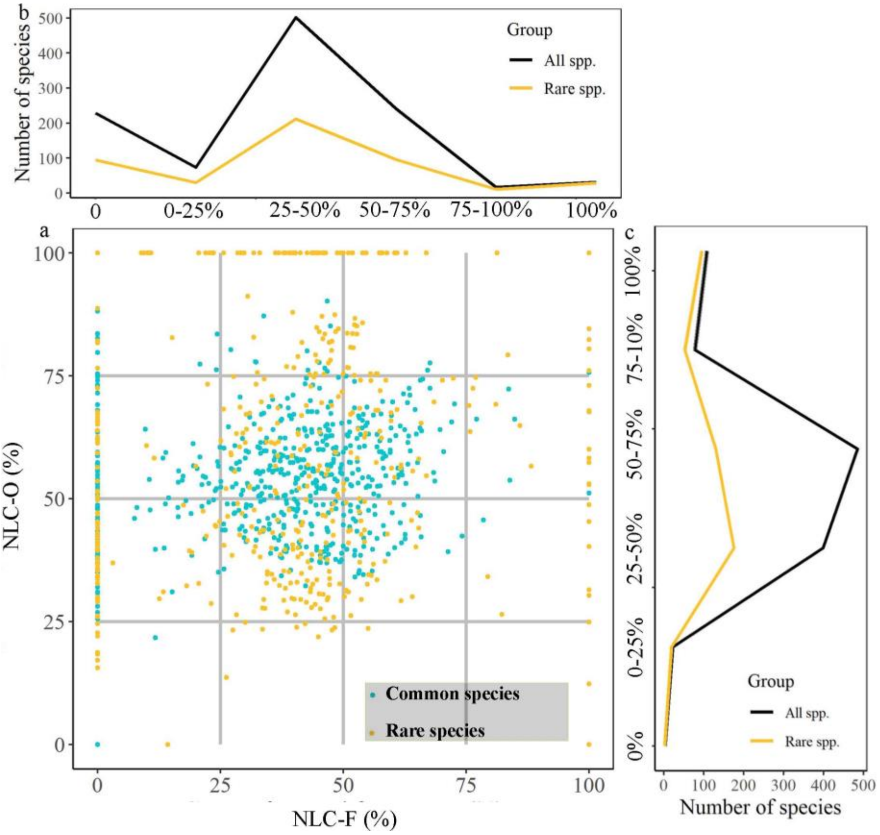
Summary	All species
Min.	0.0
1st Qu.	43.3
Median	55.0
Mean	57.6 ± 0.6
3rd Qu.	67.4
Max.	100.0

Summary	Unimodal species
Min.	10.6
1st Qu.	42.0
Median	52.9
Mean	52.7 ± 0.5
3rd Qu.	62.6
Max.	91.2

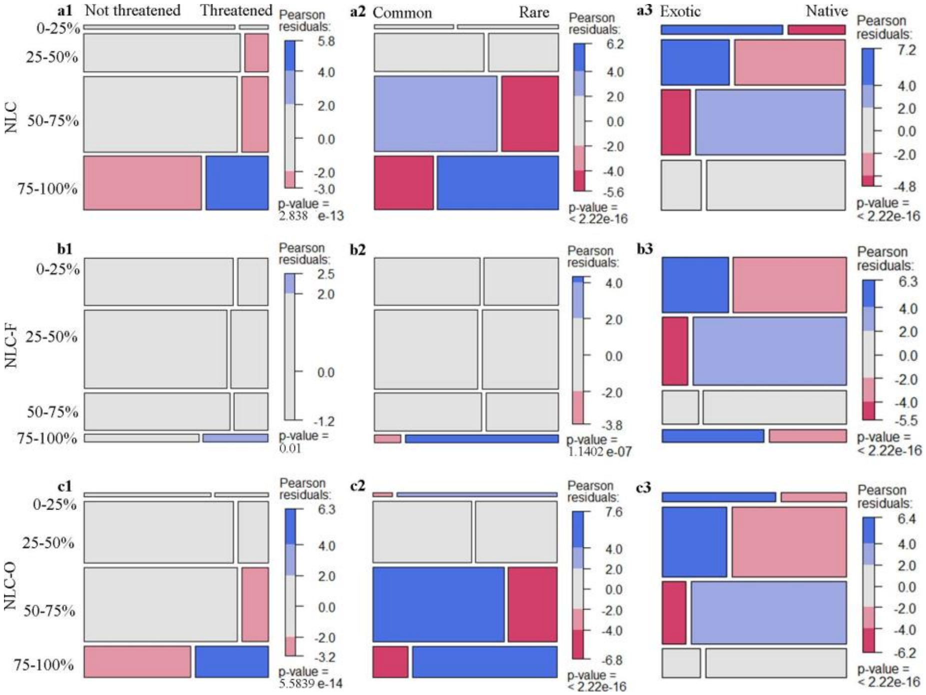
S6 Fig. 1 121 native plant species responding to the cover of natural open area (NLC-O). 4 species with 'U-shaped' responses were omitted as not ecologically realistic. **a-h**, Response curves of plant species to NLC-O. **k-l**, Summary statistics of preferred NLC-Os. **a,** Summary of all 1 121 native plants responding to NLC-O (with percentages in parentheses). **b-d,** Response curves of species with decreasing (each red line indicates one species) (**b**), unimodal (each blue line indicates one species) (**c**) and increasing (each green line indicates one species) (**d**) relations with NLC-O. The dark black line is the average response curve of each species group. The yellow line indicates the standardized proportion of grids with different NLC-O in the Netherlands. Both the occurrence probability and the standardized proportion (percentage) range from 0% to 100% and are indicated by the y axis. **e-h**, Species with unimodal shapes are split into four categories based on their preferred NLC-Os (**e**, species with preferred NLC-Os ranging from 0-25%; **f**, species with preferred NLC-Os ranging from 25-50%; **g**, species with preferred NLC-Os ranging from 50-75%; **h**, species with preferred NLC-Os ranging from 75-100%). **i-j**, Statistics of preferred NLC-Os of all 1 121 native plant species (**i**, summary of 1 121 plant species' preferred NLC-Os; **j**, percentage of species in different categories, including 0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%). **k-l**, Statistics of preferred NLC-Os of species with unimodal shapes (**k**, summary of plant species' preferred NLC-Os; **l**, histogram of preferred NLC-Os of plant species with unimodal relations with NLC-Os). All mean values are means ± SE.



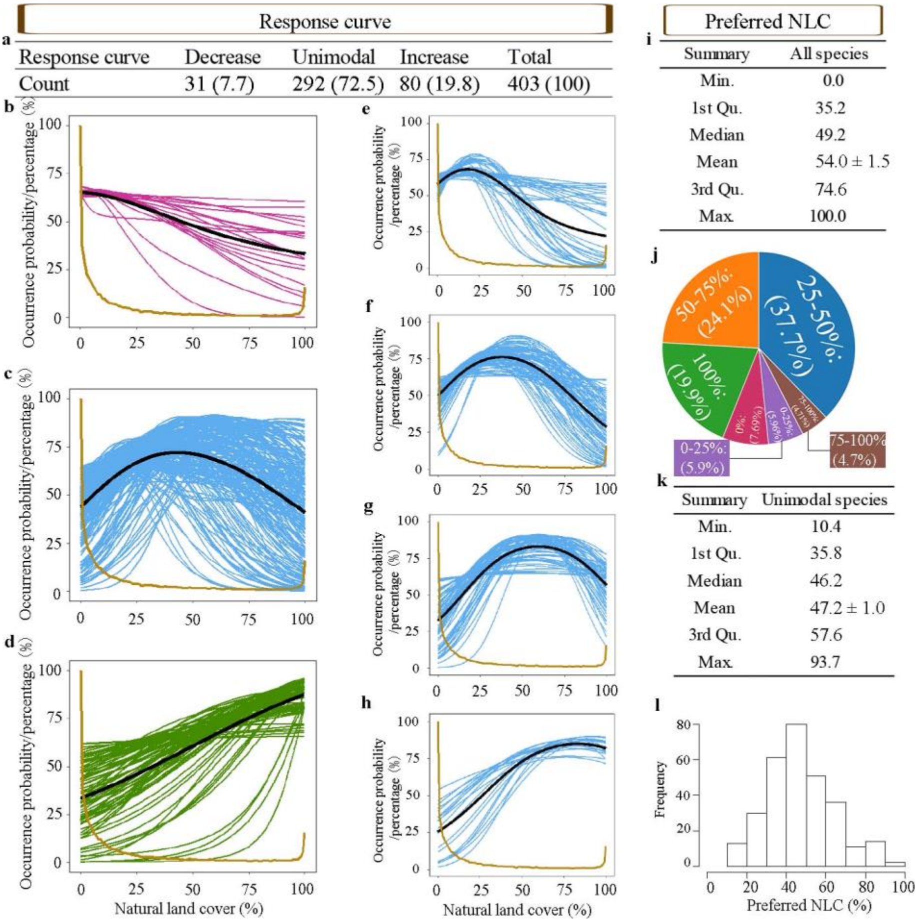
S7 Fig. Preferred NLC-F and NLC-O of native plant species, which are classified into threatened and not threatened species. a, Two-dimensional plot indicating the preferred NLC-F and NLC-O of each species. Each dot indicates one species. Red dots indicate threatened species and blue dots indicate not threatened species. **b**, Number of dots within each subgroup along the x axis (0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%). **c**, Number of dots within each subgroup along the y axis (0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%).



S8 Fig. Preferred NLC-F and NLC-O of native plant species, which are classified into rare and common species. a, Two-dimensional plot indicating the preferred NLC-F and NLC-O of each species. Each dot indicates one species. Yellow dots indicate rare species and turquoise dots indicate common species. **b**, Number of dots within each subgroup along the x axis (0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%). **c**, Number of dots within each subgroup along the y axis (0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%).



S9 Fig. Contingency Analysis on whether threatened status, rarity and origin affect the preferred NLC, NLC-F and NLC-O. a1-a3, Differences of preferred NLC within groups of threatened status, rarity and origin. **b1-b3**, Differences of preferred NLC-F within groups of threatened status, rarity and origin. **c1-c3**, Differences of preferred NLC-O within groups of threatened status, rarity and origin. Preferred NLC, NLC-F and NLC-O mean the preferences for natural land cover (preferred NLC), the cover of natural forest area (preferred NLC-F) and the cover for natural open area (preferred NLC-O).



Response curve

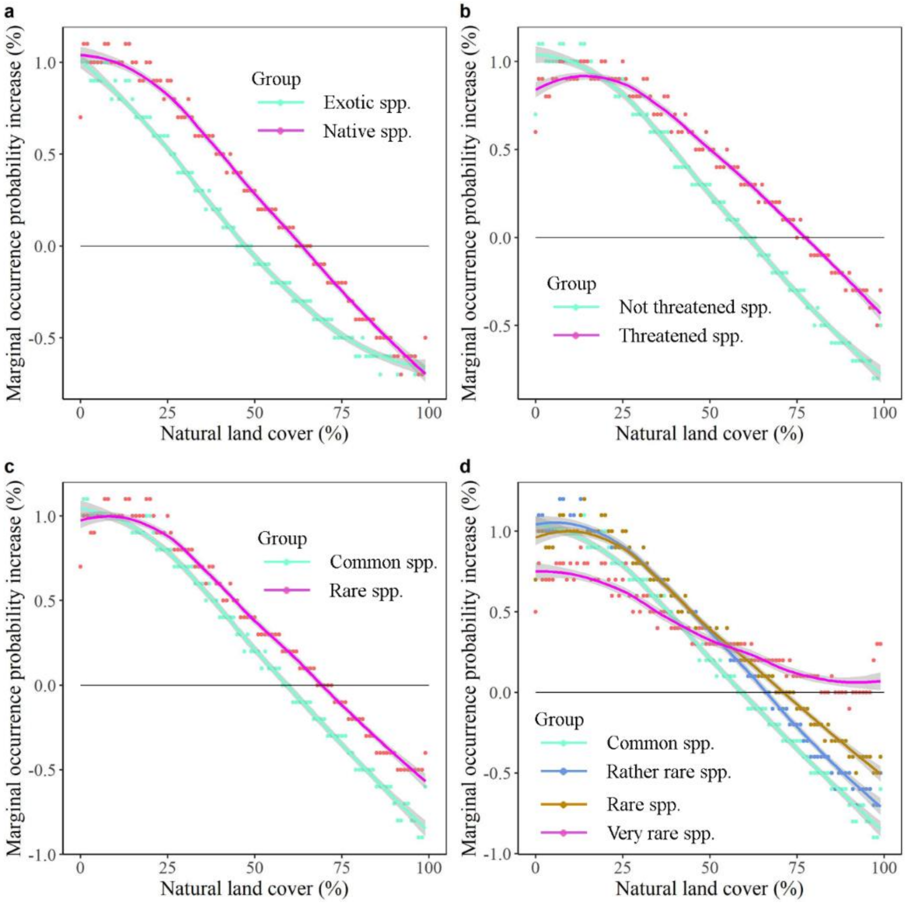
Response curve	Decrease	Unimodal	Increase	Total
Count	31 (7.7)	292 (72.5)	80 (19.8)	403 (100)

Preferred NLC

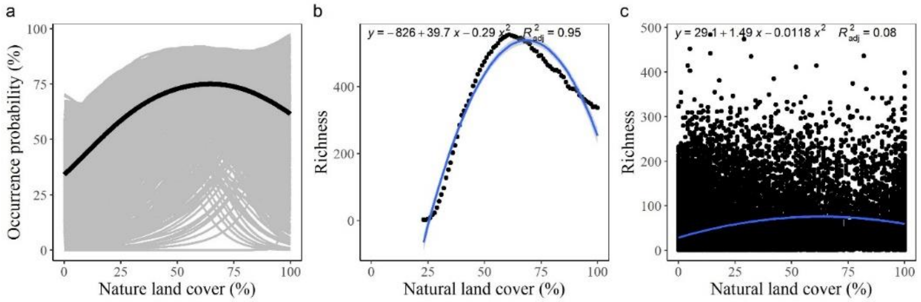
Summary	All species
Min.	0.0
1st Qu.	35.2
Median	49.2
Mean	54.0 ± 1.5
3rd Qu.	74.6
Max.	100.0

Summary	Unimodal species
Min.	10.4
1st Qu.	35.8
Median	46.2
Mean	47.2 ± 1.0
3rd Qu.	57.6
Max.	93.7

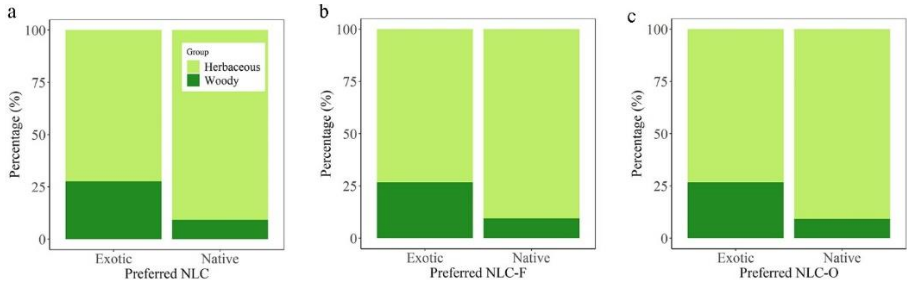
S10 Fig. 403 exotic plant species responding to natural land cover (NLC). 7 species with a significantly neutral (without a relationship, named ‘None’) response were omitted as not preferring any NLC. **a-h**, Response curves of plant species to NLC. **k-l**, Summary statistics of preferred NLCs. **a**, Summary of all 403 exotic plants responding to NLC (with percentages in parentheses). **b-d**, Response curves of species with decreasing (each red line indicates one species), unimodal (each blue line indicates one species) and increasing (each green line indicates one species) relations with NLC. The dark black line is the average response curve of each species group. The yellow line indicates the standardized proportion of grids with different NLC in the Netherlands. Both the occurrence probability and the standardized proportion (percentage) range from 0% to 100% are indicated by the y axis. **e-h**, species with unimodal shapes are split into four categories based on their preferred NLCs (**e**, species with preferred NLCs ranging from 0-25%; **f**, species with preferred NLCs ranging from 25-50%; **g**, species with preferred NLCs ranging from 50-75%; **h**, species with preferred NLCs ranging from 75-100%). **i-j**, Statistics of preferred NLCs of all 403 exotic plant species (**i**, summary of 403 plant species’ preferred NLCs; **j**, percentage of species in different categories, including 0%, 0-25%, 25-50%, 50-75%, 75-100% and 100%). **k-l**, Statistics of preferred NLCs of species with unimodal shapes (**k**, summary of plant species' preferred NLCs; **l**, histogram of preferred NLCs of plant species with unimodal relations with NLC). All mean values are means ± SE.



S11 Fig. The average marginal occurrence probability change of different species groups. a, All native species vs exotic species. b, Threatened species vs not threatened species. c, Rare species vs common species. d, Rare species vs common species, but rare species are classified into three categories (i.e. very rare, rare, rather rare) according to the Red List of Vascular Plants of the Netherlands [1]. Lines represent the best-fit regressions. The average marginal occurrence probability change means the average occurrence probability change with 1% natural land cover increase, e.g. natural land cover at 1x1 km resolution increases from 10% to 11%)



S12 Fig. Plants responding to natural land cover (NLC) at species-level and community-level. a, The occurrence probability of 1 122 native plant species responding to NLC. Each grey line indicates one species, and the dark line means the average response of all 1 122 native species. **b**, Predicted relationships of richness responding to NLC, with a best fitting quadratic model. **c**, Relationships of plant species richness responding to NLC based on observations, with a best fitting quadratic model. Lines represent the best-fit regressions.



S13 Fig. The percentage of woody and herbaceous species within each species category (native species vs exotic species).

References

Clark, C.M., Simkin, S.M., Allen, E.B., Bowman, W.D., Belnap, J., Brooks, M.L., Collins, S.L., Geiser, L.H., Gilliam, F.S., Jovan, S.E., Pardo, L.H., Schulz, B.K., Stevens, C.J., Suding, K.N., Throop, H.L., Waller, D.M., 2019. Potential vulnerability of 348 herbaceous species to atmospheric deposition of nitrogen and sulfur in the United States. Nat plants 5, 697–705.

Rachelle, E. Desrochers, Jeremy, T. Kerr, David, J. Currie, 2011. How, and how much, natural cover loss increases species richness. Glob Ecol Biogeogr 20, 857–867.

Marshall L. Wild bee diversity across space and time: the role of land use/land cover and climate. Presses universitaires de Namur; 2018.

Chapter 3

The distributions of insect-, wind- and self-pollination of plants in the Netherlands in relation to habitat types and 3D vegetation structure

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Abstract

Plants can be pollinated in many ways, with insect, wind and selfing as the most common modes. While it seems likely that the occurrence of pollination modes is correlated with environmental conditions, e.g. vegetation structure, and this remains uncertain. Here, we mapped the composition of pollination modes of different plant groups (woody species, herbs, and grasses) across (semi-)natural habitats and their distributions in relation to 3D vegetation structure in the Netherlands. We found insect-pollination is the most common mode across (semi-)natural habitats for woody species and herbs. Woody species pollinated by insects showed an even higher percentage in dune, river swamp and swamp peat than in other habitat types, whereas herbs showed a higher percentage of insect-pollination in dune than in other habitat types. Grasses were always pollinated by wind or wind-self in all habitats. Woody plants pollinated by wind showed a positive relationship with canopy densities in three different strata from 2 to 20 m vegetation, while insect-pollination showed a positive relationship with the canopy density of 0.5 to 2 m vegetation. All grass presented negative relationships with canopy density. Herbs showed different relationships with canopy densities of different strata dependent on pollination modes. Insect-pollinated species increased with canopy densities of low strata but decreased with canopy density of high strata, whereas wind-pollinated species decreased with canopy density of both low and high strata. We conclude that habitat and vegetation structure are important factors driving the distribution of pollination modes.

Keywords: Pollination mode, Vascular plants, (Semi-)natural habitats, Vegetation structure, Growth form, Spatial distribution

Introduction

Pollination is a critical event in the reproduction of flowering plants (Shivanna and Tandon 2014). Insect-pollination (allogamy), wind-pollination (allogamy) and self-pollination (autogamy) account for the majority of plant species in temperate areas (Kühn et al., 2006). The importance of animal pollination for plant species is well documented, particularly regarding insect-pollinations (Ollerton et al., 2011; Briggs et al., 2019), while the importance of wind- and self-pollination are less reported. Although, at the global scale, most flowering plants (around 80%) depend on insect-pollination, wind-pollination is still essential for the reproduction of approximately 12% plants (Ollerton et al., 2011; Rodger et al., 2021). In addition, most insect- or wind-pollinated plants are also auto-fertile (potentially self-pollinated), and 9% flowering plants are mainly auto-fertility (Rodger et al., 2021). However, it is not clear whether this pattern of occurrence in pollination modes (insect >> wind > self) is consistent across different semi-natural habitats at the local scale. We hypothesize that the occurrence of pollination modes varies across semi-natural habitats, because they also differ in their use intensity, their biotic and abiotic conditions (Culley et al., 2002; Kühn et al., 2006; Rech et al., 2016). In addition, differences in pollinator abundance and diversity between habitats may affect the occurrence of pollination modes (Taki et al., 2011; Winfree et al., 2011).

Until now, many studies have shown that environmental conditions, including temperature, wind speed, humidity, and precipitation, influence the spatial patterns in pollination modes. For example, the occurrence of insect and wind-pollination varies with proportions of distinct habitat types (Kühn et al., 2006), temperature, precipitation and plant richness (Kühn et al., 2006; Hoiss et al., 2012; Rech et al., 2016). Self-pollination is considered to provide reproductive assurance (Schoen et al., 1996; Kalisz et al., 2004; Rech et al., 2018), particularly in poor environments (e.g. pollinators or mates are absent; (Baker, 1955)).

Furthermore, the effect of 3D vegetation structure, which means the canopy heights and densities of different vegetation strata, is likely to be an important factor driving the variation in richness of pollination modes in different communities. Although some studies suggest vegetation structure (openness of a habitat) might be an important driver (Culley et al., 2002; Kühn et al., 2006; Varassin and Sazima 2012; Rech et al., 2016), it remains unclear how the occurrence of pollination modes changes with the density of vegetation.

Vegetation structure is suggested to be highly influential for insect pollinator diversity (Aguirre-Gutiérrez et al., 2017) due to the different microclimatic conditions it can represent, e.g. temperature, light, and moisture (Luskin and Potts 2011; Varassin and Sazima 2012; Frenne et al., 2013). In addition, vegetation structure may affect the availability of nesting and feeding resources of pollinators (Grundel et al., 2010; Berg et al., 2011; Montero-Castaño and Vilà 2012; Varassin and Sazima 2012). It is unclear to what extent vegetation structure may be a more important explanatory factor to understand the richness of pollination modes than habitat classifications. However, pollination modes are non-randomly distributed among plant growth forms and types. Grasses are only wind-pollinated, whereas the frequency of insect and wind-pollination among woody species and herbs may also be different. This in turn may determine the relationship between habitat type and vegetation structure, with wind-pollination more effective in open, windy habitats and insect-pollination more effective in insect-rich areas (Rech et al., 2016).

In this study, we address two questions: (i) What is the distribution of the composition of insect-, wind-, and self-pollination across Dutch (semi-)natural habitats, and whether this distribution varies between woody plants, grasses, and herbs? We expect a higher proportion of insect-pollination in open habitats, while a higher proportion of wind-pollination in grassland and forested habitats. (ii) Is there a correlation between 3D vegetation structure and the occurrence of each pollination mode within (semi-)natural habitats, and does this vary for woody plants, grasses, and herbs? We expect that the richness of insect-pollinated plants will increase with herb layers while wind-pollinated species will either increase with grassland or forest habitats, and these relationships may vary between woody plants, grasses and herbs. Finally, we assess the interaction between habitat type and 3D vegetation as determinants of pollination mode occurrence.

Material and methods

Habitat types

To derive a complete national dataset from which habitat types could be obtained, we extracted 175 different habitat types at the country scale from three national sources: *Informatiemodel natuurbeheer* (Inter Provinciaal Overleg 2016), *basisregistratie gewaspercelen* (Ministerie van Economische Zaken (EZK) 2015), and *bestand bodemgebruik* (Centraal Bureau voor de Statistiek (CBS) 2012) using ESRI ArcGIS Desktop 10.2 (https://desktop.arcgis.com/en/). These 175 classes were aggregated into 15 habitat types, within which 7 are natural or semi-natural habitats, at a resolution of 10 × 10 m. However, as most vegetation plots were sampled in natural or semi-natural areas, we retained plots in 7 natural and semi-natural habitat types to further compare the distribution of plants pollinated by three different modes. The following habitats are included in this study: Dune (coastal dune habitats), Heather (heathlands with shrubs and woody elements managed as nature but often through sheep grazing), River swamp (swamps and marshlands along the rivers and streams, mosaic of open and woody elements), Semi-natural forest (forests with primarily nature function), Semi-natural grassland (grasslands with primarily nature function but often managed extensively through grazing), Swamp peat (marshes and swamps in both peaty inland areas and brackish coastal areas) and Production forest (forests with both a production and nature function). The data of habitat types was rescaled to 100 × 100 m, and only grid cells with 100% of a single habitat type were kept to make sure habitat types precisely matched the vegetation plots.

Vegetation structure data

LIDAR data were used to analyse the vegetation structure across the Netherlands. We used four different strata of vegetation heights (0.5-2, 2-5, 5-10 and 10-20 m) and calculated the canopy density of each stratum in each grid cell with 100 × 100 m resolution. It means a grid cell with dense forests will have a high value in the 10-20 m category and probably in the 5-10 m as well and may have low values in the 0.5-2 m layer representing the herb and shrub layers. The data was calculated from nationwide LIDAR data in the Netherlands (http://www.ahn.nl) collected from 2007 to 2012. For a full description of the vegetation structure calculation, see (Aguirre-Gutiérrez et al., 2017).

Plant community data

We obtained vegetation plot data representing vascular plant species composition across the Netherlands from 2010-2017 to match with the habitat and vegetation structure data. The vegetation data originates from the Dutch Vegetation Database (Hennekens 2018). Following Večeřa (Večeřa et al., 2021), plots without geo-referenced information or without sample size (i.e. the size of each sampled plot) or sample size < 1 m^2 or $> 1{,}000$ m^2 were excluded from this study. Based on these criteria, the dataset comprised 1,249 native species in 53,011 plots located in 33,289 grid cells with 1 ha area. These plots were assigned to grid cells of 100 m^2 to match with the habitat and vegetation structure data. The final filtered dataset, matched with the habitat types and vegetation structure data, contained 904 species in 11,937 geo-referenced plots with sample sizes ranging from 1 to 1,000 m^2 (Fig. 1). These ranges reflect the sample sizes traditionally used by the European phytosociology (Westhoff et al., 1978) to capture plant species in ecosystems from grassland to forest, and the datasets have been used in other studies (Hämmerle et al., 2018; Večeřa et al., 2021).

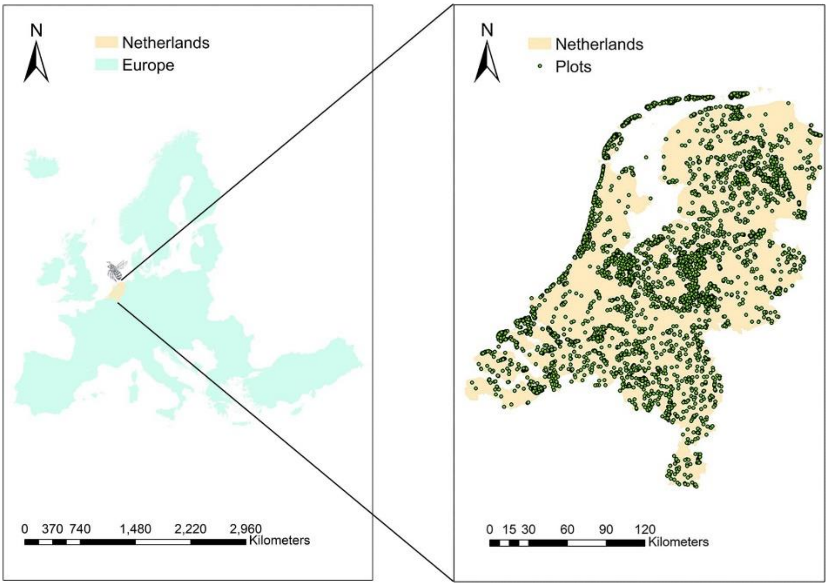

Figure 1. The distribution of 11,937 plots with coordinates and sample sizes between 1-1000 m^2 and matched with the habitat types map. Map projection: EPSG:28992, Amersfoort / RD New.

Pollination modes and growth forms

Data of pollination modes were collected from Biobase (CSB 2003), which includes pollination modes of all Dutch vascular plants. Pollination modes were classified into insect-pollination, wind-pollination and self-pollination, and all plants were adapted to a binary classification in consideration of each of three pollination modes (Table1). Further, specialization in pollination mode (named specialized insect-pollination, specialized wind-pollination and specialized self-pollination) was assigned to plants that exhibit only one pollination mode. Pollination modes were attributed to every plant species observed in each plot. However, pollination modes are non-randomly distributed among plant growth forms and types. Grasses are only wind-pollinated, whereas the frequency of insect and wind-pollination among woody species and herbs may also be different. This, in turn, may determine the relationship with habitat type and vegetation structure. Moreover, the effectiveness of pollination also depends on the type of plant. A woody plant species pollinated by wind is less likely to be affected by the cover of the upper vegetation layer in a habitat, whereas for a herb or grass, wind-pollination may be hampered by high vegetation surrounding it. Thus, we obtained data of growth forms, which includes herbs, grasses (grasses here refer to all grass-like plants in the families Poaceae (grasses), Juncaceae (rushes) and Cyperaceae (sedges)) and woody species, from Biobase (CSB 2003). The numbers of plant species pollinated by different modes in different growth form groups were in Table1.

Table 1. The number of species with different pollination modes and growth forms.

Pollination mode	Herb	Grass	Woody (Tree/Shrub)
Insect	526	0	79 (17/62)
Wind	66	173	48 (41/7)
Self	387	7	23 (3/20)
Specialized insect	159	0	51 (10/41)
Specialized wind	22	166	42 (37/5)
Specialized self	14	0	0

Percentage of species with different pollination modes in all grid cells and 7 (semi-)natural habitats

In each grid cell, we first calculated the number of species pollinated by different modes in each plot within the grid cell. Second, since there might be more than one plot in each grid cell, we calculated the average number of species pollinated by different modes based on all plots in each grid cell. Third, averaged richness of species pollinated by different pollination modes were calculated based on richness of different pollination modes in all grid cells in each habitat type. The Euclidean distances between habitats were calculated by functions of acomp and dist from package *compositions* (version 2.0-1) (van den Boogaart and Tolosana-Delgado 2008) and hclust function with the ward.D2 method was used to get clusters of seven habitat types by the package *stats* (version 4.1.2) (R Core Team 2013). Since there are only 3 pollination modes, within which either wind- or self-pollination counted a lower proportion than the other two pollination modes in all habitat types, the maximum number of clusters was limited to 3 (i.e. the proportion of animal pollination = the proportion of wind-pollination or self-pollination, the proportion of animal pollination > the proportion of wind-pollination or self-pollination, the proportion of animal pollination < the proportion of wind-pollination or self-pollination). The number of clusters were obtained based on three criteria: (1) if (the minimum proportion of animal pollination - the maximum proportion of wind-pollination or self-pollination) > 0.5, we only kept 1 cluster, (2) if -0.5 <= (the minimum proportion of animal pollination - the maximum proportion of wind- or self-pollination) <= 0.5, we kept 2 clusters, (3) if 0.5 < |(the minimum proportion of animal pollination - the maximum proportion of wind- or self-pollination)|, we kept 3 clusters. A ternary plot (Hamilton and Ferry 2018) was used to compare which species group accounts for a higher percentage in each grid cell and habitat type.

Drivers of 3D vegetation structure on the diversity of species pollinated by different modes

We assessed bivariate correlations among four variables of vegetation structure (canopy densities of 0.5-2, 2-5, 5-10 and 10-20 m vegetation strata) and found none of them with high correlations (Pearson's correlation coefficients > |.7|, (Dormann et al., 2013)). We further assessed multivariate correlations among predictors using VIFs (Variance inflation factors). We interpret our results using a conventional cutoff for VIF of 10.0. Finally, four variables were included in the final set of variables used during the modeling step.

We used a generalized linear mixed model with a poisson distribution to assess whether and how 3D vegetation structure drives the diversity of species pollinated by different pollination modes at a landscape level. Canopy densities of 0.5-2, 2-5, 5-10 and 10-20 m vegetation strata were taken as fixed effects. Since more than one plot may fall in the same 100 × 100 m grid cell and vegetation plots in our datasets were of different sizes, we used grid cell identity and sample size as random factors. All analyses were conducted in R (version 4.1.0) (R Core Team 2013) with the package *glmmTMB* (version 1.1.2.2) (Brooks et al., 2017).

We compared the importance of vegetation structure on driving the occurrence of pollination modes to habitat type to make this study comparable to peer-reviewed papers emphasizing the effect of habitat (e.g. Kühn et al., 2006). Since we only want to know the influential effects of vegetation structure and habitat on the richness of all plants pollinated by different modes in a community, analysis was conducted based on all plants instead of different plant types. We first constructed a full generalized linear mixed model (m1) with a poisson distribution. This model includes habitat type (a categorical variable including dune, heather, semi-natural grassland, river swamp, swamp peat, semi-natural forest and production forest) and four vegetation structure variables (canopy densities of 0.5-2, 2-5, 5-10 and 10-20 m vegetation strata) as fixed effects. Interactions between habitat type and vegetation structure were included. Grid cell identity and sample size were maintained as random effects. Secondly, we constructed three other generalized linear mixed models by excluding interactions between habitat and vegetation structure (m2), removing canopy densities of four vegetation strata (m3) and habitat type (m4) from the full model each time, and each of these three models was compared to the full model (m1) by ANOVA. A model with a significantly larger AIC (Akaike information criterion) value than the full mode (m1) means the excluded interaction or removed variable is significantly important.

Results

Distribution of pollination modes composition across Dutch (semi-)natural habitats

Across all (semi-)natural habitats in the Netherlands, insect-pollinated species (35%) and wind-pollinated species (38%) were more common than self-pollinated species (27%) (Appendix IV). Wind-pollinated species were more common in heather (49%) and production forest (43%) (Fig. 2A). Insect-pollinated species were more common in dune (40%) and river swamp (42%) (Fig. 2A). There was much variation between the different plots within habitat types (Appendix V A). For plants specially pollinated by one mode, wind-pollination was most common in all habitats (Appendix VI A, Appendix VII A).

When splitting plants into different groups of growth type, insect-pollination was the most common pollination mode across (semi-)natural habitats for woody species and herbs (Fig. 2B-C, Appendix V B-C). However, the insect-pollination of woody species in dune, river swamp and swamp peat were more common than in other habitat types, whereas insect-pollination of herbs in dunes was more common than in other habitats. Wind-pollination was the most common pollination mode across (semi-)natural habitats for grasses (Fig. 2D, Appendix V D).

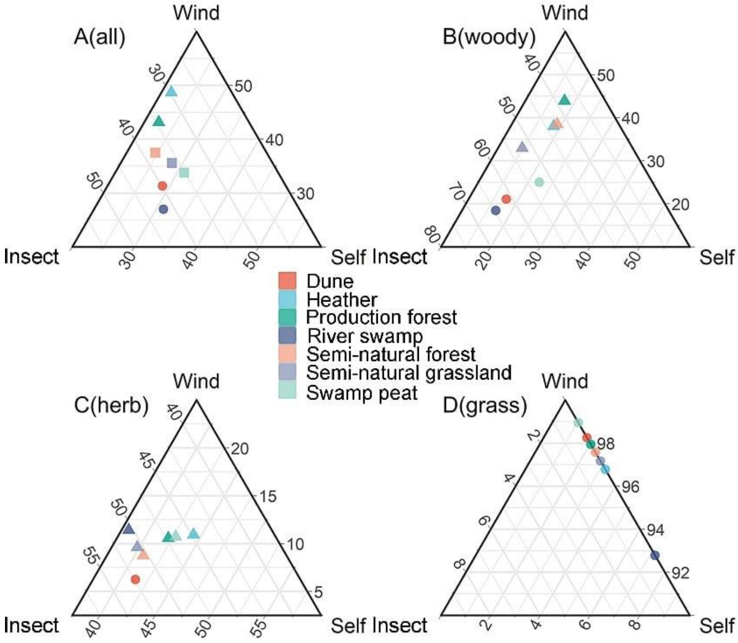

Figure 2. Percentages of species with different pollination modes in each of seven habitat types for (A) all plants, (B) woody species, (C) herbs and (D) grasses. In this ternary graph, different colors indicate distinct habitat types and different shapes mean statistically different clusters (cluster analysis by *compositions*). The average number of species in each habitat type can be found in Appendix I.

The distribution of pollination modes related to 3D vegetation structure

In our final generalized linear mixed mode with 904 plant species, we included canopy densities of 4 vegetation strata as fixed effects. Grid identity and sample sizes were taken as random effects. Our model showed that of 904 plant species, insect- and self-pollinated species showed similar patterns and increased with denser herb and shrub (strata < 5 m) layers (Fig. 3A, Appendix VIII), whereas they decreased if the canopy density of high strata (> 5 m) increased. Wind-pollinated plants, on the other hand, decreased with denser canopy of low strata. Specialized insect-pollinated plants also increased with canopy density of low vegetation strata (< 5 m) but decreased with canopy density of high vegetation strata (Fig. 3B, Appendix XII).

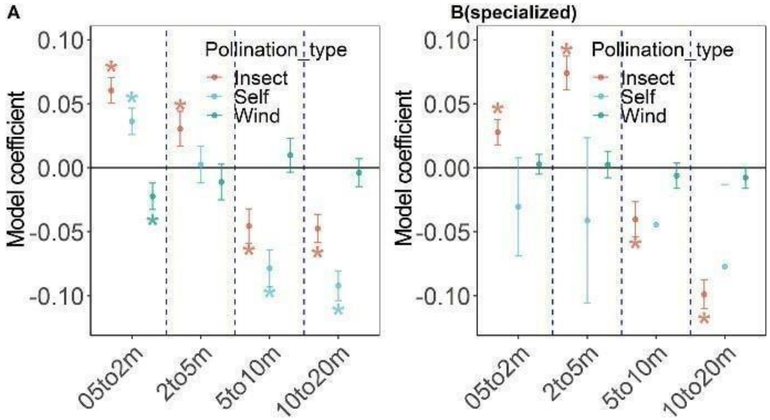

Figure 3. Model coefficients from the generalized linear mixed model (GLMM) of species richness in relation to canopy densities of four vegetation strata. Analysis was conducted within (A) three groups of insect-pollination, wind-pollination and self-pollination and (B) three groups of specialized insect-pollination, specialized wind-pollination and specialized self-pollination. 05to2m means the canopy density of 0.5-2 m vegetation strata. 2to5m means the canopy density of 2-5 m vegetation strata. 5to10m means the canopy density of 5-10 m vegetation strata. 10to20m means the canopy density of 10-20 m vegetation strata. Y axes indicate coefficients of predictors, which are also listed in Appendix II.

For woody species, only wind-pollinated plants decreased with denser vegetation canopy of low strata (< 2 m height) (Fig. 4A, Appendix IX). Grasses, no matter if they are wind- or self-pollinated, decreased with denser canopy density (Fig. 4E, Appendix X). For herbs, insect- and self-pollinated species showed similar patterns. Both decreased with denser vegetation layers between 5 and 20 m (Fig. 4C, Appendix XI), whereas insect-pollinated plants increased with canopy density of low strata (< 5 m). Wind-pollinated herbs decreased with denser 0.5-2 m and 10-20 m vegetation.

Woody plants only had two specialized pollination modes (i.e. insect and wind) (Fig. 4B, Appendix XIII). Insect-pollinated woody plants increased with denser canopy of low strata (< 5 m) but decreased with denser tree layer (> 10 m). In contrast, wind-pollinated plants increased with canopy density of strata above 2 m but decreased with canopy density of strata below 2 m. Wind-pollination was the only specialized pollination mode of grasses (Fig. 4F, Appendix XIV), which decreased with the canopy density of high strata (> 5 m). Although there were three specialized pollination modes of herbs (Fig. 4D, Appendix XV), only insect-pollinated species showed significant patterns. Those species increased with canopy density of strata from 2 to 5 m but decreased with denser canopies of other vegetation strata.

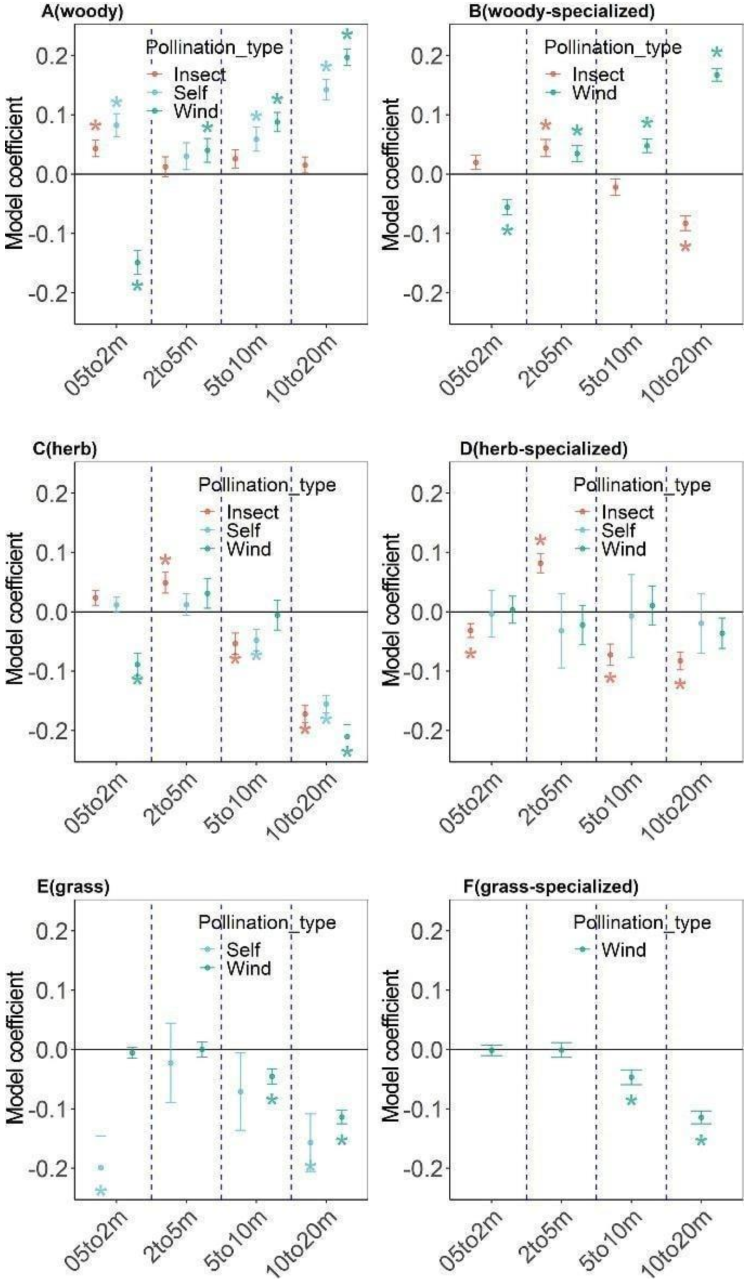

Figure 4. Model coefficients from the generalized linear mixed model (GLMM) of species richness in relation to canopy densities of four vegetation strata. A-B, for woody species with analysis conducted (A) within three groups of insect-pollination, wind-pollination and self-pollination and (B) within three groups of specialized insect-pollination, specialized wind-pollination and specialized self-pollination. C-D, for herbs with analysis conducted (C) within three groups of insect-pollination, wind-pollination and self-

pollination and (D) within three groups of specialized insect-pollination, specialized wind-pollination and specialized self-pollination. E-F, for grasses with analysis conducted (E) within three groups of insect-pollination, wind-pollination and self-pollination and (F) within three groups of specialized insect-pollination, specialized wind-pollination and specialized self-pollination. 05to2m means the canopy density of 0.5-2 m vegetation strata. 2to5m means the canopy density of 2-5 m vegetation strata. 5to10m means the canopy density of 5-10 m vegetation strata. 10to20m means the canopy density of 10-20 m vegetation strata. Y axes indicate coefficients of predictors, which are also listed in Appendix II.

When comparing the influence of vegetation structure on the occurrence of pollination mode to habitat type, we found that although habitat type was more important than vegetation structure, both had a strong influence on the occurrence of the different pollination modes and that their relationship was not independent since removing either of habitat or vegetation structure or their interactions will make the AIC value higher (Table 2, Appendix XVI-XVII).

Table 2. Comparisons between each individual model (m2-m4) and the full model (m1). **m1**: richness ~ canopy densities of 0.5-2 m vegetation * habitat type + canopy densities of 2-5 m vegetation * habitat type + canopy densities of 5-10 m vegetation * habitat type + canopy densities of 10-20 m vegetation * habitat type. **m2**: richness ~ canopy densities of 0.5-2 m vegetation + canopy densities of 2-5 m vegetation + canopy densities of 5-10 m vegetation + canopy densities of 10-20 m vegetation + habitat type. **m3**: richness ~ habitat type. **m4**: richness ~ canopy densities of 0.5-2 m vegetation + canopy densities of 2-5 m vegetation + canopy densities of 5-10 m vegetation + canopy densities of 10-20 m vegetation.

Specialized	Pollination mode	Model	AIC	*P*.Value (compare to m1)	Significance
	Insect	m1	61097.08	-	*
-	Insect	m2	61171.36	<0.001	*
-	Insect	m3	61279.10	<0.001	*
-	Insect	m4	62543.69	<0.001	*
	Self	m1	55183.43	-	*

-	Self	m2	55243.16	<0.001	*
-	Self	m3	55323.67	<0.001	*
-	Self	m4	56447.58	<0.001	*
-	Wind	m1	56167.93	-	*
-	Wind	m2	56273.08	<0.001	*
-	Wind	m3	56289.06	<0.001	*
-	Wind	m4	57366.12	<0.001	*
Specialized	Insect	m1	26532.72	-	*
Specialized	Insect	m2	26533.91	0.002	*
Specialized	Insect	m3	26627.18	<0.001	*
Specialized	Insect	m4	26664.11	<0.001	*
Specialized	Self	m1	2687.69	-	
Specialized	Self	m2	2640.07	1	
Specialized	Self	m3	2633.05	1	
Specialized	Self	m4	2629.68	1	

Specialized	Wind	m1	51872.57	-	*
Specialized	Wind	m2	51928.90	<0.001	*
Specialized	Wind	m3	51934.45	<0.001	*
Specialized	Wind	m4	52878.98	<0.001	*

Discussion

The distribution of pollination modes composition across Dutch (semi-)natural habitats

The pattern of pollination modes over the whole Netherlands is different from that found in Germany (Kühn et al., 2006), where less wind- and self-pollination were found. More wind-pollinated plants in the Netherlands might be due to flatter landscapes, as indicated in previous studies (Kühn et al., 2006; Rech et al., 2016). However, the finer scale used in our study may also explain part of the difference.

We further detected different distributions of three pollination modes in seven (semi-)natural habitat types, and the distributions were different between woody plants, herbs, and grasses. Insect-pollination is more common in dunes and river swamp habitats, while wind-pollination is more common in open heathland, probably because of the high proportion of grasses, and production forest, which is less diverse in plants and insect pollinators than semi-natural forest (Aubin et al., 2008; Taki et al., 2011). Our study supports the hypothesis of Rech et al., (Rech et al., 2016) that higher plant diversity in a habitat contributes to higher insect-pollination, as the Dutch dunes and river swamps have more plant species, while heathland and forest are often dominated by few (dwarf) shrubs and trees. Fewer insect pollinators may contribute to a failure of insect-pollination in forests (Winfree et al., 2011; Hanula et al., 2016).

Within plant types, pollination modes showed different distributions among habitats. Woody species largely mirrored the pattern of all plants, with insect-pollination being more common in dunes and river swamp, but also in swamp peat habitats. Most woody species in these habitats are shrubs, which are insect-pollinated, whereas the main big trees in production forest (and semi-natural forest) tend to be wind-pollinated (Regal 1982). Grasses are the main feature of semi-natural grassland and heathland and are wind-pollinated. This may explain the higher frequency of wind-pollination in these habitats compared to dunes, river swamp and swamp peat. Herbs show quite different patterns compared to all plants. Insect-pollination is the most common pollination mode of herbs across all (semi-)natural habitats, particularly in dunes.

3D vegetation structure is correlated with the occurrence of pollination modes

According to previously published studies, pollination mode can be explained by wind speed, temperature, humidity, precipitation, plant richness and openness of habitats. In this study, we found that plants using insect-pollination increased with denser vegetation in low strata and decreased with denser vegetation in high strata. This is in line with previous findings. For example, dense canopies in high strata may cause a lower temperature underneath, which decreases nectar production by understory plants and affects pollinator foraging (Polatto et al., 2014; Hanula et al., 2016; Rech et al., 2016) and limits pollinator flight ability and activity (Hodkinson 2005). In fact, forest understories are often poor in plant species (Rech et al., 2016).

Wind-pollination decreased with increasing canopy density in the 0.5-2 m vegetation stratum, probably because wind-pollinated species benefit from more open vegetation for pollen dispersal (Culley et al., 2002; see also Kühn et al., 2006; Rech et al., 2016). Rech et al. (2016) hypothesize that wind-pollination is facilitated by open vegetation as denser vegetation, in high strata might mechanically restrict pollen dispersal..

We found that woody species, herbs and grasses differ in their correlation with 3D vegetation structure. Compared to all plants, woody species pollinated by wind have positive correlations with canopy densities of 2-20 m vegetation. Most of these species are trees, for which wind-pollination is less affected by surrounding vegetation. This result differs from (Rech et al., 2016), where wind-pollination is more frequent in open fields probably due to more diverse species composition in lower latitudes. Insect-pollination only increased with canopy density of 0.5-2 m vegetation, which reflects mostly shrubs common in relatively open habitats. However, occurrences of plants that are obligate insect-pollinated increased with canopy density of 2-5 m vegetation but decreased with canopy density of 10-20 m vegetation, probably due to lower abundance and diversity of insect pollinators in forested areas and better wind-pollination conditions in opener habitats. Grasses decreased with canopy density of 5-20 m vegetation, probably (as argued above) due to lower effectiveness of wind-pollination (the main pollination mode of grasses) in forests (Culley et al., 2002; Davis et al., 2004; Saunders 2018). Similarly, wind-pollinated herbs also showed negative relationships with canopy densities of both low and high strata, probably because of surrounding shrubs and trees limiting wind-pollination. Compared to all plants, herbs pollinated by insects did not show a significant response to the canopy density of 0.5-2 meters. Furthermore, strict insect-pollination decreased with the canopy density of 0.5-2 meters probably because too open habitats are suitable for wind-pollination instead of insect-pollination (Culley et al., 2002).

The importance of vegetation structure on driving the occurrence of pollination modes compared to habitat type

Overall, we found that insect-pollination occurs more frequently in habitats covered by herbs or shrubs than in habitats with dense tree layers. These habitats are often related to dune, river swamp and swamp peat (Appendix III, Appendix XVIII). However, swamp peat has few insect-pollinated species. It means other environmental conditions, e.g. temperature, moisture, light, feeding resources in different habitats are also important factors driving the richness of different pollination modes (Regal 1982; Culley et al., 2002). However, the occurrence of wind-pollination in habitats largely depends on different plant types. More wind-pollinated trees occur in habitats with a higher proportion of tree layers, which are corresponding to diverse wind-pollinated species in production forest or semi-natural forest, while grasses occur in open habitats. Our results also showed that although habitat type is important, which was also shown by Kühn et al. (Kühn et al. 2006), both habitat and vegetation structure are important factors driving the occurrence of different pollination modes and they are not independent. We suggest future studies identifying the effect of land use on pollination mode should not only focus on habitat type, but also vegetation structure and its interactions with habitat type.

Conclusion

We show that compositions of pollination modes are different across (semi-)natural habitats. In conclusion, insect-pollination is more common in opener habitats, while wind-pollination is more common in forested habitats. Within open habitats, wind-pollination is more common in habitats with a higher proportion of grasses. This pattern is slightly different for woody species, herbs, and grasses due to different dominating modes for each plant group. For each pollination mode, its occurrence is related to vegetation structure. More insect-pollination occurs in habitats covered by herbs or shrubs but not by large trees, whereas the occurrence of wind-pollination in habitats with different vegetation structures depends on plant types. More wind-pollinated trees occur in habitats with denser upper-layer trees, but grasses are more likely to occur in open habitats. For woody and herb species, specialized insect-pollination has a different response to vegetation structure compared to insect-pollination due to its high dependence on pollinators. Our study reveals that 3D vegetation structure might affect plant richness by affecting pollination modes. Thus, the conservation and management of plant species richness may actually require a different focus from the pollination mode.

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References

Aguirre-Gutiérrez J, WallisDeVries MF, Marshall L, van't Zelfde M, Villalobos-Arámbula AR, Boekelo B, Bartholomeus H, Franzén M, Biesmeijer JC (2017) Butterflies show different functional and species diversity in relationship to vegetation structure and land use. Global Ecology and Biogeography 26:1126–1137.

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Brooks, M. M (2017) glmmTMB: Generalized Linear Mixed Models using Template Model Builder. R Package Version 0.2. 0. Available online at: https://cran.r-project.org/web/packages/glmmTMB/glmmTMB.pdf.

Aubin I, Messier C, Bouchard A (2008) Can plantations develop understory biological and physical attributes of naturally regenerated forests? Biological Conservation 141:2461–2476. Available online at: https://www.sciencedirect.com/science/article/pii/S0006320708002619.

Baker HG (1955) Self-Compatibility and Establishment After 'Long-Distance' Dispersal. Evolution 9:347.

Berg Å, Ahrné K, Öckinger E, Svensson R, Söderström B (2011) Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. Biological Conservation 144:2819–2831.

Briggs H, Ayers CA, Armsworth PR, Brosi BJ (2019) Testing how antagonistic interactions impact the robustness of plant-pollinator networks. Journal of Pollination Ecology 25.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal 9:378–400. Available online at: https://www.research-collection.ethz.ch/handle/20.500.11850/239870.

Centraal Bureau voor de Statistiek (CBS) (2012) Bestand Bodemgebruik Productbeschrijving.

CSB (2003) Biobase 2003. Biodiversity Register. CBS. Voorburg/Heerlen.

Culley TM, Weller SG, Sakai AK (2002) The evolution of wind pollination in angiosperms. Trends in ecology & evolution 17:361–369. Available online at: https://www.sciencedirect.com/science/article/pii/S0169534702025405.

Davis HG, Taylor CM, Lambrinos JG, Strong DR (2004) Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (Spartina alterniflora). Proceedings of the National Academy of Sciences of the United States of America 101:13804–13807. Available online at: https://www.pnas.org/content/101/38/13804.full.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JR, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Frenne P de, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J, Decocq GM, Dierschke H, Eriksson O, Gilliam FS, Hédl R, Heinken T, Hermy M, Hommel P, Jenkins MA, Kelly DL, Kirby KJ, Mitchell FJ, Naaf T, Newman M, Peterken G, Petrík P, Schultz J, Sonnier G, van Calster H, Waller DM, Walther G-R, White PS, Woods KD, Wulf M, Graae BJ, Verheyen K (2013) Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciences of the United States of America 110:18561–18565.

Grundel R, Jean RP, Frohnapple KJ, Glowacki GA, Scott PE, Pavlovic NB (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecological applications : a publication of the Ecological Society of America 20:1678–1692.

Hamilton NE, Ferry M (2018) ggtern : Ternary Diagrams Using ggplot2. Journal of Statistical Software. 87:1–17. Available online at: https://www.jstatsoft.org/index.php/jss/article/view/v087c03.

Hämmerle AI, Wessely J, Baatar U-O, Essl F, Moser D, Jiménez-Alfaro B, Jandt U, Agrillo E, Stančić Z, Dirnböck T, Dullinger S (2018) A new method for jointly assessing effects of climate change and nitrogen deposition on habitats. Biological Conservation 228:52–61.

Hanula JL, Ulyshen MD, Horn S (2016) Conserving Pollinators in North American Forests: A Review. Natural Areas Journal 36:427–439. Available online at: https://bioone.org/journals/natural-areas-journal/volume-36/issue-4/043.036.0409/Conserving-Pollinators-in-North-American-Forests-A-Review/10.3375/043.036.0409.full.

Hennekens S (2018) Dutch Vegetation Database (LVD). v1.6. Alterra, Wageningen UR. Dataset/Samplingevent.

Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80:489–513. Available online at: https://www.cambridge.org/core/journals/biological-reviews/article/terrestrial-insects-along-elevation-gradients-species-and-community-responses-to-altitude/A8824BF3780E0624F744D5D9219B851F.

Hoiss B, Gaviria J, Leingärtner A, Krauss J, Steffan-Dewenter I (2012) Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. Diversity and Distributions 19:n/a-n/a. Available online at: https://onlinelibrary.wiley.com/doi/full/10.1111/j.1472-4642.2012.00941.x.

Inter Provinciaal Overleg (2016) Informatiemodel natuurbeheer (IMNAB): Index Natuur en Landschap.

Kalisz S, Vogler DW, Hanley KM (2004) Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating. Nature 430:884–887. Available online at: https://www.nature.com/articles/nature02776.

Kühn I, Bierman SM, Durka W, Klotz S (2006) Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods.

The New phytologist 172:127–139. Available online at: https://nph.onlinelibrary.wiley.com/doi/full/10.1111/j.1469-8137.2006.01811.x.

Luskin MS, Potts MD (2011) Microclimate and habitat heterogeneity through the oil palm lifecycle. Basic and Applied Ecology 12:540–551.

Ministerie van Economische Zaken (EZK) (2015) Basisregistratie Gewaspercelen (BRP).

Montero-Castaño A, Vilà M (2012) Impact of landscape alteration and invasions on pollinators: a meta-analysis. Journal of Ecology 100:884–893. Available online at: https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2745.2012.01968.x.

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321–326.

Polatto LP, Chaud-Netto J, Alves-Junior VV (2014) Influence of Abiotic Factors and Floral Resource Availability on Daily Foraging Activity of Bees. Journal of Insect Behavior 27:593–612. Available online at: https://idp.springer.com/authorize/casa?redirect_uri=https://link.springer.com/article/10.1007/s10905-014-9452-6&casa_token=ahojnsrdidmaaaaa:jzsqmsyvbxaqmtszcju_a5p3y-5iikovq-7ib1hag32bbu5m5z1lnqyctrtuoe_6ejqfnydzw9fitbhujzq.

R Core Team (2013) R: A language and environment for statistical computing.

Rech AR, Dalsgaard B, Sandel B, Sonne J, Svenning J-C, Holmes N, Ollerton J (2016) The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. Plant Ecology & Diversity 9:253–262.

Rech AR, Jorge LR, Ollerton J, Sazima M (2018) Pollinator availability, mating system and variation in flower morphology in a tropical savanna tree. Acta Botanica Brasilica. 32:462–472. Available online at: https://www.scielo.br/j/abb/a/WMrYfYZtzX74PqZKSjdwp5M/?lang=en.

Regal PJ (1982) Pollination by Wind and Animals: Ecology of Geographic Patterns. Annual Review of Ecology and Systematics. 13:497–524.

Rodger JG, Bennett JM, Razanajatovo M, Knight TM, van Kleunen M, Ashman T-L, Steets JA, Hui C, Arceo-Gómez G, Burd M, Burkle LA, Burns JH, Durka W, Freitas L, Kemp JE, Li J, Pauw A, Vamosi JC, Wolowski M, Xia J, Ellis AG (2021) Widespread vulnerability of flowering plant seed production to pollinator declines. Science Advances 7:eabd3524.

Saunders ME (2018) Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. Insect Conservation and Diversity 11:13–31. Available online at: https://onlinelibrary.wiley.com/doi/full/10.1111/icad.12243.

Schoen DJ, Morgan MT, Bataillon T. (1996) How does self-pollination evolve? Inferences from floral ecology and molecular genetic variation. Philosophical Transactions of the Royal Society B 351:1281–1290.

Shivanna KR, Tandon R (2014) Pollination Ecology. In: Shivanna K (ed) Reproductive ecology of flowering plants. A manual. Springer, New York, pp 63–96.

Taki H, Yamaura Y, Okabe K, Maeto K (2011) Plantation vs. natural forest: matrix quality determines pollinator abundance in crop fields. Scientific Report 1:132. Available online at: https://www.nature.com/articles/srep00132.

van den Boogaart KG, Tolosana-Delgado R (2008) “compositions”: A unified R package to analyze compositional data. Computers & Geosciences 34:320–338.

Varassin IG, Sazima M (2012) Spatial heterogeneity and the distribution of bromeliad pollinators in the Atlantic Forest. Acta Oecologica 43:104–112. Available online at: https://www.sciencedirect.com/science/article/pii/S1146609X12000756.

Večeřa M, Axmanová I, Padullés Cubino J, Lososová Z, Divíšek J, Knollová I, Aćić S, Biurrun I, Boch S, Bonari G, Campos JA, Čarni A, Carranza ML, Casella L, Chiarucci A, Ćušterevska R, Delbosc P, Dengler J, Fernández-González F, Gégout J-C, Jandt U, Jansen F, Jašková A, Jiménez-Alfaro B, Kuzemko A, Lebedeva M, Lenoir J, Lysenko T, Moeslund JE, Pielech R, Ruprecht E, Šibík J, Šilc U, Škvorc Ž, Swacha G, Tatarenko I, Vassilev K, Wohlgemuth T, Yamalov S, Chytrý M (2021) Mapping species richness of plant families in European vegetation. Journal of Vegetation Science 32.

Westhoff V, Van der Maarel E, Whittaker RH (1978) Classification of plant communities. The Hague.

Winfree R, Bartomeus I, Cariveau DP (2011) Native Pollinators in Anthropogenic Habitats. Annual Review of Ecology, Evolution, and Systematics. 42:1–22.

Appendix I. The average number of species in each habitat type.

	Habitat types	Insect ± sd	Wind ± sd	Self ± sd
All	Dune	7.6 ± 5.0	5.9 ± 3.1	5.5 ± 3.6
	Heather	3.0 ± 3.2	4.9 ± 2.5	2.2 ± 2.5
	Production_forest	4.5 ± 3.7	5.6 ± 2.7	2.9 ± 2.8
	River_swamp	7.4 ± 5.4	4.8 ± 3.0	5.5 ± 4.2
	Semi_natural_forest	5.9 ± 4.5	5.8 ± 2.8	3.8 ± 3.3
	Semi_natural_grassland	7.1 ± 5.1	7.0 ± 3.7	5.5 ± 3.9
	Swamp_peat	4.1 ± 3.7	3.9 ± 2.5	3.6 ± 2.7
Woody	Dune	2.0 ± 1.6	0.7 ± 0.7	0.6 ± 0.9
	Heather	1.9 ± 1.1	1.7 ± 1.1	0.8 ± 0.8
	Production_forest	2.8 ± 1.9	3.2 ± 1.7	1.3 ± 1.0
	River_swamp	2.1 ± 1.5	0.6 ± 1.0	0.6 ± 0.8
	Semi_natural_forest	3.1 ± 2.2	2.8 ± 1.7	1.4 ± 1.2
	Semi_natural_grassland	1.6 ± 1.4	1.0 ± 1.1	0.5 ± 0.8
	Swamp_peat	1.4 ± 1.3	0.7 ± 0.7	0.6 ± 0.8
Herb	Dune	6.7 ± 4.4	0.8 ± 0.9	5.3 ± 3.4
	Heather	2.6 ± 3.4	0.6 ± 0.7	2.5 ± 2.7
	Production_forest	3.0 ± 3.5	0.7 ± 0.9	2.7 ± 2.9
	River_swamp	6.9 ± 4.9	1.6 ± 1.3	5.2 ± 3.9
	Semi_natural_forest	4.4 ± 4.1	0.8 ± 1.0	3.6 ± 3.3
	Semi_natural_grassland	7.0 ± 4.9	1.3 ± 1.2	5.5 ± 3.7
	Swamp_peat	4.0 ± 3.4	0.9 ± 1.0	3.7 ± 2.5
Grass	Dune	0.0 ± 0.0	4.9 ± 2.7	0.1 ± 0.3
	Heather	0.0 ± 0.0	3.2 ± 1.9	0.1 ± 0.4
	Production_forest	0.0 ± 0.0	2.5 ± 1.9	0.1 ± 0.2
	River_swamp	0.0 ± 0.0	3.5 ± 2.1	0.3 ± 0.5
	Semi_natural_forest	0.0 ± 0.0	3.2 ± 2.2	0.1 ± 0.3
	Semi_natural_grassland	0.0 ± 0.0	5.5 ± 3.1	0.2 ± 0.4
	Swamp_peat	0.0 ± 0.0	3.1 ± 2.1	0.0 ± 0.2

Appendix II. Estimates from GLMMs.

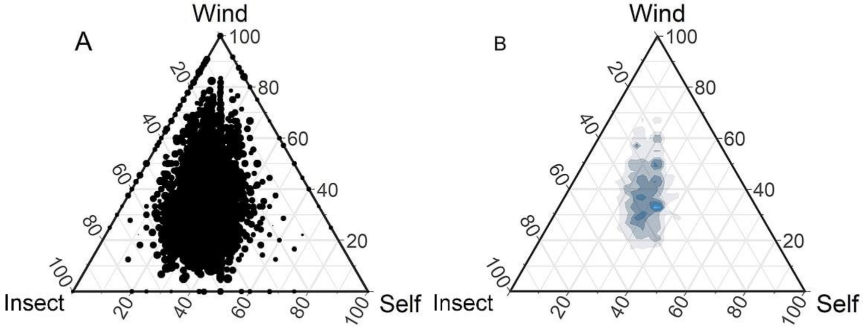
Specialized pollination	Growth_form	Pollination_mode	Intercept	05to2 m	10to20 m	2to5 m	5to10 m
-	All_species	Insect	1.67	0.06	-0.05	0.03	-0.05
-	All_species	Self	1.39	0.04	-0.09	0	-0.08
-	All_species	Wind	1.66	-0.02	0	-0.01	0.01
-	Grasses	Self	-2.4	-0.2	-0.16	-0.02	-0.07
-	Grasses	Wind	1.29	-0.01	-0.11	0	-0.05
-	Herbs	Insect	1.48	0.02	-0.17	0.05	-0.05
-	Herbs	Self	1.29	0.01	-0.16	0.01	-0.05
-	Herbs	Wind	-0.18	-0.09	-0.21	0.03	-0.01
-	Woody_species	Insect	0.94	0.04	0.02	0.01	0.03
-	Woody_species	Self	-0.02	0.08	0.14	0.03	0.06
-	Woody_species	Wind	0.63	-0.15	0.2	0.04	0.09
Specialized	All_species	Insect	0.94	0.03	-0.1	0.07	-0.04
Specialized	All_species	Self	0.12	-0.03	-0.08	-0.04	-0.04
Specialized	All_species	Wind	1.63	0	-0.01	0	-0.01
Specialized	Grasses	Wind	1.29	0	-0.11	0	-0.05
Specialized	Herbs	Insect	0.92	-0.03	-0.08	0.08	-0.07
Specialized	Herbs	Self	0.16	0	-0.02	-0.03	-0.01
Specialized	Herbs	Wind	0.23	0	-0.04	-0.02	0.01

Specialized	Woody_species	Insect	0.59	0.02	-0.08	0.04	-0.02
Specialized	Woody_species	Wind	0.82	-0.06	0.17	0.03	0.05

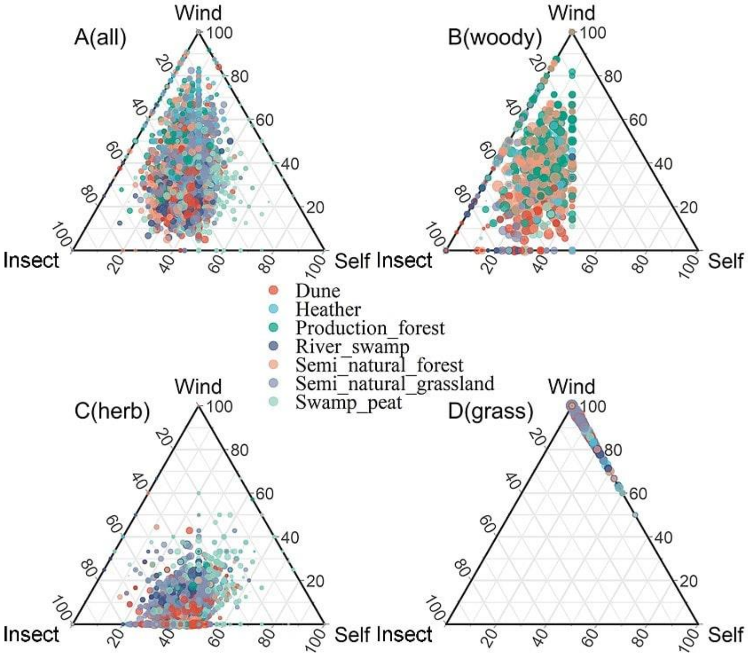
Appendix III. Canopy densities of four vegetation strata in each habitat type.

Strata	Habitat types	Min	Max	Mean ± sd
0.5to2 m	Dune	0	27.3	3.2 ± 5.1
0.5to2 m	Heather	0	29.8	1.2 ± 2.4
0.5to2 m	Production_forest	0	19.3	2.4 ± 2.0
0.5to2 m	River_swamp	0	23.3	3.5 ± 4.5
0.5to2 m	Semi_natural_forest	0	44.6	3.2 ± 3.5
0.5to2 m	Semi_natural_grassland	0	56.8	1.1 ± 2.8
0.5to2 m	Swamp_peat	0	43.9	2.4 ± 5.0
2to5 m	Dune	0	28.5	1.9 ± 4.0
2to5 m	Heather	0	39.6	2.3 ± 3.7
2to5 m	Production_forest	0	24.5	5.3 ± 3.8
2to5 m	River_swamp	0	33.2	4.7 ± 6.5
2to5 m	Semi_natural_forest	0	46.5	7.1 ± 5.6
2to5 m	Semi_natural_grassland	0	34.3	1.3 ± 3.2
2to5 m	Swamp_peat	0	42.4	1.1 ± 3.2
5to10 m	Dune	0	40.0	0.7 ± 2.8
5to10 m	Heather	0	32.7	2.8 ± 4.9
5to10 m	Production_forest	0	54.2	11.2 ± 7.8

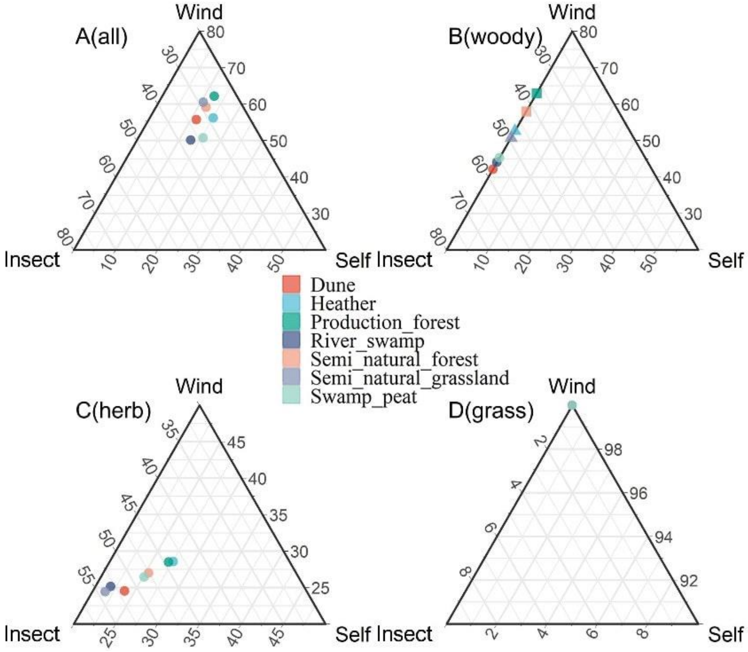
5to10 m	River_swamp	0	34.0	4.0 ± 6.8
5to10 m	Semi_natural_forest	0	52.6	12.5 ± 8.3
5to10 m	Semi_natural_grassland	0	33.1	1.2 ± 3.4
5to10 m	Swamp_peat	0	18.3	0.4 ± 1.7
10to20 m	Dune	0	24.8	0.2 ± 1.5
10to20 m	Heather	0	47.5	1.5 ± 4.8
10to20 m	Production_forest	0	68.1	31.2 ± 13.0
10to20 m	River_swamp	0	35.0	3.3 ± 6.6
10to20 m	Semi_natural_forest	0	70.3	28.1 ± 15.0
10to20 m	Semi_natural_grassland	0	65.3	1.3 ± 5.6
10to20 m	Swamp_peat	0	23.4	0.1 ± 1.0



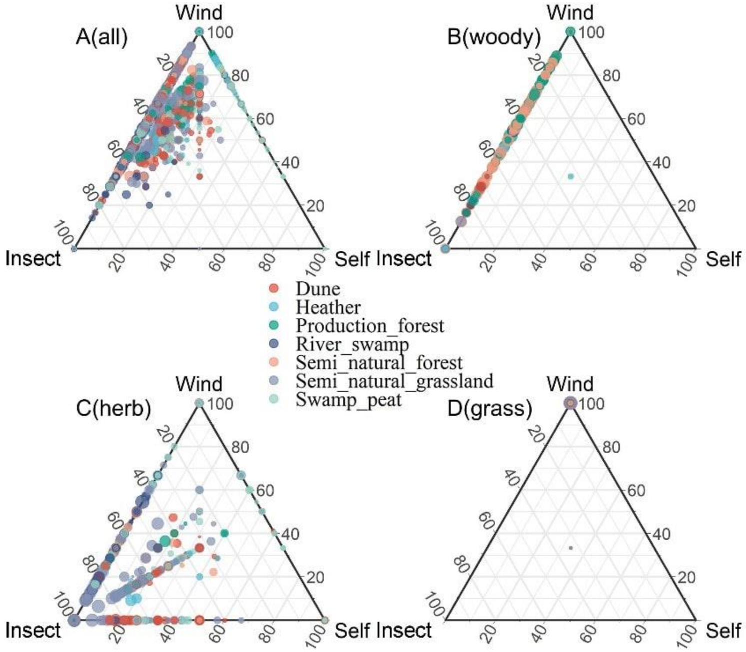
Appendix IV. Percentages of species with different pollination modes in each of seven habitat types. (A) the percentages of insect-, wind- and self-pollinated species in all grid cells. (B) the density of plots with different percentages of insect-, wind- and self-pollinated species in all grid cells.



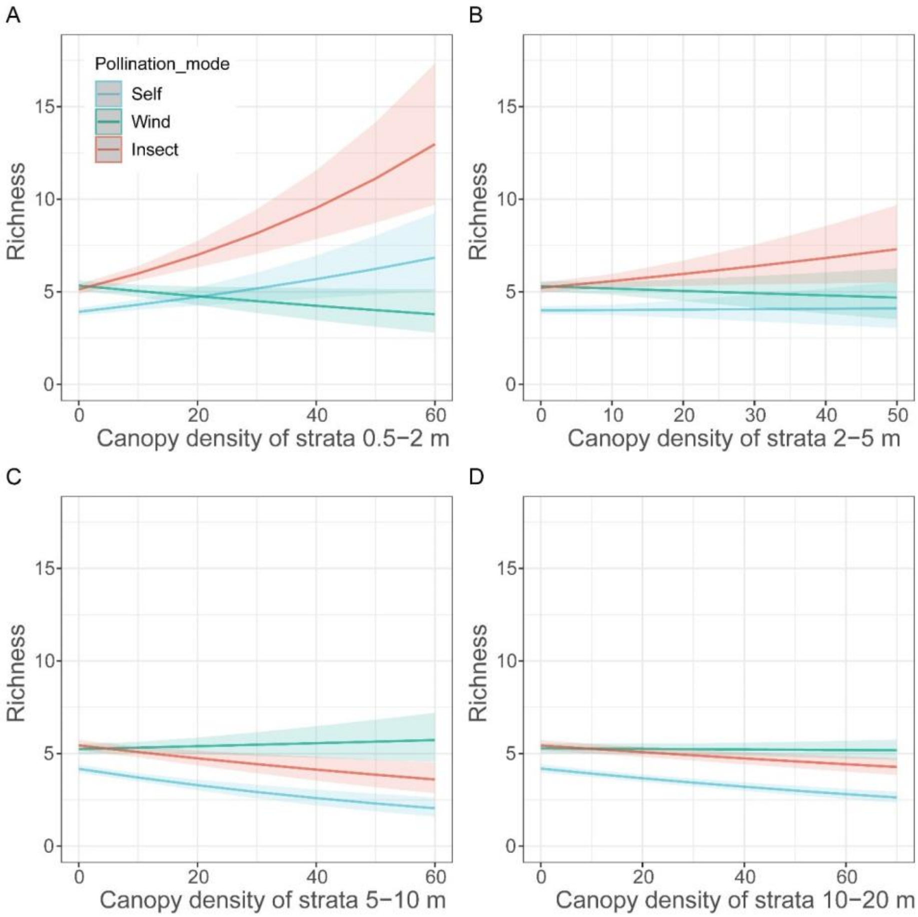
Appendix V. Percentages of species with different pollination modes in all grid cells for (A) all plants, (B) woody species, (C) herbs and (D) grasses. In this ternary graph, each colour indicates one habitat type.



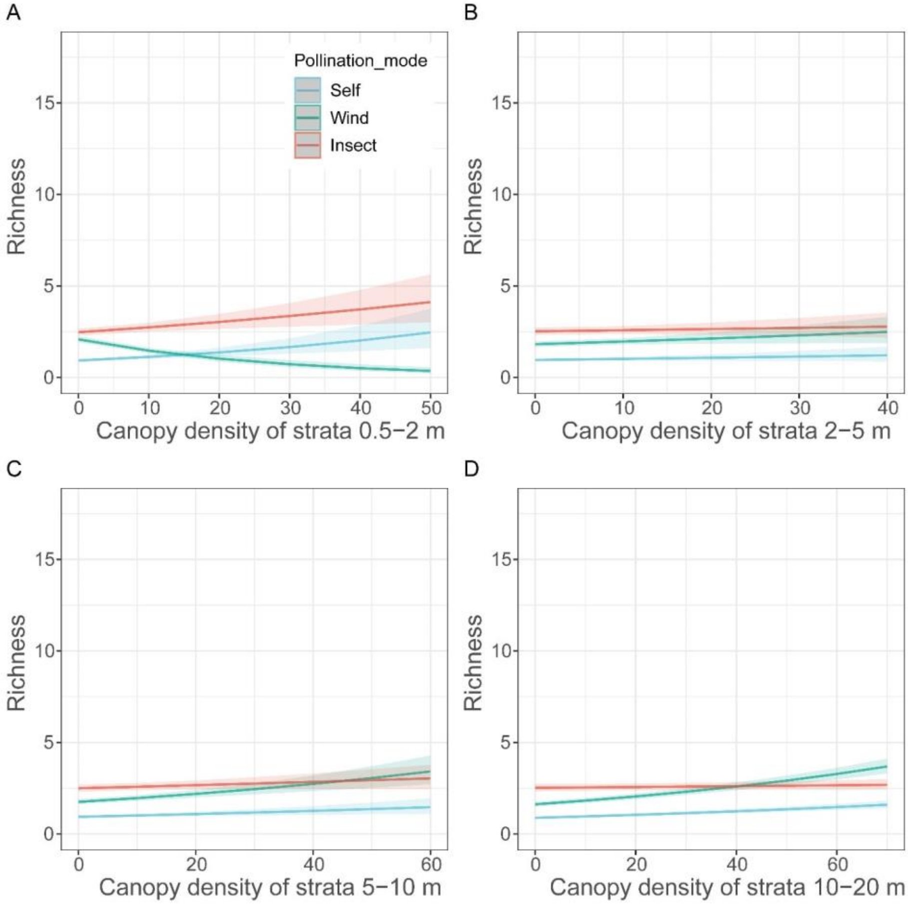
Appendix VI. Percentages of species with different specialized pollination modes in each of seven habitat types for (A) all plants, (B) woody species, (C) herbs and (D) grasses. In this ternary graph, different colours indicate different habitat types and different shapes mean statistically different clusters (cluster analysis by *compositions*).



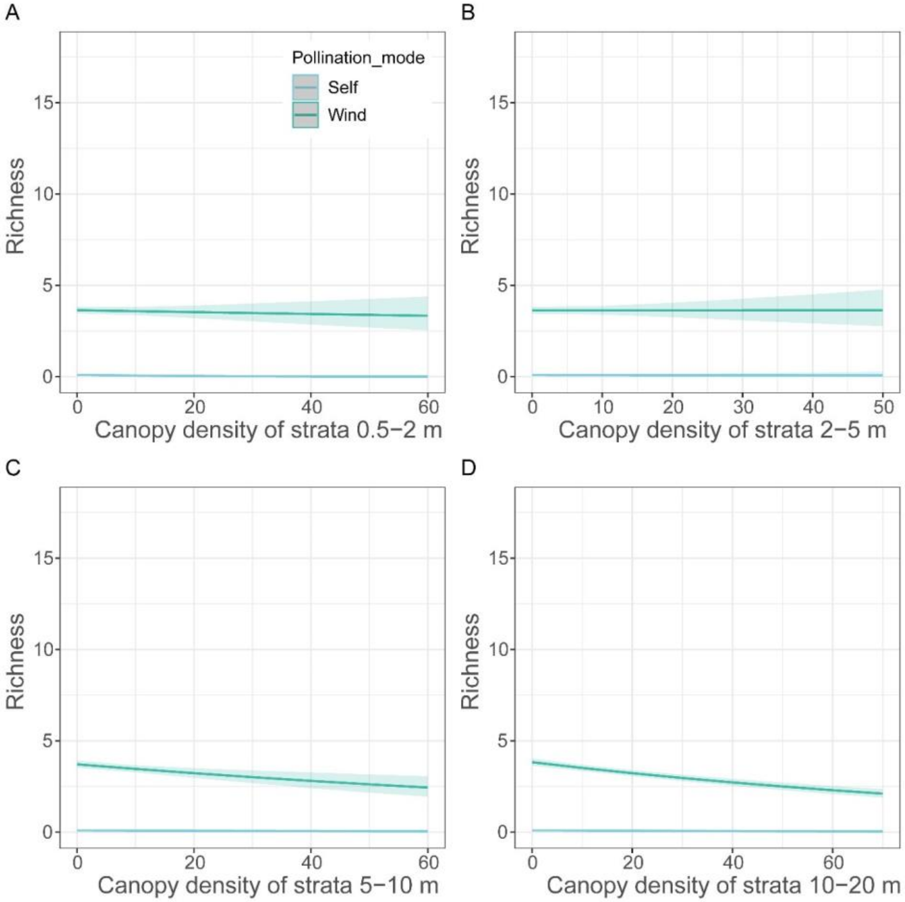
Appendix VII. Percentages of species with different specialized pollination modes in all grid cells for (A) all plants, (B) woody species, (C) herbs and (D) grasses. In this ternary graph, each colour indicates one habitat type.



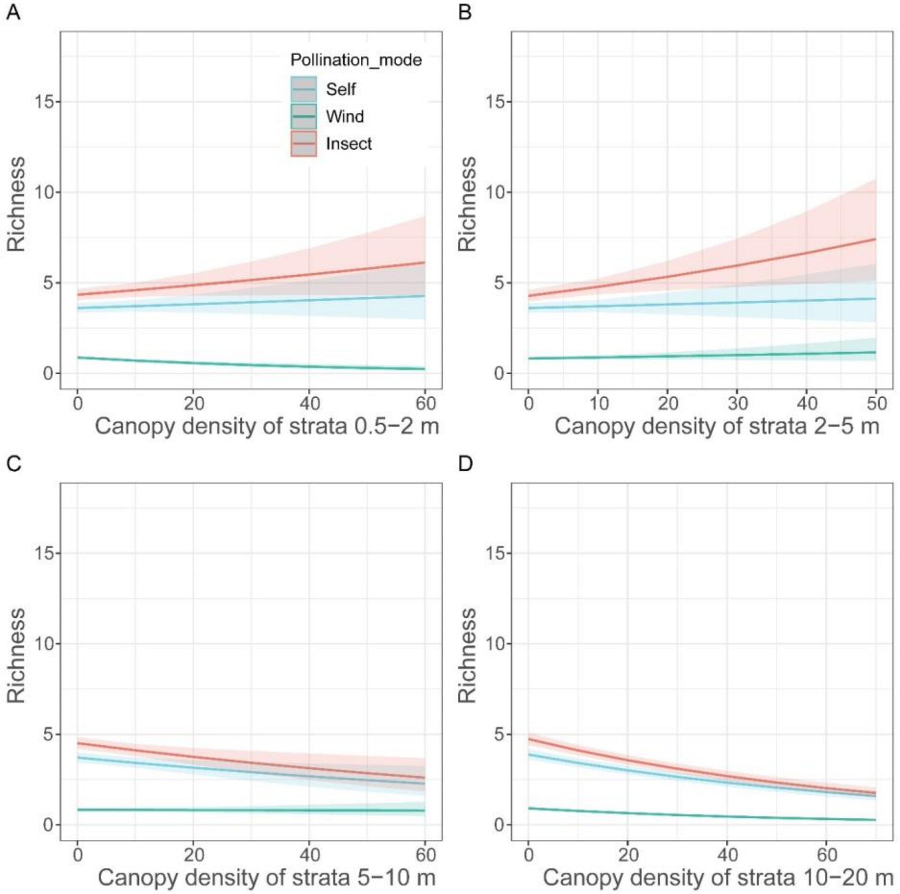
Appendix VIII. Responses of richness of all plants with different pollination modes to vegetation structure.



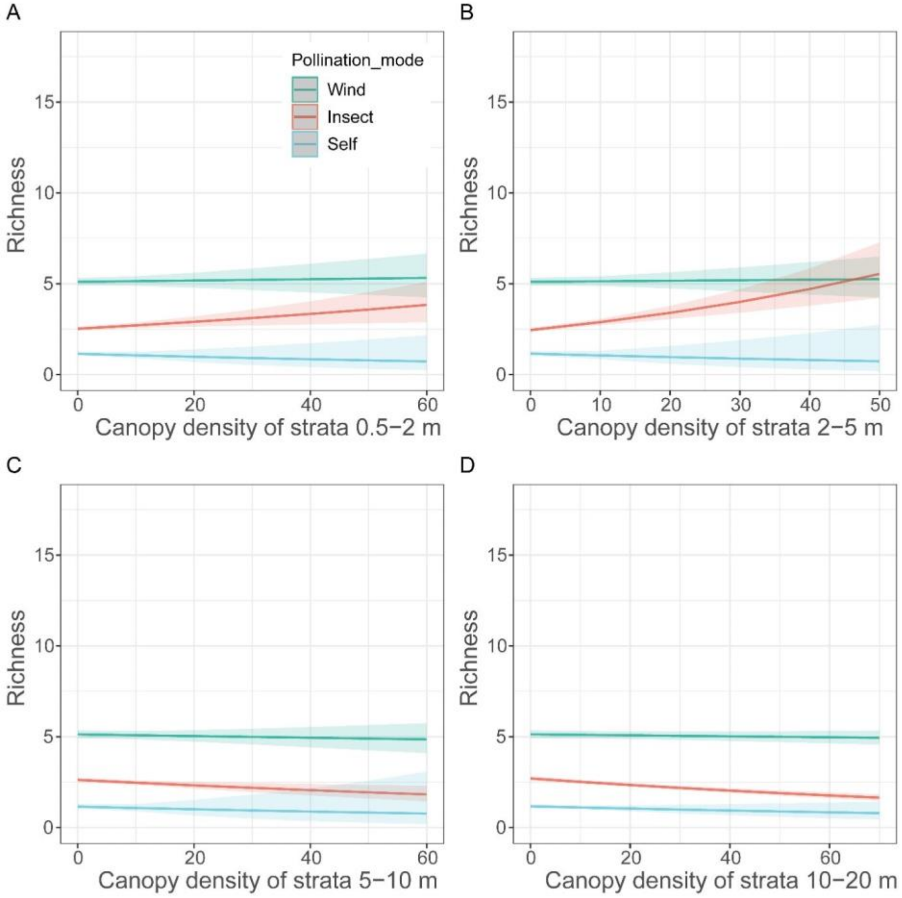
Appendix IX. Responses of richness of woody plants with different pollination modes to vegetation structure.



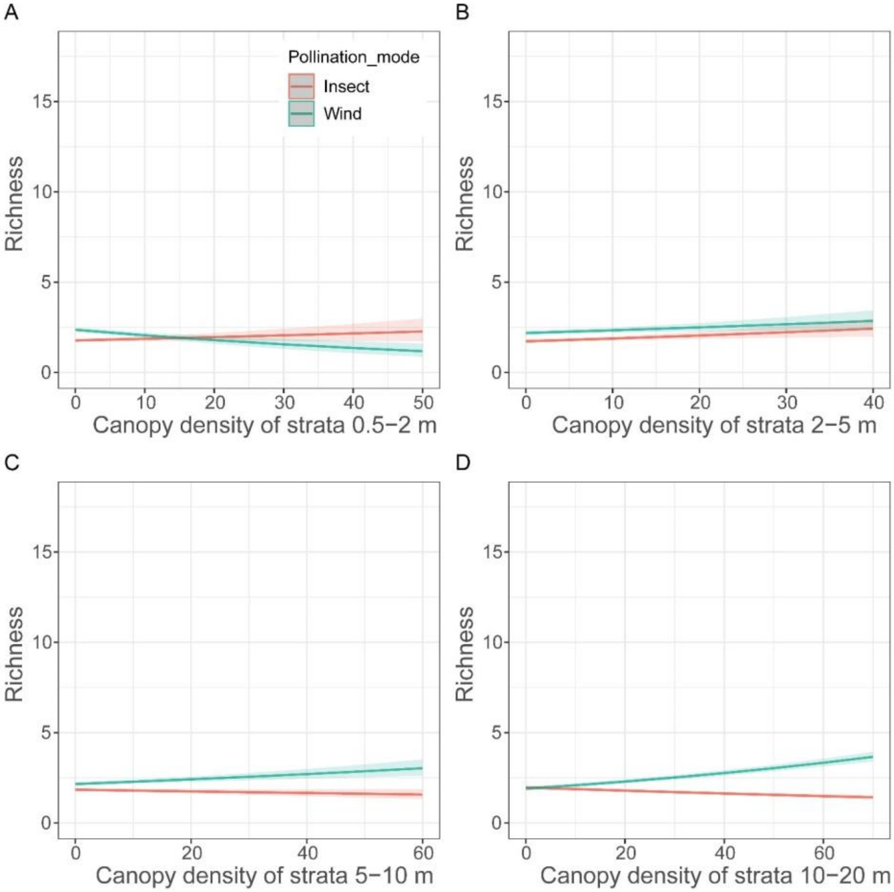
Appendix X. Responses of richness of grasses with different pollination modes to vegetation structure.



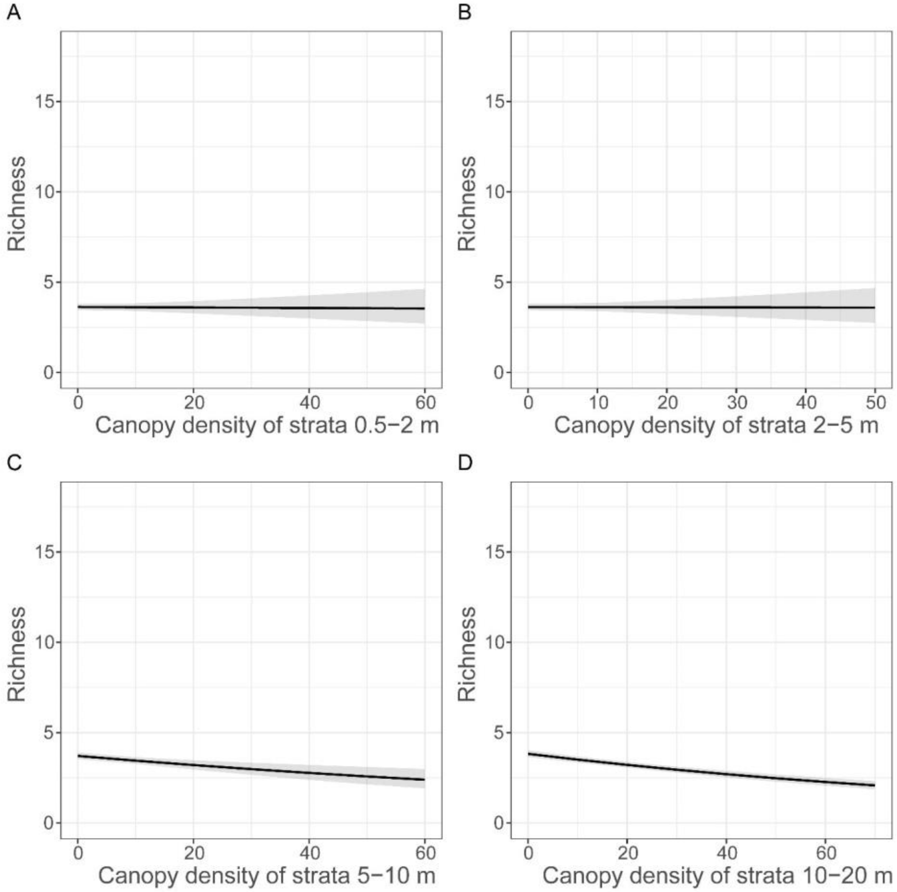
Appendix XI. Responses of richness of herbs with different pollination modes to vegetation structure.



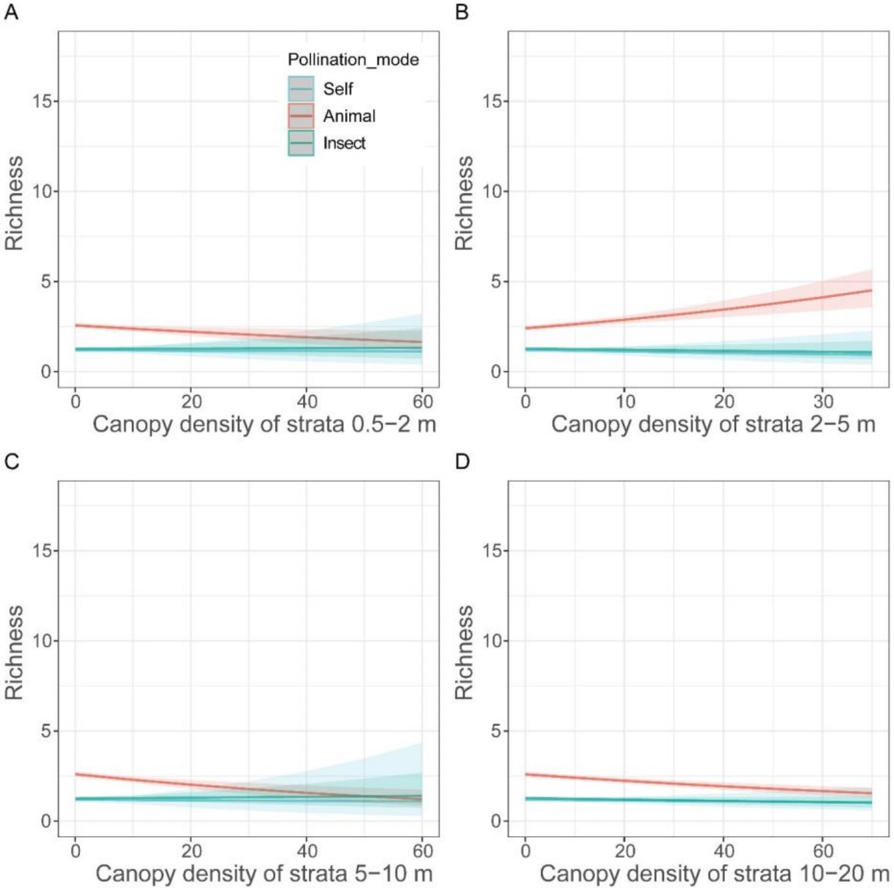
Appendix XII. Responses of richness of all plants with different specialized pollination modes to vegetation structure.



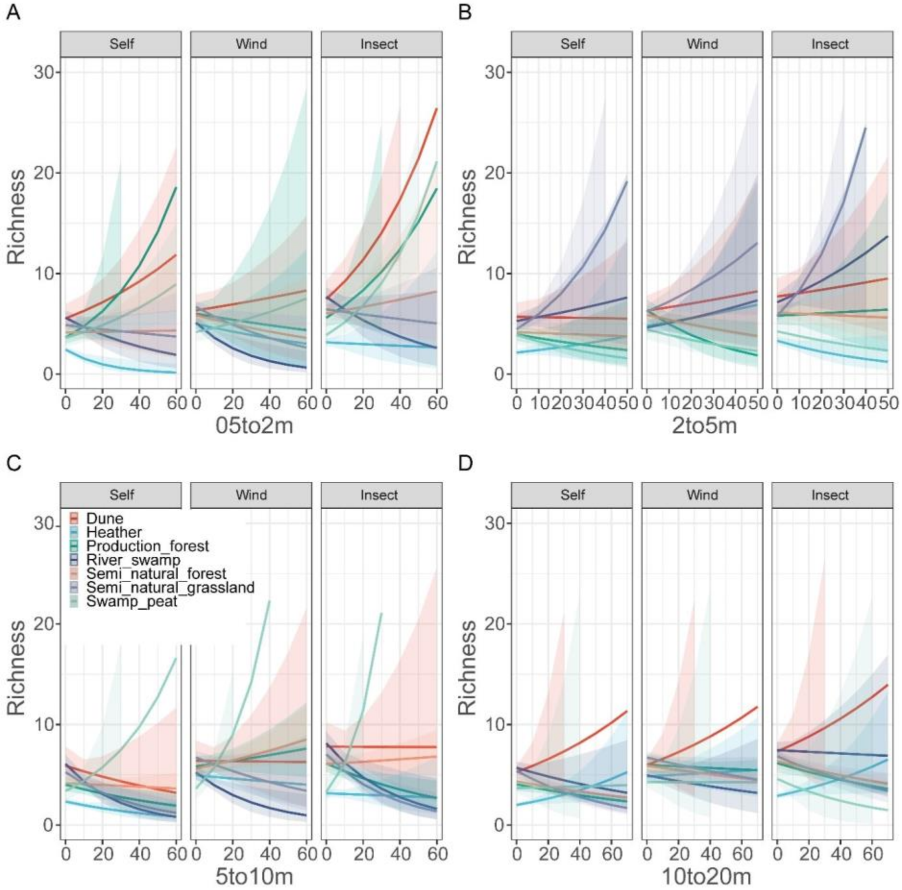
Appendix XIII. Responses of richness of woody plants with different specialized pollination modes to vegetation structure.



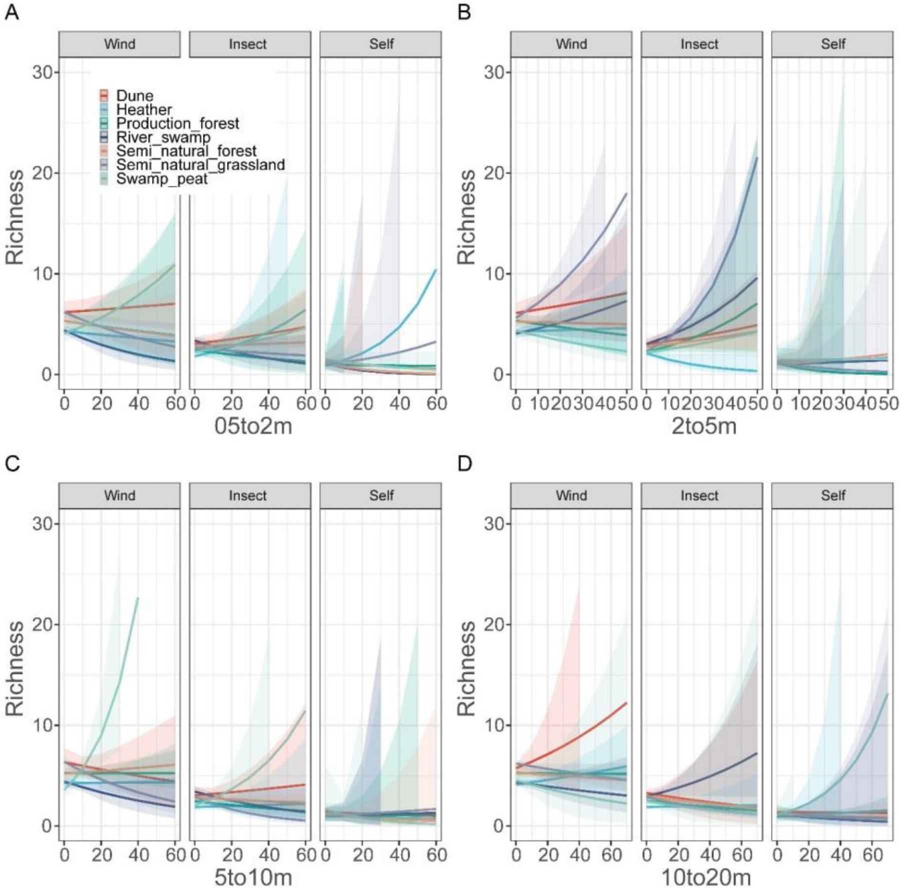
Appendix XIV. Responses of richness of grasses with different specialized pollination modes to vegetation structure.



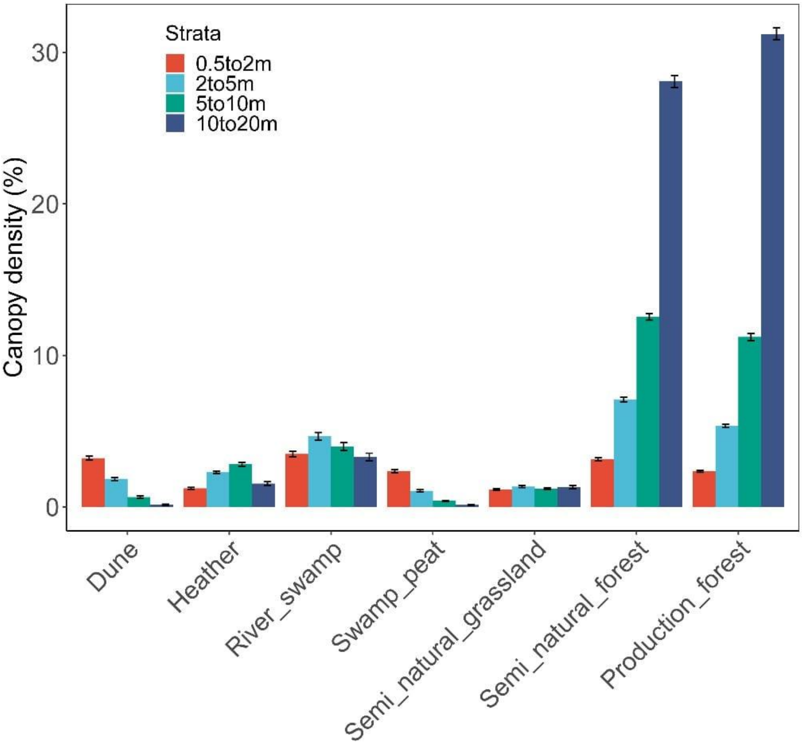
Appendix XV. Responses of richness of herbs with different specialized pollination modes to vegetation structure.



Appendix XVI. Responses of richness of plants with different pollination modes to each variable in the full mode. (A) for a canopy density of 0.5-2 m vegetation stratum. (B) for a canopy density of 2-5 m vegetation stratum. (C) for a canopy density of 5-10 m vegetation stratum. (D) for a canopy density of 10-20 m vegetation stratum.



Appendix XVII. Responses of richness of plants with different specialized pollination modes to each variable in the full mode. (A) for a canopy density of 0.5-2 m vegetation stratum. (B) for a canopy density of 2-5 m vegetation stratum. (C) for a canopy density of 5-10 m vegetation stratum. (D) for a canopy density of 10-20 m vegetation stratum.



Appendix XVIII. Average canopy densities of four vegetation strata in each habitat type.

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Chapter 4

Dutch landscapes are losing insect-pollinated plants

Kaixuan Pan, Leon Marshall, Geert R. de Snoo & Koos Biesmeijer

In revision for Journal of Biogeography

Abstract

Aim: The interruption of plant-pollinator interactions may threaten global plant diversity, food security and ecosystem stability. Recent reports of strong declines of both insects and plants seem to point to insect decline as a driver of plant decline. However, it is still unknown whether these trends are linked and to what extent plant declines are related to insect-pollination, as plants often produce seeds without the need for insect pollinators. In this study, we hypotheses that the decline of pollinators may have shifted our plant communities away from insect-pollination over time.

Location: The Netherlands

Taxon: Pollinated plants

Methods: We combine 625,247 vegetation plot data from 1930 to 2017 and plant traits to assess the changes in occurrences of plants pollinated by different modes.

Results: The proportion of obligately insect-pollinated plants has declined ~10.4% while obligately wind-pollinated plants have increased ~9.6% over the last 87 years. The proportion of facultatively insect-pollinated plants has declined ~6.4% while facultatively wind-pollinated plants have increased ~9.6%. This proportional change reflects an absolute decline in the number of insect-pollinated species and increase in the number of wind-pollinated species over time in the Netherlands.

Main conclusion: In conclusion, Dutch landscapes are losing insect-pollinated plant species, which are being replaced by wind-pollinated species, due to declines in pollination service. Based on our results, we encourage policies to address the conservation of insect pollinators to mitigate the decline of plants.

Significance statement: Studies have reported alarming declines in insect or bee-pollinated plants at national scale. However, it remains unknown whether and to what extent insect-pollinated species have declined in our ecosystem at the community level. Here we show declines in pollinator has shifted natural plant community away from insect-pollination.

Keywords: Temporal trends, Plant diversity, Plant community composition, Plant-insect interaction, Pollination modes, Insect-pollination decline, Natural landscapes

Introduction

Plant-pollinator interactions rate among the most critical relationships in our planet's ecosystems (Potts et al., 2016a; Potts et al., 2016b). Pollinator-dependent plants are an important component of global plant biodiversity and provide humans with 85% of the most important crops (Potts et al., 2010; Huang et al., 2021; Tscharntke, 2021; Dicks et al., 2021; Wei et al., 2021). Evidence suggests that approximately 80% of flowering plants are pollinated by insects, and that half would suffer over 80% reductions in seed production despite the fact that plants can often produce seed by wind or selfing (Ollerton et al., 2011; Rodger et al., 2021).

In parallel, other studies show strong declines in the richness of terrestrial insects (Janzen & Hallwachs, 2021), hoverflies (Hallmann et al., 2021) and butterflies (Warren et al., 2021), in the abundance of terrestrial insects (van Klink et al., 2020), hoverflies(Hallmann et al., 2021) and butterflies (Forister et al., 2021; Warren et al., 2021), and in the biomass of flying insects (Hallmann et al., 2021). This has raised the interest in understanding the role of insects in our ecosystems, in insect-plant interactions and insect conservation (Harvey et al., 2020). Biesmeijer et al. (2006) found evidence of declines in bees and insect-pollinated plants between two periods at the national scale in the Netherlands and the UK. Moreover, bee species decline is linked to loss of their preferred food plants (Scheper et al., 2014); plant species in the diet of declining bumblebee species were themselves declining, in contrast to those in the diet of stable and increasing species (Kleijn & Raemakers, 2008). It remains unclear, however, whether the declines in insects and insect-pollinated plants are linked, and to what extent the relative and absolute occurrence of insect-pollinated plants have shifted in relation to plants pollinated through selfing or by wind in natural ecosystems at the level of plant communities over time.

Here we assess whether the pollination mode of plants (insect, wind, selfing) is correlated with their past and present occurrence in Dutch landscapes, hypothesising that the decline of pollinators may have shifted our plant communities away from insect-pollination. We assume that this shift might be more crucial to obligate outcrossers (Biesmeijer et al., 2006), therefore we analyse obligate (i.e. a species only pollinated by a single mode, Table S1) and facultative (i.e. a species pollinated by more than one mode, Table S1) pollination separately. To adequately demonstrate such a shift, for each group, we evaluate temporal changes in both relative (i.e. proportion) and absolute richness of plants pollinated by different modes at the vegetation plot level by using long-term plot monitoring data of plant assemblages in the Netherlands (Hennekens, 2018). The 625,247 plots are spread over the Netherlands (Figure S1), and they span 87 years (1930 to 2017), with 1,425 native plant species included in the analysis. Some plots have been recorded multiple times (named resampled plots). We use them to assess fixed-site vegetation shifts.

Materials and Methods

Plant plot data

We obtained vegetation plot data representing complete vascular plant species composition across the Netherlands from 1930-2017, from the Dutch Vegetation Database (Hennekens, 2018). Plot sizes vary with habitat types and they reflect those traditionally used by European phytosociology (Westhoff et al., 1978). All spore plants were excluded since they do not reproduce via pollination. In a small number of cases, data are reported for subspecies, but we conducted analyses at the level of taxonomic species, thus trinomials were collapsed to binomials in the dataset before further analyses.

Pollination modes

Data of pollination modes were extracted from Biobase (2003), and included the pollination modes (insect, wind and selfing) of all native Dutch vascular plants. In this study, we used two pollination groups: obligate pollination (i.e. a species only pollinated by one mode) and facultative pollination (i.e. a species pollinated by more than one mode, e.g. a species is pollinated by insect, but also with other modes like wind or selfing as complementary in its pollination service), which represent different pollination strategies. Firstly, pollination modes were classified into insect-pollination, wind-pollination and self-pollination, and all plants were assigned a facultative classification for each of the three pollination modes (Table S1). Facultative pollination mode includes all species and each species may be assigned to one or more than one of the 3 categories (e.g. if a species is both insect and self-pollinated). Obligate pollination includes plants that only exhibit a single pollination mode (i.e. obligate insect-pollination, obligate wind-pollination and obligate self-pollination). Species which exhibit more than one pollination mode (facultative) are excluded in the obligate pollination categorization.

The proportions of plants pollinated by different modes change over time

From 1930 on, all plant plot data was classified into eight time periods: [1930, 1939], [1940, 1949], [1950, 1959], [1960, 1969], [1970, 1979], [1980, 1989], [1990, 1999], [2000-2017]. In each time period, for either facultative or obligate group, we calculated the proportion of plant species pollinated by each of three modes (P_i) in each plot,

$$P_i = N_i/N$$

N_i is the number of species pollinated by mode *i* (i.e. insect, wind or selfing). *N* is the sum of the number of insect, wind and self-pollinated species in each plot.

We used a generalized linear model (GLM) with a logit distribution to assess temporal trends in the proportion of each pollination mode (P_i) over the 8 time periods. Since we only measure the proportion of each pollination mode in each plot, we excluded the effect of plot sizes and locations. The final GLM formula is: The proportion of plant species pollinated by each mode ~ Time period*Pollination mode. These analyses were conducted in R version 4.0.3 (R Core Team, 2020) using the glmmTMB (Brooks et al., 2017) packages.

The richness of plants pollinated by different modes change over time

In each of the eight time periods, we calculated the species richness of each pollination mode in each plot. Due to the species-area relationship, we only kept plots which included sample size information, which will be treated as a random effect in the statistical models.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution, which deals with overdispersion in a Poisson distribution, to assess temporal trends in the richness of each pollination mode. The plot size was treated as a random effect in the model. The final GLMM formula is: The richness of plant species pollinated by each mode ~ Time period*Pollination mode + (1|plot size). Analyses were conducted in R version 4.0.3 (R Core Team, 2020) using the glmmTMB (Brooks et al., 2017) packages.

Comparison of the Ellenberg values (nitrogen) of plants pollinated by different modes

The Ellenberg values were obtained from JUICE (https://www.sci.muni.cz/botany/juice/). Ellenberg values were assigned to species in our study. Finally, we got 1,071 species with Ellenberg values from JUICE. Tata was tested with a Kruskal-Wallis test and a post hoc multiple comparison test.

Results and Discussion

To disentangle the percentage changes of pollination modes in vegetation communities, we performed generalized linear models with a logit distribution. Results show a shift at community level of -1.3% for obligately insect-pollinated plants and +1.2% increase for obligately wind-pollinated plants per decade (Figure 1 a-b). Compared to obligate insect-pollination, we found a weaker but still significant decline in the occurrence of facultative insect-pollination which we estimated to be decreasing by ~0.8% per decade (Figure 1 c-d), although these species are less vulnerable to declines in insect-pollination services (Aguilar et al., 2006). The proportion of obligately self-pollinated plant species increased (~0.1% per decade), but facultatively self-pollinated plants decreased (~0.5% per decade) over time (Figure 1), due to the fact that most insect-pollinated plants are also facultative selfers. Our fixed-site analysis based on plots recorded multiple times shows the same trend (Figure S2-3).

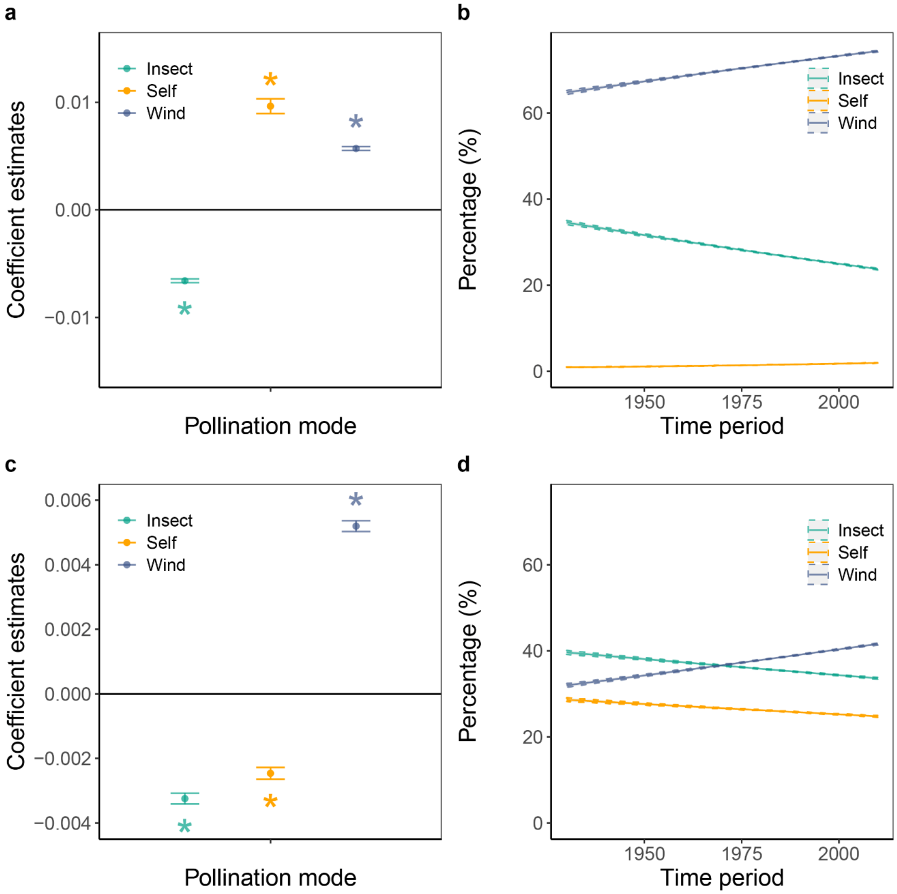

Figure 1 Shifts in the occurrence of pollination modes over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) for obligate pollination, and model coefficient estimates (± s.e. indicated by bars) (c) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (d) for facultative pollination, both from the generalized linear model (GLM) with a logit distribution (Table S2). In a and c, asterisks mean statistically significant ($P < 0.05$).

To find out whether the shift of pollination modes in vegetation communities is due to changes in plant richness, we performed generalized linear mixed models with a negative binomial distribution. We show that, on average, vegetation plots in the Netherlands have lost three species during the 87 year period (Figure S7). Insect-pollinated plants account for most of the loss, with wind-pollinated plants showing a slight increase in richness over time (Figure 2 c-d). Plants that are obligate insect, wind or self-pollinated show similar patterns, with a gain in obligate wind pollinators (mostly grasses) and loss of insect-pollinated species, adding up to a slight increase of plants with obligate pollination modes overall (Figure 2 a-b, Figure S6). The decreasing trend for insect-pollinated species is consistent with previous findings from NW Europe (Biesmeijer et al., 2006; Carvalheiro et al., 2013; Goulson et al., 2015) and may result from a deficiency of insect pollinators (Lennartsson, 2002; Pauw & Hawkins, 2011). In summary, Dutch landscapes are losing insect-pollinated plant species, which are being replaced by wind-pollinated species. This is probably also happening in other areas of the world where pollinating insects are also declining. Since insect-pollinated plants represent ~80% of the earth's flowering plants (Ollerton et al., 2011; Rodger et al., 2021), such a loss may greatly affect the future of our ecosystems and the services they provide. Results from analysis based on resampled plots (fixed sites) also show a great decline in facultative insect-pollination and self-pollination while increase in facultative and obligate wind-pollination (Figure S4-5, 8-9).

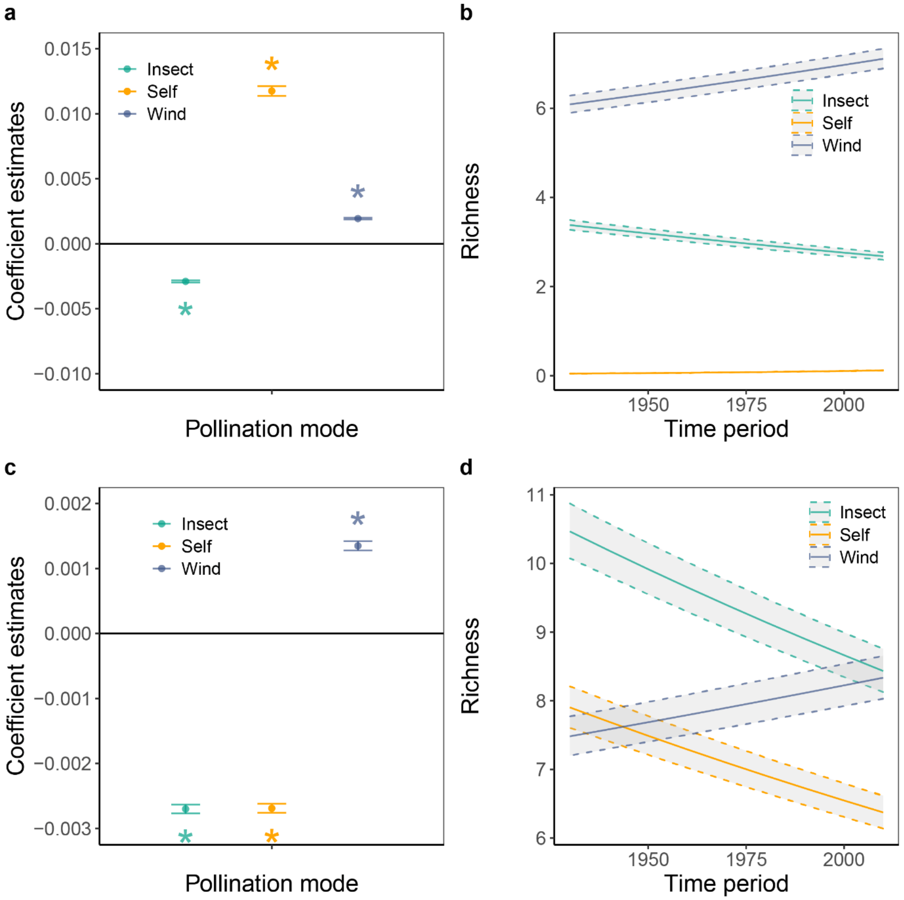

Figure 2 Shifts in the richness of pollination modes over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) for the obligate pollination, and model coefficient estimates (± s.e. indicated by bars) (c) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (d) for facultative pollination, both from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S3). In a and c, asterisks mean statistically significant (*P* < 0.05).

Our estimates of 1.3% decline in obligate insect-pollinated plants and 0.8% decline in facultative insect-pollinated plants per decade in the Netherlands reveal that plant communities have shifted away from insect-pollination in the last 87 years. This estimated loss rate fills the critical knowledge gap of quantifying the extent of decline in insect-pollination at a level of plant communities (vegetation plot level) compared to previous findings (Biesmeijer et al., 2006), where bees and insect-pollinated plants declined at the national scale between two periods.

Such a decline raises concern given the critical role of plant-pollinator networks for ecosystem functioning. Changes in plants within these networks may reflect the declines observed for some bee and hoverfly pollinators (Potts et al., 2010; Dicks et al., 2021). Even though a correlative study such as ours cannot definitively assign causality, the confluence of findings from controlled experiments of changes in plant-pollinator interactions over different period (Lennartsson, 2002), historical pollination rates from specimen (Pauw & Hawkins, 2011), and species occurrence tracked through time (Biesmeijer et al., 2006), all suggest that the decline of insect pollinators alter plant community composition. Moreover, the absence of a correlation between plant pollination modes and their Ellenberg values for nitrogen indicates that the observed decline of insect-pollinated plants is not simply explained by nitrogen change tolerance of plants (Figure 3-4). Carvalheiro et al. (2020) found a greater decline in richness of plants that are dependent on pollinators and prefer nutrient-rich environments than plants that are not dependent on pollinators and prefer nutrient-rich environments, which supports our conclusion.

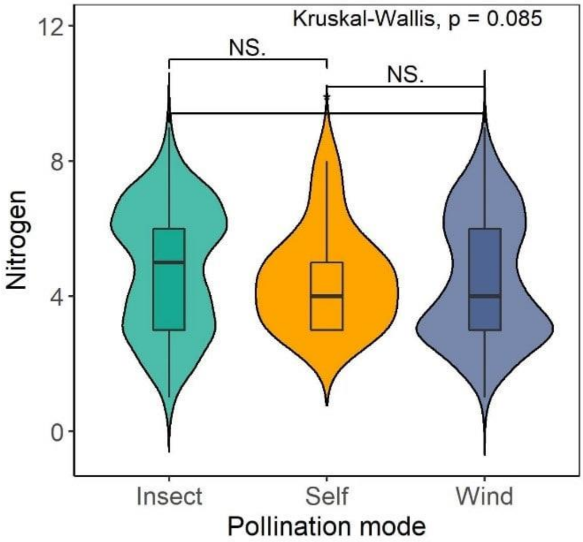

Figure 3 Comparison of the Ellenberg values (nitrogen) of plants obligately pollinated by different modes (n = 527, d.f. = 2, $\chi 2$ = 4.942). Boxplots show the range of Ellenberg values calculated across 1,071 plant species. Upper and lower box bounds represent the

75th and 25th percentiles, respectively, and the horizontal line represents the median value. Observed values are shown with asterisks. The database of Ellenberg values is from JUICE (https://www.sci.muni.cz/botany/juice/).

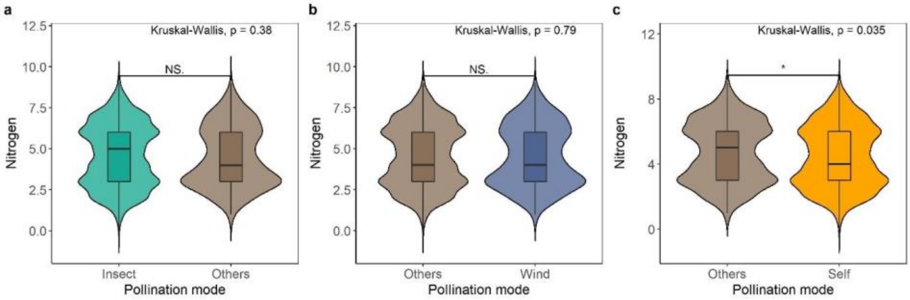

Figure 4 Comparison of the Ellenberg values (nitrogen) of plants facultatively pollinated by different modes. a, nitrogen values between facultive insect-pollination and other pollination modes (n = 1,071, d.f. = 1, χ2 = 0.785). b, nitrogen values between facultive wind-pollination and other pollination modes (n = 1,071, d.f. = 1, χ2 = 0.069). c, nitrogen values between facultive self-pollination and other pollination modes (n = 1,071, d.f. = 1, χ2 = 4.449). Boxplots show the range of Ellenberg values calculated across 1,071 plant species. Upper and lower box bounds represent the 75th and 25th percentiles, respectively, and the horizontal line represents the median value. Observed values are shown with asterisks. The database of Ellenberg values is from JUICE (https://www.sci.muni.cz/botany/juice/).

These results suggest that insect-pollination is important for plant persistence and for the composition of plant communities. Without mitigation efforts, declines of insect-pollinated plants and their pollinators may continue in natural communities. This implies that policies should take effective strategies (e.g. habitat protection and reduce chemical pollution (Stefanescu et al., 2004; Goulson et al., 2015; Warren et al., 2021; Aguirre-Gutiérrez et al., 2017)) to protect insect pollinators and mitigate declines in insect-pollinated plants. An inspiration for this could be the IPBES pollinator report (Potts et al., 2016b), the EU Pollinator Initiative (https://ec.europa.eu/environment/nature/conservation/species/pollinators/policy_en.htm) and other initiatives such as the Coalition of the Willing on Pollinators (https://promotepollinators.org/) and the Dutch Delta Plan for Biodiversity Recovery (https://www.samenvoorbiodiversiteit.nl/themas).

Conflict of Interest

The authors declare no competing interests.

Data availability

Plot data for analysis during this study is from public domain resource, which is indicated in this article. Data of plant trait will be made available in the Zenodo upon acceptance for publication.

Code availability

The R code used in this study will be made available in the Zenodo upon acceptance for publication.

References

Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. (2006). Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.*, **9**, 968–980.

Aguirre-Gutiérrez, J., Kissling, W.D., Biesmeijer, J.C., WallisDeVries, M.F., Reemer, M. & Carvalheiro, L.G. (2017). Historical changes in the importance of climate and land use as determinants of Dutch pollinator distributions. *J. Biogeogr.*, **44**, 696–707.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Biobase (2003). Centraal Bureau voor de Statistiek, Voorburg/Heerlen, The.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M. & Bolker, B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *RJ*, **9**, 378–400.

Carvalheiro, L.G., Biesmeijer, J.C., Franzén, M., Aguirre-Gutiérrez, J., Garibaldi, L.A., Helm, A., Michez, D., Pöyry, J., Reemer, M., Schweiger, O., van Leon den, B., WallisDeVries, M.F. & Kunin, W.E. (2020). Soil eutrophication shaped the composition of pollinator assemblages during the past century. *Ecography*, **43**, 209–221.

Carvalheiro, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R., Groom, Q., Hennekens, S., van Landuyt, W., Maes, D., van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.P.M., Schaminée, J., WallisDeVries, M.F. & Biesmeijer, J.C. (2013). Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecol. Lett.*, **16**, 870–878.

Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J. & Potts, S.G.

(2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.*, **5**, 1453–1461.

Forister, M.L., Halsch, C.A., Nice, C.C., Fordyce, J.A., Dilts, T.E., Oliver, J.C., Prudic, K.L., Shapiro, A.M., Wilson, J.K. & Glassberg, J. (2021). Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. *Science*, **371**, 1042–1045.

Goulson, D., Nicholls, E., Botías, C. & Rotheray, E.L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, **347**, 1255957.

Hallmann, C.A., Ssymank, A., Sorg, M., Kroon, H. de & Jongejans, E. (2021). Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. *Proc. Natl. Acad. Sci. U.S.A.*, **118**.

Harvey, J.A., Heinen, R., Armbrecht, I., Basset, Y., Baxter-Gilbert, J.H., Bezemer, T.M., Böhm, M., Bommarco, R., Borges, P.A.V., Cardoso, P., Clausnitzer, V., Cornelisse, T., Crone, E.E., Dicke, M., Dijkstra, K.-D.B., Dyer, L., Ellers, J., Fartmann, T., Forister, M.L., Furlong, M.J., Garcia-Aguayo, A., Gerlach, J., Gols, R., Goulson, D., Habel, J.-C., Haddad, N.M., Hallmann, C.A., Henriques, S., Herberstein, M.E., Hochkirch, A., Hughes, A.C., Jepsen, S., Jones, T.H., Kaydan, B.M., Kleijn, D., Klein, A.-M., Latty, T., Leather, S.R., Lewis, S.M., Lister, B.C., Losey, J.E., Lowe, E.C., Macadam, C.R., Montoya-Lerma, J., Nagano, C.D., Ogan, S., Orr, M.C., Painting, C.J., Pham, T.-H., Potts, S.G., Rauf, A., Roslin, T.L., Samways, M.J., Sanchez-Bayo, F., Sar, S.A., Schultz, C.B., Soares, A.O., Thancharoen, A., Tscharntke, T., Tylianakis, J.M., Umbers, K.D.L., Vet, L.E.M., Visser, M.E., Vujic, A., Wagner, D.L., WallisDeVries, M.F., Westphal, C., White, T.E., Wilkins, V.L., Williams, P.H., Wyckhuys, K.A.G., Zhu, Z.-R. & Kroon, H. de (2020). International scientists formulate a roadmap for insect conservation and recovery. *Nat. Ecol. Evol.*, **4**, 174–176.

Hennekens, S. (2018). Dutch Vegetation Database (LVD). *v1.6. Alterra, Wageningen UR. Dataset/Samplingevent.*

Huang, H., Tu, C. & D'Odorico, P. (2021). Ecosystem complexity enhances the resilience of plant-pollinator systems. *One Earth*, **4**, 1286–1296.

Janzen, D.H. & Hallwachs, W. (2021). To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. *Proc. Natl. Acad. Sci. U.S.A.*, **118**.

Kleijn, D. & Raemakers, I. (2008). A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology*, **89**, 1811–1823.

Lennartsson, T. (2002). Extinction thresholds and disrupted plant–pollinator interactions in fragmented plant populations. *Ecology*, **83**, 3060–3072.

Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.

Pauw, A. & Hawkins, J.A. (2011). Reconstruction of historical pollination rates reveals linked declines of pollinators and plants. *Oikos*, **120**, 344–349.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.*, **25**, 345–353.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J. & Vanbergen, A.J. (2016a).

Safeguarding pollinators and their values to human well-being. *Nature,* **540**, 220–229.

Potts, S.G., Ngo, H.T., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J. & Vanbergen, A. (2016b). The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production.

R Core Team (R Foundation for Statistical Computing, 2020). *R: A language and environment for statistical computing*.

Rodger, J.G., Bennett, J.M., Razanajatovo, M., Knight, T.M., van Kleunen, M., Ashman, T.-L., Steets, J.A., Hui, C., Arceo-Gómez, G., Burd, M., Burkle, L.A., Burns, J.H., Durka, W., Freitas, L., Kemp, J.E., Li, J., Pauw, A., Vamosi, J.C., Wolowski, M., Xia, J. & Ellis, A.G. (2021). Widespread vulnerability of flowering plant seed production to pollinator declines. *Sci. Adv.*, **7**, eabd3524.

Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T.J., Schaminée, J.H.J., Siepel, H. & Kleijn, D. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proc. Natl. Acad. Sci. U.S.A.*, **111**, 17552–17557.

Stefanescu, C., Herrando, S. & Páramo, F. (2004). Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *J. Biogeogr.*, **31**, 905–915.

Tscharntke, T. (2021). Disrupting plant-pollinator systems endangers food security. *One Earth*, **4**, 1217–1219.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A. & Chase, J.M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, **368**, 417–420.

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D. & Ellis, S. (2021). The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proc. Natl. Acad. Sci. U.S.A.*, **118**.

Wei, N., Kaczorowski, R.L., Arceo-Gómez, G., O'Neill, E.M., Hayes, R.A. & Ashman, T.-L. (2021). Pollinators contribute to the maintenance of flowering plant diversity. *Nature*, **597**, 688–692.

Westhoff V, Van der Maarel E, Whittaker RH (1978). *Classification of plant communities.* The Hague.

Biosketch

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Author contributions

K.P., G.R. de S. and K.B. conceived the idea and designed the study. L.M. and K.B. developed the idea of results validating by resampled plots. K.B. provided the trait data. K.P. conducted all analysis. L.M. checked the model developed by K.P. K.P. wrote the first manuscript draft. K.B. and G.R. de S. further contributed to the interpretation of results and K.B. contributed to the writing of discussion in the final manuscript. All authors commented on and edited the manuscript. G.R. de S. and K.B. jointly supervised the study.

Supplementary Information

Temporal trends in the proportions of plants pollinated by different modes in resampled grid cells at 1 km resolution in the same location (fixed sites) and recorded in different years

To further support our analysis and test whether observed changes in the proportion of pollination modes is consistent at the site scale, we selected plots with georeferenced information and matched them with grid cells at 1 km resolution covering the whole Netherlands. Only grid cells that were sampled at multiple time points were retained (resampled grid cells). Since there might be more than one plot in each grid cell, we first calculate the average number of each pollination mode AN_i in each grid cell. Then, at each grid cell in each year, the proportion of each pollination mode (GP_i) in each grid cell was calculated

$$GP_i = AN_i / \sum AN_i$$

We used a generalized linear mixed model (GLMM) with a logit distribution to assess temporal trends in the proportion of each pollination mode. The grid cell location was treated as a random effect in the model. The final GLMM formula is: The proportion of plant species pollinated by each mode ~ Year*Pollination mode + (1|grid cell location). Analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

Temporal trends in the richness of plants pollinated by different modes in resampled plots with the same size and within the same grid cell at 1 km resolution (fixed sites) and recorded in different years

In each grid cell at 1 km resolution, for each plot size category, we kept a set of plots that shared the sample plot size and were recorded in multiple years. Those plot size categories that were only recorded once were excluded. For each set of resampled plots, we calculated the species richness of each pollination mode in each plot.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to assess temporal trends in the richness of each pollination mode. The plot size and location were treated as random effects in the model. The final GLMM formula is: The richness of plant species pollinated by each mode ~ Year*Pollination mode + (1|plot size) + (1|plot location). These analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

Temporal trends in the total richness of obligate and facultative pollination groups

To test whether the total richness of species which exhibit multiple pollination modes (facultative) and exhibit only one mode (obligate) in vegetation plots change over time, in each of the eight time periods defined ([1930, 1939], [1940, 1949], [1950, 1959], [1960, 1969], [1970, 1979], [1980, 1989], [1990, 1999], [2000-2017]), we calculated the total species richness of facultative or obligate pollination plants in each plot. Due to the species-area relationship, we only kept plots which included sample size information, which will be treated as a random effect in the statistical models.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to assess temporal trends in the total richness. The plot size was treated as a random effect in the model. The final GLMM formula is: The total richness ~ Time period + (1|plot size). These analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

Temporal trends in the total richness of pollination plants in resampled plots with the same size and within the same grid cell at 1 km resolution (fixed sites) and recorded in different years

In each grid cell at 1 km resolution, for each plot size category, we kept a set of plots that shared the sample plot size and were recorded in multiple years. Those plot size categories that were only recorded once were excluded. For each set of resampled plots, we calculated the total species richness of facultative or obligate pollination plants in each plot.

We used a generalized linear mixed model (GLMM) with a negative binomial distribution to assess temporal trends in the total richness. The plot size and location were treated as random effects in the model. The final GLMM formula is: The total richness ~ Year + (1|plot size) + (1|plot location). These analyses were conducted in R version 4.0.3 (R Core Team, R Foundation for Statistical Computing, 2020) using the glmmTMB (Brooks *et al.*, 2017) packages.

Table S1 Number of plant species with different pollination modes included in the analysis.

Group	Pollination_mode	Freq	Definition
Obligate	Insect	411	all plants only with insects as their pollination
Obligate	Wind	310	all plants only with wind as their pollination
Obligate	Self	32	all plants only with selfing as their pollination
Facultative	Insect	1055	all plants with insect as one of their pollination modes
Facultative	Wind	387	all plants with wind as one of their pollination modes
Facultative	Self	674	all plants with selfing as one of their pollination modes

Table S2 Significance of the factor year in GLMs testing effects on the proportion of plants pollinated by different modes based on all plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Proportions of obligate plants ~ year*pollination mode (binomial distribution) : n = 1,857,282;	Intercept (insect)	33.93	<0.001	12.09 ± 0.356
	Year (insect)	-36.74	<0.001	-0.007 ± 0
	Intercept (wind)	-29.618	<0.001	-10.397 ± 0.351
	Year (wind)	32.252	<0.001	0.006 ± 0
	Intercept (self)	-17.04	<0.001	-23.292 ± 1.367
	Year (self)	14.0153	<0.001	0.01 ± 0.001
Proportions of facultative plants ~ year*pollination mode (binomial distribution) : n = 1,875,741;	Intercept (insect)	17.6243	<0.001	5.841 ± 0.331
	Year (insect)	-19.438	<0.001	-0.003 ± 0
	Intercept (wind)	-32.627	<0.001	-10.784 ± 0.331
	Year (wind)	31.2261	<0.001	0.005 ± 0
	Intercept (self)	10.6327	<0.001	3.837 ± 0.361
	Year (self)	-13.541	<0.001	-0.002 ± 0

Table S3 Significance of the fixed factor year in GLMMs testing effects on the richness of plants pollinated by different modes based on all plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligate plants ~ year*pollination mode (negative binomial distribution) : n = 1,313,091;	Intercept (insect)	43.0383	<0.001	6.801 ± 0.158
	Year (insect)	-36.589	<0.001	-0.003 ± 0
	Intercept (wind)	-14.487	<0.001	-1.938 ± 0.134
	Year (wind)	29.0493	<0.001	0.002 ± 0
	Intercept (self)	-34.38	<0.001	-25.762 ± 0.749
	Year (self)	31.2262	<0.001	0.012 ± 0
Richness of facultative plants ~ year*pollination mode (negative binomial distribution) : n = 1,324,680;	Intercept (insect)	56.1556	<0.001	7.558 ± 0.135
	Year (insect)	-40.29	<0.001	-0.003 ± 0
	Intercept (wind)	-4.1996	<0.001	-0.592 ± 0.141
	Year (wind)	19.208	<0.001	0.001 ± 0
	Intercept (self)	51.5003	<0.001	7.257 ± 0.141
	Year (self)	-38.296	<0.001	-0.003 ± 0

Table S4 Significance of the fixed factor year in GLMMs testing effects on the proportion of plants pollinated by different modes based on resampled plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Proportions of obligate plants ~ year*pollination mode (binomial distribution) : n = 364,683;	Intercept	15.1599	<0.001	10.814 ± 0.713
	Year (insect)	-16.446	<0.001	-0.006 ± 0
		-14.106	<0.001	-9.986 ± 0.708
	Year: wind	15.333	<0.001	0.005 ± 0
		-5.6421	<0.001	-20.29 ± 3.596
	Year: self	4.36778	<0.001	0.008 ± 0.002
Proportions of facultative plants ~ year*pollination mode (binomial distribution) : n = 366,669;	Intercept (insect)	7.76959	<0.001	5.254 ± 0.676
	Year (insect)	-8.5825	<0.001	-0.003 ± 0
	Intercept (wind)	-15.917	<0.001	-11.004 ± 0.691
	Year (wind)	15.1676	<0.001	0.005 ± 0
	Intercept (self)	5.58468	<0.001	4.121 ± 0.738
	Year (self)	-6.9958	<0.001	-0.003 ± 0

Table S5 Significance of the fixed factor year in GLMMs testing effects on the richness of plants pollinated by different modes based on resampled plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligate plants ~ year*pollination mode (negative binomial distribution) : n = 382,122;	Intercept (insect)	9.6639	<0.001	2.68 ± 0.277
	Year (insect)	-6.2071	<0.001	-0.001 ± 0
	Intercept (wind)	-22.701	<0.001	-5.371 ± 0.237
	Year (wind)	30.3959	<0.001	0.004 ± 0
	Intercept (self)	-7.0754	<0.001	-9.477 ± 1.339
	Year (self)	5.13044	<0.001	0.003 ± 0.001
Richness of facultative plants ~ year*pollination mode (negative binomial distribution) : n = 384,525;	Intercept	21.624	<0.001	4.7 ± 0.217
	Year (insect)	-12.37	<0.001	-0.001 ± 0
		-27.246	<0.001	-6.267 ± 0.23
	Year: wind	35.8696	<0.001	0.004 ± 0
		25.202	<0.001	5.784 ± 0.23
	Year: self	-17.783	<0.001	-0.002 ± 0

Table S6 Significance of the factor year in GLMMs testing effects on the total richness of pollinated plants based on all plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligately pollinated plants ~ year (negative binomial distribution) : n = 437,697;	Intercept	12.47	<0.001	1.511 ± 0.121
	Year	6.14	<0.001	0 ± 0
Richness of facultatively pollinated plants ~ year (negative binomial distribution) : n = 441,560;	Intercept	44.52	<0.001	5.935 ± 0.133
	Year	-20.94	<0.001	0.001 ± 0

Table S7 Significance of the fixed factor year in GLMMs testing effects on the total richness of pollinated plants based on resampled plots.

Model description	**Fixed effects**	**Z value**	***P* (two-sided)**	**Coefficients ± SE**
Richness of obligately pollinated plants ~ year (negative binomial distribution) : n = 127,374;	Intercept	-7.4	<0.001	-1.634 ± 0.221
	Year	17.18	<0.001	0.002 ± 0
Richness of facultatively pollinated plants ~ year (negative binomial distribution) : n = 128,175;	Intercept	13.529	<0.001	3.246 ± 0.24
	Year	-0.986	0.324	0 ± 0

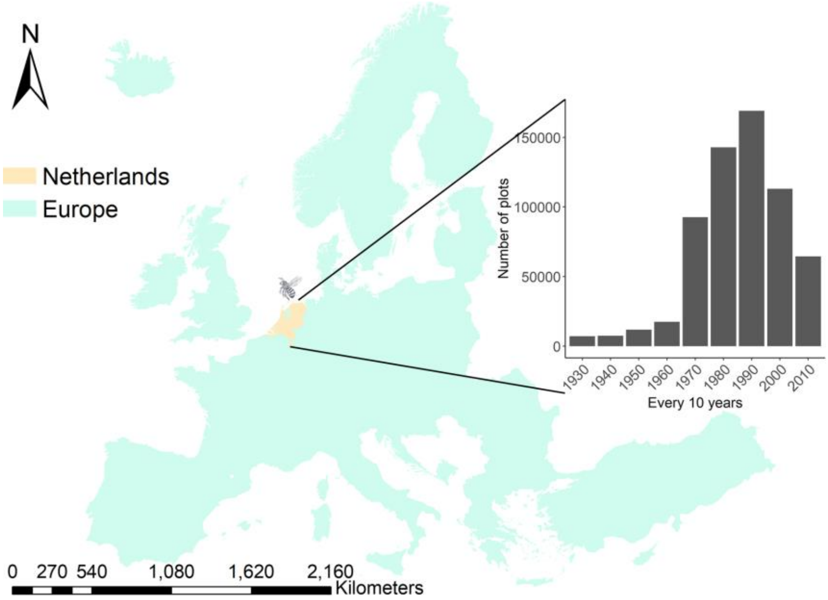

Figure S1 Numbers of vegetation plots over time in the Netherlands.

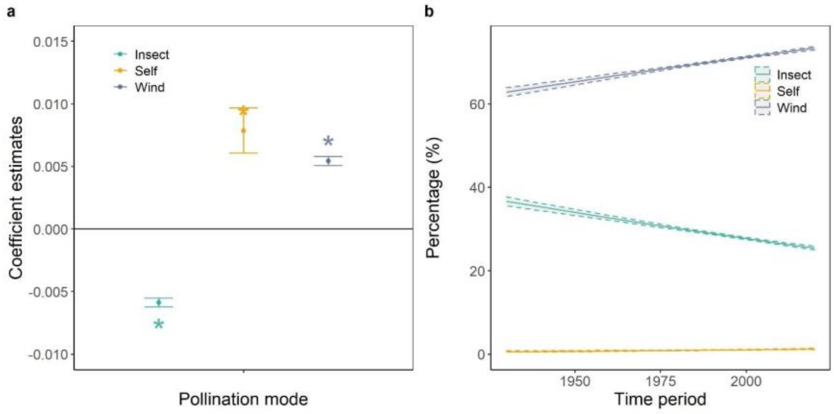

Figure S2 Shifts in the occurrence of obligate pollination modes (obligate insect-, wind- and self-pollination) in resampled grid cells over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a logit distribution (Table S4). In a, asterisks mean statistically significant ($P < 0.05$).

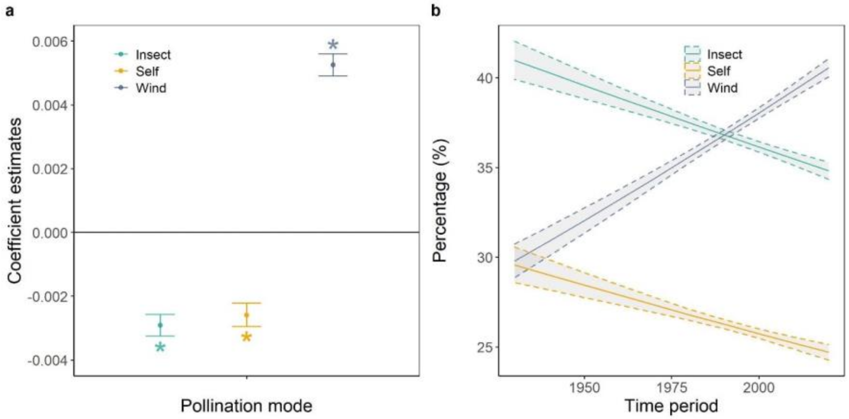

Figure S3 Shifts in the occurrence of facultative pollination modes (facultative insect-, wind- and self-pollination) in resampled grid cells over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a logit distribution (Table S4). In a, asterisks mean statistically significant ($P < 0.05$).

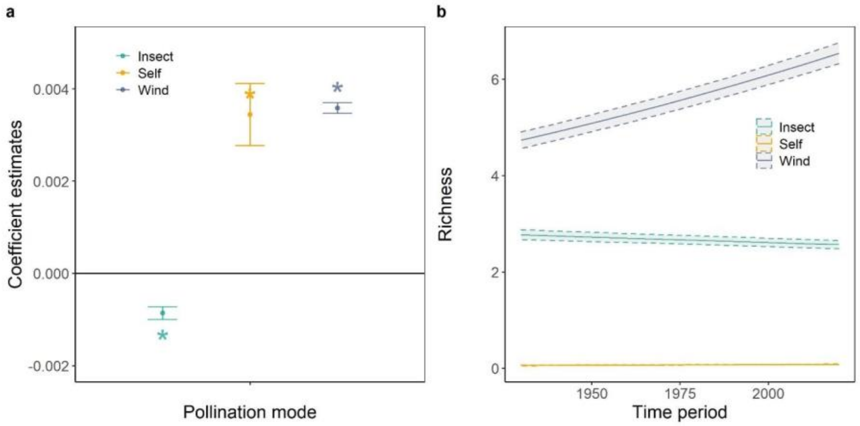

Figure S4 Shifts in the richness of obligate pollination modes in resampled plots over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S5). In a, asterisks mean statistically significant (*P* < 0.05).

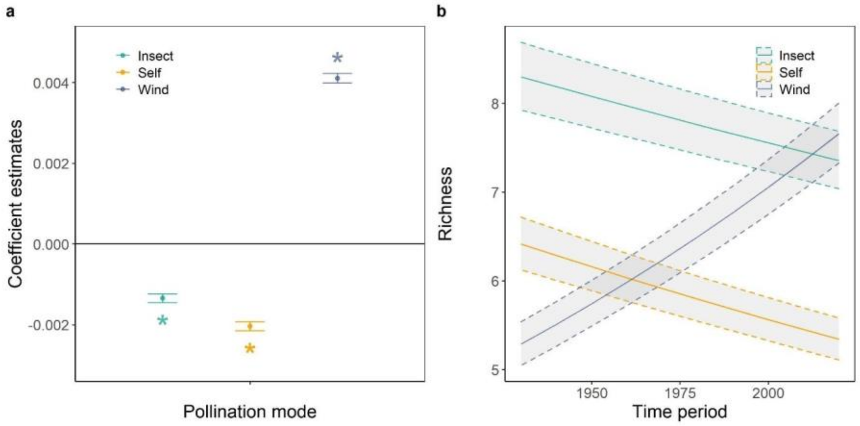

Figure S5 Shifts in the richness of facultative pollination modes in resampled plots over time. Given are model coefficient estimates (± s.e. indicated by bars) (a) and best fits with solid lines indicating estimated changes and dashed lines indicating 95% CIs (b) from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S5). In a, asterisks mean statistically significant (*P* < 0.05).

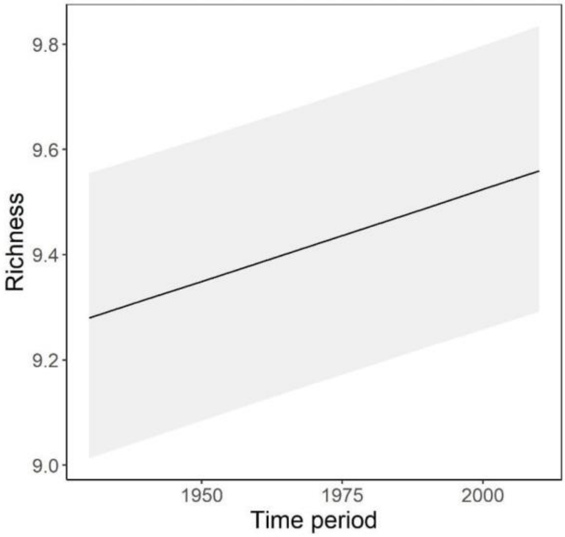

Figure S6 The total richness of three obligate pollination modes (obligate insect-, wind- and self-pollination) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S6).

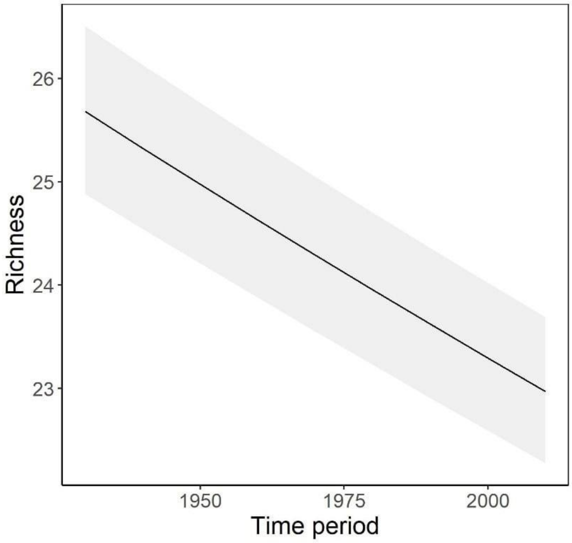

Figure S7 The total richness of three facultative pollination modes (facultative insect, wind and self) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S6).

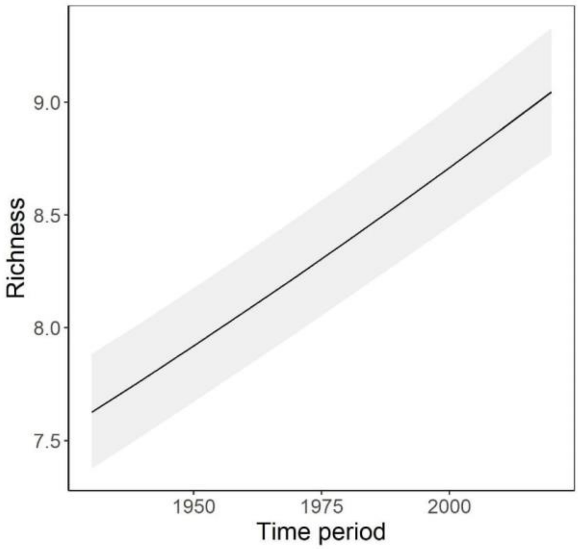

Figure S8 The total richness of three obligate pollination modes (obligate insect-, wind- and self-pollination) in resampled plots (same location but recorded in different years) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S7).

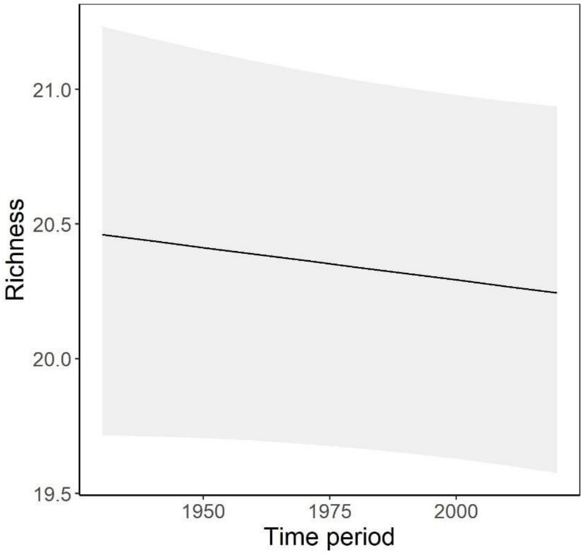

Figure S9 The total richness of three facultative pollination modes (facultative insect, wind and self) in resampled plots (same location but recorded in different years) respond to time from the generalized linear mixed model (GLMM) with a negative binomial distribution (Table S7).

References

R Core Team (R Foundation for Statistical Computing, 2020). *R: A language and environment for statistical computing*.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M. & Bolker, B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *RJ*, **9**, 378–400.

Chapter 5

Plant conservation needs more than natural and protected areas

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Abstract

Decision-makers increasingly seek scientific guidance for their investment in biodiversity conservation, but questions remain on the effectiveness of protected areas and the role of different land-use types in species conservation at different scales. Using data from 19,477 sites, we assessed plant diversity in three main land-use types (natural, rural and urban habitats) and the level of nature protection (being part of Netherlands' Nature Network, Nature 2000 or not). Our results support protected areas and natural habitats as important refugees due to the highest gamma diversity. Protected areas and natural habitats sustain a high α-diversity of threatened and rare species, while unprotected areas and urban habitats sustain a high α-diversity of total plant species and native species across different scales. Our research supports the idea of valuing protected areas and natural habitats for species conservation, but also emphasizes the importance of unprotected areas and urban habitats as complementary methods for preserving biodiversity.

Introduction

Biodiversity is fundamental to the functioning of Earth's ecosystems, and it provides humans with food, goods, clean water, suitable climate and many other ecosystem services (IPBES, 2019, 2022). However, we are currently experiencing what has been termed the sixth mass extinction (Ceballos *et al.*, 2015), with up to half a million species under imminent threat of extinction within a few decades (Ceballos *et al.*, 2015; Vos *et al.*, 2015; Johnson *et al.*, 2017). Accelerating human impacts in the anthropocene are reshaping Earth's ecosystems (IPBES, 2019, 2022). The abundance (Dornelas *et al.*, 2019; Daskalova *et al.*, 2020), richness (Baeten *et al.*, 2010; Vellend *et al.*, 2013; Dornelas *et al.*, 2014) and composition (Dornelas *et al.*, 2014) of biodiversity all over the world is being altered due to multiple drivers all associated with human activity, e.g. habitat conversion, climate change and nitrogen deposition (Sala *et al.*, 2000; Brook *et al.*, 2008; Cusack *et al.*, 2016; Schulte To Bühne *et al.*, 2021). It remains a question whether and how we can conserve biodiversity in a human-dominated world.

The traditional approach to conserve biodiversity is to put land, particularly the most intact natural areas or biodiversity hotspots, under protection (Brooks *et al.*, 2006; Watson *et al.*, 2016; Veach *et al.*, 2017; Watson *et al.*, 2018; Wintle *et al.*, 2019). Ambitious policy targets include protected area targets of 30% of the planet by 2030 (Dinerstein *et al.*, 2019) or even half of the terrestrial biota by 2050 (Locke, 2013; Dinerstein *et al.*, 2017; Watson & Venter, 2017). However, given the failure of the 2011 - 2020 strategy of the CBD (Visconti *et al.*, 2019; Hirsch *et al.*, 2020) and conflict between species conservation and economy development (Brockington & Wilkie, 2015), it seems difficult to halt or even reverse the current trends of species decline by restricting conservation efforts to the protection of intact natural areas (Leclère *et al.*, 2020; Obura *et al.*, 2021). Besides, there is no assessment on whether these protected areas alone can sustain viable populations of all species of conservation concern. In fact, unprotected (natural) areas, i.e. areas not part of a nature protection regime, may also play an important role in biodiversity conservation.

Natural habitats are often considered as the best areas for species conservation as they (mostly) lack major human disturbance, and includes the original environments of many species (Ridder, 2007; Bawa *et al.*, 2020; Díaz *et al.*, 2020). However, natural habitats only account for ~23% of the terrestrial habitat (Watson *et al.*, 2018) with 2-3% being ecologically intact (Plumptre *et al.*, 2021) and a minority of species being endemic to natural habitats (18% of plants and 10% of terrestrial vertebrates) (Mittermeier *et al.*, 2003). The percentage of natural habitats will continue to decline with human activities leading to their conversion to other land-uses, e.g. agriculture, infrastructure, industry and housing. Others suggest, however, that agricultural and urban habitats may be just as important as natural habitats for biodiversity conservation (Li *et al.*, 2020; Lomba *et al.*, 2020; Turo & Gardiner, 2020; Uchida *et al.*, 2021).

Agricultural land makes up about a third of the Earth's terrestrial surface (Li *et al.*, 2020; Lomba *et al.*, 2020) and is considered to be a major direct driver of Anthropocene biodiversity loss (IPBES, 2019, 2022). However, agricultural practices are not detrimental to all species everywhere. Over the course of centuries of agricultural development, many wild species have adapted to or even became dependent on farmland habitats (Magioli *et al.*, 2019). In fact, 'wildlife-friendly' farmlands are often seen as valuable ecosystems for biodiversity conservation, e.g. high nature value (HNV) farmlands in Europe (Fischer *et al.*, 2012; Sutcliffe *et al.*, 2015; Lomba *et al.*, 2020).

Urban habitats, particularly urban greenspaces, are also increasingly recognized as valuable habitats for species conservation and biodiversity management (Dearborn & Kark, 2010; Shaffer, 2018; Soanes & Lentini, 2019; Soanes *et al.*, 2019; Aronson *et al.*, 2014). Urban habitats may harbour many threatened and rare species (Ives *et al.*, 2016), and the species inhabiting cities are capable of changing rapidly in response to anthropogenic environments (Alberti, 2015; Donihue & Lambert, 2015; Rivkin *et al.*, 2019).

To what extent natural, urban and agricultural habitats are important to wild species is not yet fully understood. In addition, it may be context, species or habitat dependent, and will vary given the spatial scale and layout of the habitats in our landscapes.

The overall aim of this study is to explore to what extent the three main land-use types (natural, rural and urban habitats) and the level of nature protection (not protected areas, areas being part of Netherlands' Nature Network or being part of the Netherlands EU Natura 2000 network) contribute to the occurrences of different plant species. Our three research questions are: what is the contribution of land-use types (i.e. natural, rural and urban habitats) and the protection status of areas to (1) the occurrence of plant species at the level of the landscape (γ-diversity)? (2) plant occurrence at the site level (α-diversity)? and (3) the similarity of plant assemblages across neighbouring similar habitats (β-diversity)? We assess this at the level of all plant species, all native plants and for the latter also in relation to their rarity and threat levels. We address question 2 and 3 at different spatial scales: from small scale (0.5 km squared) to landscape scale (two square kilometres) as occurrence patterns may be different at these scales.

Materials and Methods

Figure 1 summarises the workflow used to address each of the questions from the assignment of areas ('grid cells') to the different land-use types (natural, rural and urban) and to the different nature protection regimes (NNN=Netherlands' Nature Network; Natura 2000), the selection of the well-sampled cells (WSC) to be included in the different analyses, the calculation of the alpha, beta and gamma diversity of plant species for the focal land-use and protection type and, for questions 2 and 3 at the scales of 0.5 km, 1 km and 2 km (Figure 1).

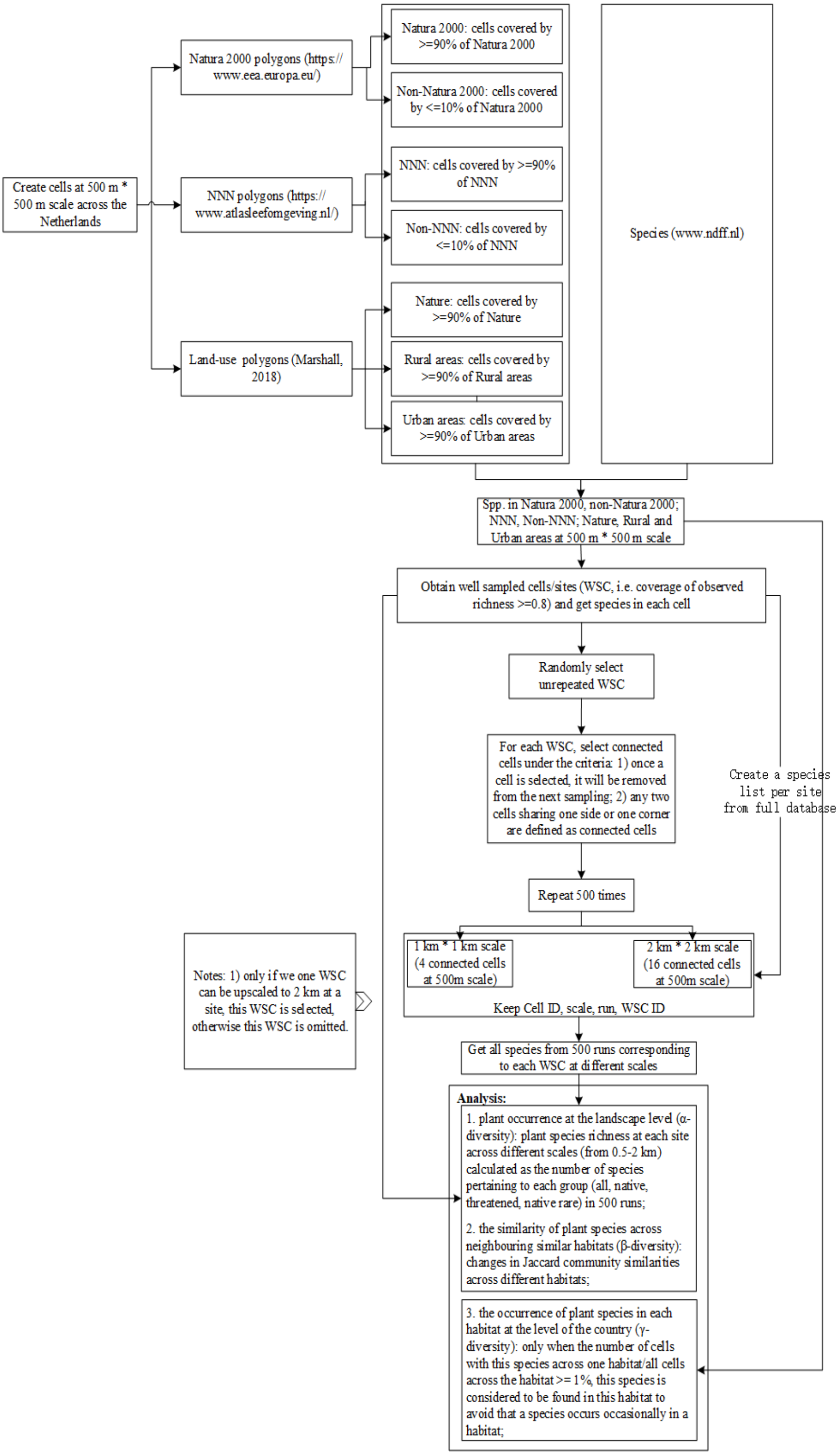

Create cells at 500 m * 500 m scale across the Netherlands
Natura 2000 polygons (https://www.eea.europa.eu/)
NNN polygons (https://www.atlasleefomgeving.nl/)
Land-use polygons (Marshall, 2018)
Natura 2000: cells covered by >=90% of Natura 2000
Non-Natura 2000: cells covered by <=10% of Natura 2000
NNN: cells covered by >=90% of NNN
Non-NNN: cells covered by <=10% of NNN
Nature: cells covered by >=90% of Nature
Rural areas: cells covered by >=90% of Rural areas
Urban areas: cells covered by >=90% of Urban areas
Species (www.ndff.nl)
Spp. in Natura 2000, non-Natura 2000; NNN, Non-NNN; Nature, Rural and Urban areas at 500 m * 500 m scale
Obtain well sampled cells/sites (WSC, i.e. coverage of observed richness >=0.8) and get species in each cell
Randomly select unrepeated WSC
For each WSC, select connected cells under the criteria: 1) once a cell is selected, it will be removed from the next sampling; 2) any two cells sharing one side or one corner are defined as connected cells
Create a species list per site from full database
Repeat 500 times
1 km * 1 km scale (4 connected cells at 500m scale)
2 km * 2 km scale (16 connected cells at 500m scale)
Keep Cell ID, scale, run, WSC ID
Notes: 1) only if we one WSC can be upscaled to 2 km at a site, this WSC is selected, otherwise this WSC is omitted.
Get all species from 500 runs corresponding to each WSC at different scales
Analysis:
1. plant occurrence at the landscape level (α-diversity): plant species richness at each site across different scales (from 0.5-2 km) calculated as the number of species pertaining to each group (all, native, threatened, native rare) in 500 runs;
2. the similarity of plant species across neighbouring similar habitats (β-diversity): changes in Jaccard community similarities across different habitats;
3. the occurrence of plant species in each habitat at the level of the country (γ-diversity): only when the number of cells with this species across one habitat/all cells across the habitat >= 1%, this species is considered to be found in this habitat to avoid that a species occurs occasionally in a habitat;

Figure 1 Flow chart detailing all analytical steps. NNN refers to the 'Netherlands' Nature Network, which includes all existing protected natural areas. WSC refers to well-sampled cells (see methods for detailed explanation).

Study area

The Netherlands has experienced a huge transformation in land-use from (semi-)natural habitats to human-used habitats (Hauser *et al.*, 2016; The European environment, 2019), with an alarming decline in biodiversity (Biesmeijer *et al.*, 2006; van Strien *et al.*, 2019; The European environment, 2019). Nowadays, most of the country consists of human-dominated landscapes with over 60% of the terrestrial surface being urban and rural habitats, and around 23% of terrestrial surface being (semi-)natural landscapes, including natural reserves spread across the whole country.

Land-use and Natural reserves

Natural, rural and urban habitats all have the potential to be biodiversity hotspots (Ives *et al.*, 2016; Kowarik & Lippe, 2018; Salinitro *et al.*, 2018). To compare the plant diversity between these habitats we define natural habitats as all natural or (semi-)natural habitats receiving little human disturbance and management, urban habitats include urban green (open space covered by vegetation in urban environment) and urban grey (all impervious areas in urban environment), and rural habitats include all other terrestrial habitats in the country (agricultural land) (Table S1). To derive a complete national dataset from which three habitat types could be obtained, we combined data from three national sources on land-use and land cover: summary of nature management in the Netherlands (Inter Provinciaal Overleg, 2016), basic registration of crops and agricultural parcels (Ministerie van Economische Zaken (EZK), 2015), and urban land-use (Centraal Bureau voor de Statistiek (CBS), 2012) using ESRI ArcGIS Desktop 10.2 (https://desktop.arcgis.com/en/). Three datasets included 175 land-use classes, which are aggregated into 14 terrestrial land-use classes at a resolution of 10 x 10 m by Marshall (2018). We further re-classified 14 classes into the three land-use types: natural, rural and urban habitats (Table S1). Next, we calculated the proportions of natural, rural and urban habitats in each 0.5 x 0.5 km cell using ArcGIS. We assigned a cell to a natural, rural or urban habitat if that type of habitat covered more than 90% (>= 90%) (following Zwaan *et al.*, 2022). Only cells with <10% open water (equalling a land surface proportion of =>90% in each cell) were included in our analysis, following Desrochers *et al.*, 2011 and Clark *et al.*, 2019. As a result, we obtained three rasters, natural, rural and urban habitats. In the Netherlands, there are different types of nature reserves. In this study, we use two nature reserve datasets: the Nature Network of the Netherlands (NNN) and Natura 2000. These two datasets represent different conservation efforts. The NNN, which is the most complete natural conservation network, includes all types of protected areas in the Netherlands (the NNN is described more fully in https://www.rijksoverheid.nl/onderwerpen/natuur-en-biodiversiteit/natuurnetwerk-nederland). Natura 2000 in the Netherlands is part of the European network of protected nature areas (https://www.government.nl/topics/nature-and-biodiversity/natura-2000) and it reflects biodiversity conservation targets in Europe

(Sundseth & Creed, 2008; Trochet & Schmeller, 2013). All Natura 2000 areas are part of NNN, but not all NNN areas are part of Natura 2000. The spatial extent of NNN and Natura 2000 was obtained from the polygons of the NNN (https://www.atlasleefomgeving.nl/) and Natura 2000 (https://www.eea.europa.eu/). At the scale of 0.5 x 0.5 km, we calculated the proportions of NNN and Natura 2000 in each cell using ArcGIS. Finally, we retained all cells that are covered by over 90% of NNN, Non_NNN, Natura2000 or Non_Natura2000.

Plant observation and plant groups

To measure plant richness, i.e. numbers of species, we used presence-only records for vascular plants, which include seed plants, conifers, ferns and club mosses, in the Netherlands from the Dutch National Database of Flora and Fauna (NDFF, www.ndff.nl) collected in the period 2010-2017. We use species-level taxonomy, so we excluded records at genus and family level or with nomina dubia (e.g. '*Geranium dissectum* / *molle* / *pusillum*'). The observations included were either point observations or polygons with areas smaller than 3 ha, with the latter indicating the presence of a species within a given area. All polygons were converted to points by taking the centroid of the polygon. Next, each observation was attributed to a 0.5 x 0.5 km cell, and only cells covered by either >= 0.9 natural habitat, rural habitat, urban habitat. Natura2000, non_Natura200, NNN or non_NNN were retained.

We analysed plant richness patterns for four nested plant species groups: all species (native+exotic spp.), native species, threatened species and (native) rare species. Data on threatened status, rarity and species origin (i.e. whether a species is a native species) were obtained from the Red List of Vascular Plants of the Netherlands (Sparrius *et al.*, 2014). Since we were interested in differences between main categories, for the threatened status of species, we omitted species assigned as Data Deficient (DD), and reclassified Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) as 'threatened'. Group classifications of species are attributed to species in each cell.

Well-sampled sites across different habitats at different scales

To investigate plant richness in different habitats across different scales, we first estimated the sampling effort in each cell at 0.5 km scale using the iNEXT package in R (version 2.0.20 (Hsieh *et al.*, 2016)). In each cell, all species and records of each species were counted and stored in a matrix, and only cells with >= 3 species and 40 observations were retained in order to estimate sampling efforts by iNEXT. We used this matrix as the abundance data input for the iNEXT function to estimate the sampling efforts in each cell based on the coverage (i.e. the percentage of species that are sampled in each cell). iNEXT estimated the coverage based on three methods: interpolation (i.e. the coverage is estimated based on subset of observed species richness), observed (i.e. the coverage is estimated based on all observed species richness) and extrapolation (i.e. the coverage is estimated based on predicted species richness). If 0.8 coverages of cells could only be reached with extrapolation, we omitted them. Other cells with 0.8 coverages reached by interpolation and observation are considered to be well sampled cells (WSCs). For our questions on alpha and beta diversity patterns at different scales, we took each WSC as the focal cell and upscaled it to 1 km (4 cells) and 2 km (16 cells) by joining neighbouring cells (any of the eight adjacent squares) of the same land-use type. We repeated this process 500 times to account for variability in the selection of neighbours. We excluded sites at 0.5 and 1 km that couldn't be aggregated to 2 km. Finally, we obtained 1836 sites in natural habitats, 1215 sites in rural habitats, 502 sites in urban habitats, 1618 sites in Natura 2000, 8288 sites in non-Natura 2000, 2087 sites in NNN and 3931 sites in non-NNN. For each site, the list of species was obtained at each scale generated from the WSC across the 500 repetitions.

Statistical Analysis

To quantify how plant richness varied between habitats, we explored this at three levels: (i) the total number of plant species (at country-level) in natural habitats, rural habitat, urban habitats, Natural2000, non_Natura2000, NNN and non_NNN (the γ-diversity of each land-use), (ii) the total number of species at small scales (0.5-2 km) (α-diversity), and (iii) the similarity in plant species across cells of similar land-use (β-diversity).

To quantify γ-diversity, we aggregated and counted all species by groups for each land-use type. For species to be assigned to a land-use or protection category, at least >=1% of cells from that category needs to be with its records, to avoid that a species occurs occasionally in a habitat.

To quantify the total number of species at different sites (α-diversity), plant species richness at each site across different scales (from 0.5-2 km) is calculated as the number of species pertaining to each group (all, native, threatened, native rare) in 500 runs. The non-parametric Kruskal-wallis test was used to test whether there are significant differences in richness between different habitats. Richness at each site across different scales is calculated as the number of species with at least 1 record.

To quantify β-diversity, we statistically tested for changes in species composition across different habitats. Firstly, we calculated Jaccard community similarities between each two sites with the vegdist in R package vegan (version 2.5-6, Oksanen, 2022). Furthermore, we tested for significant differences in community similarities between habitat types with Kruskal-wallis test. All analyses are conducted in R version 4.1.2 (R Core Team, 2021).

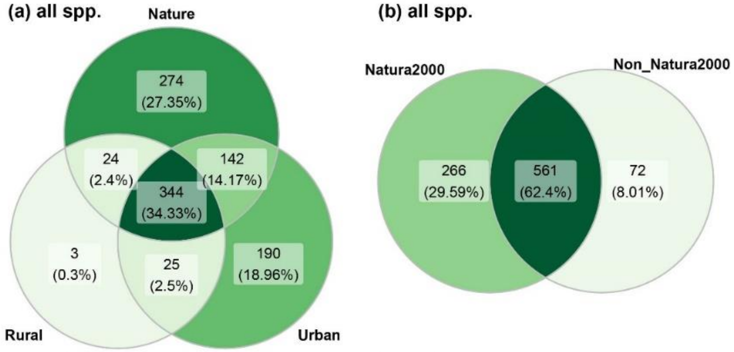
Results

Plant occurrence in relation to land-use types and habitat protection level at national level.

Plant occurrence in relation to land-use types and habitat protection level at national level.

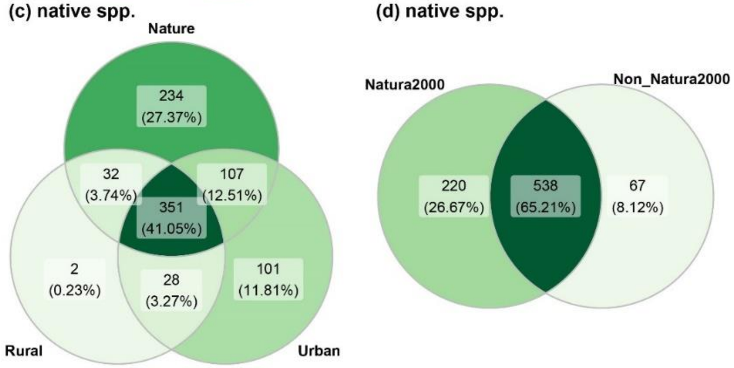
The largest group of species (344, 34.3%) was found in all three land-use types, (Figure 2a). In addition, 274 species (27.4%) were found exclusively in natural habitats, 190 species (19%) in urban habitats and 3 (0.3%) in rural habitats. More species were found exclusively in protected habitats than in unprotected habitats. Overall, 29.6% of all species were found only in Natura 2000 sites. Conversely, 8.0% of all species were found only in non-Natura 2000 sites, with 62.4% found in both Natura 2000 and non-Natura 2000 sites (Figure 2b). Native species showed similar patterns to all species (Figure 2c-d), with more species uniquely found in natural habitats (27.4% for native species), and Natura 2000 habitats (26.7% for native species) than in urban habitats (11.8% for native species), rural (0.2% for native species) habitats, and non-Natura 2000 sites (8.1% for native species).

Threatened and rare plant species showed different patterns, with a far greater proportion of species found exclusively in natural habitats (33.3% for threatened species and 42.9% for rare species) than in urban or rural habitats (Figure 2e-h). Urban habitats (15.5% for threatened species and 19.1% for rare species) sustained more unique species than rural habitats (7.5% for threatened species and 7.0% for rare species) (Figure 2e, g). More threatened species (43.4%) were found in both Natura 2000 and non-Natura 2000 sites than to one of them (Figure 2f). This is different for rare species, which were most commonly found in Natura 2000 sites (47.7%) (Figure 2h).



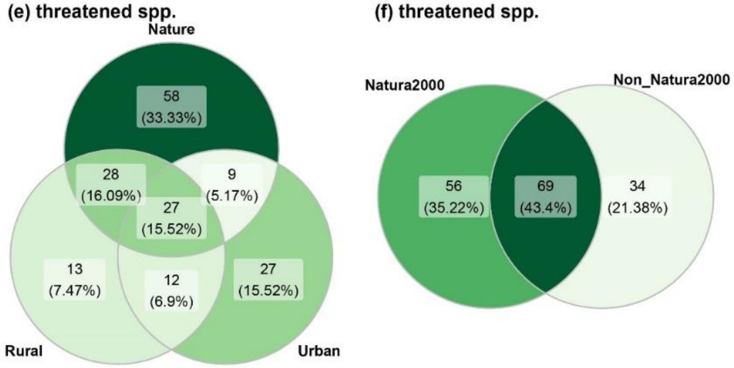
(a) all spp.

(b) all spp.



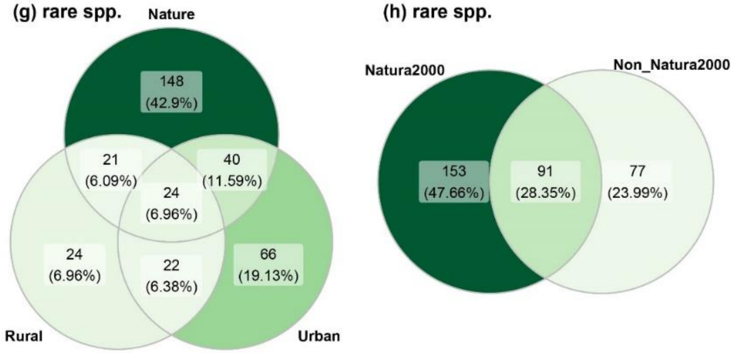
(c) native spp.

(d) native spp.



(e) threatened spp.

(f) threatened spp.



(g) rare spp.

(h) rare spp.

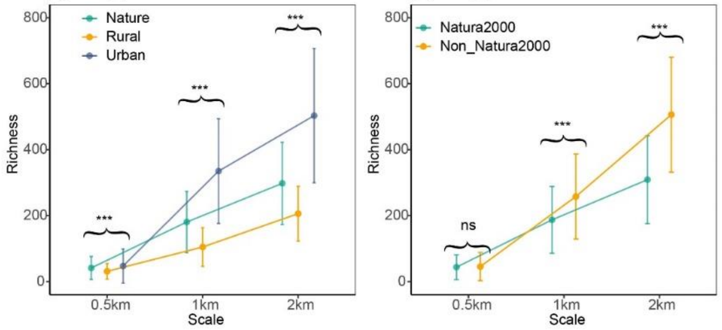
Figure 2 Plant species Richness (γ-diversity) in natural, urban or rural habitats and in habitats with different protection management (Natura 2000). a-b, numbers and proportions of all plant species that were found in different habitats (natural, rural, urban) and sites (Natura 2000 and non-Natura 2000). c-d, the same for native species. e-f, the same for threatened species. g-h, the same for native rare species.

Plant α-diversity in relation to land-use types and habitat protection level.

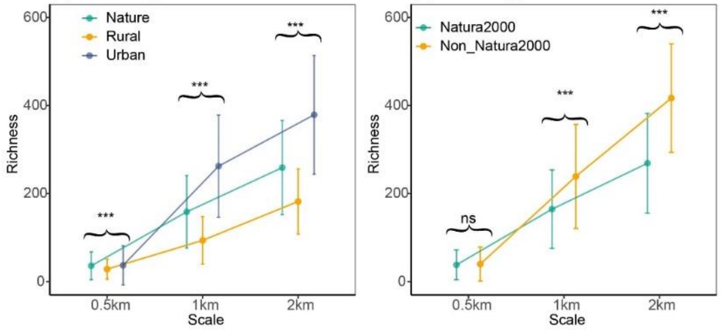
For all plants and all native plants, the number of species at a site (α-diversity) was higher in urban habitats than in natural habitats, and the richness in natural habitats was consistently higher than the richness in rural habitats across spatial scales (Figure 3a, c). The α-diversity for all plants and all native plants was higher in non-Natura 2000 habitats than in Natura 2000 habitats at different scales (Figure 3b, d). Moreover, the differences in richness between habitats increased as the scale of analysis increased from 0.5 to 2 km.

Similarly, results for rare species showed that, on average, a greater number of species were found at a single urban site than in natural and rural sites at 1 km and 2 km scale (Figure 3g). There were more rare species in natural habitats than in urban habitats at 0.5 km scale, but richness in both habitats was higher than in rural habitats. The α-diversity of rare plants in Natura 2000 habitats was significantly higher than in non-Natura 2000 habitats at 0.5 km and 1 km scales (Figure 3h).

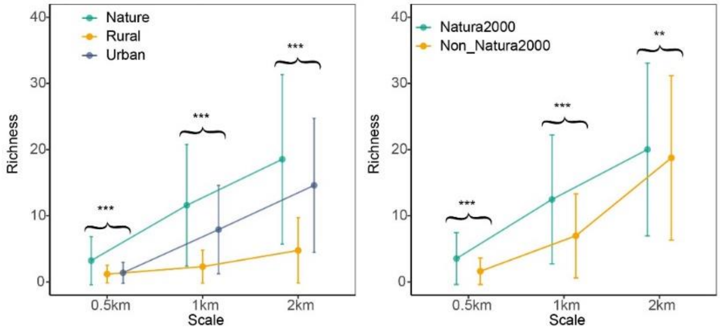
In contrast, the number of threatened plant species at a site showed a different pattern. The highest richness of threatened species was found in natural habitats, and Natura 2000 habitats (Figure 3e-f). Urban habitats sustained a higher richness than rural habitats (Figure 3e).



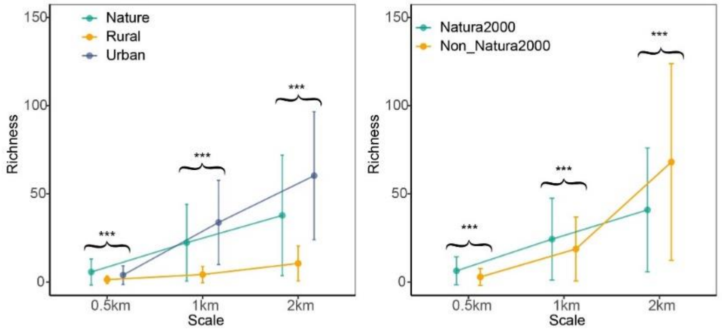
(a) all spp. (b) all spp.



(c) native spp. (d) native spp.



(e) threatened spp. (f) threatened spp.



(g) rare spp. (h) rare spp.

Figure 3 Species Richness (α-diversity) in different types of habitats or habitats with different protection management. a-b, α-diversity of all species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). c-d, α-diversity of native species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). e-f, α-diversity of threatened species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). g-h, α-diversity of rare species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). The value is mean ± sd. Significances between groups are indicated by ns (not significantly different) or stars (significantly different). Numbers of sites across each habitat and mean richness ± sd are in Table S2.

Plant β-diversity in relation to land-use types and habitat protection level.

All taxonomic groups differed significantly in their species-based community similarity coefficients (β-diversity) when categorised into natural, rural and urban sites, and Natura 2000 and non-Natura 2000 sites. Kruskal-wallis tests detected that urban habitats have the strongest similarity in species-based community (all and native plants) composition while natural habitats have the strongest dissimilarity in species-based community composition at 0.5 km scale (Figure 4a, c). Community compositions of the three groups in Natura 2000 were less similar than in non-Natura 2000 only at 0.5 km scale (Figure 4b, d).

For threatened and rare species, the dissimilarity of species across sites in Natura 2000 was stronger than in non-Natura 2000 (Figure 4f, h). Community composition of threatened species in natural habitats was less similar than in urban habitats, and rural habitats had the most homogenised species composition (Figure 4e). For rare species, natural habitats had the most heterogeneous species composition between communities at 0.5 km scale (Figure 4g). However, urban communities were more heterogeneous in rare species than natural communities at 1 km and 2 km scales, while rural habitats have the most homogenised species compositions across sites.

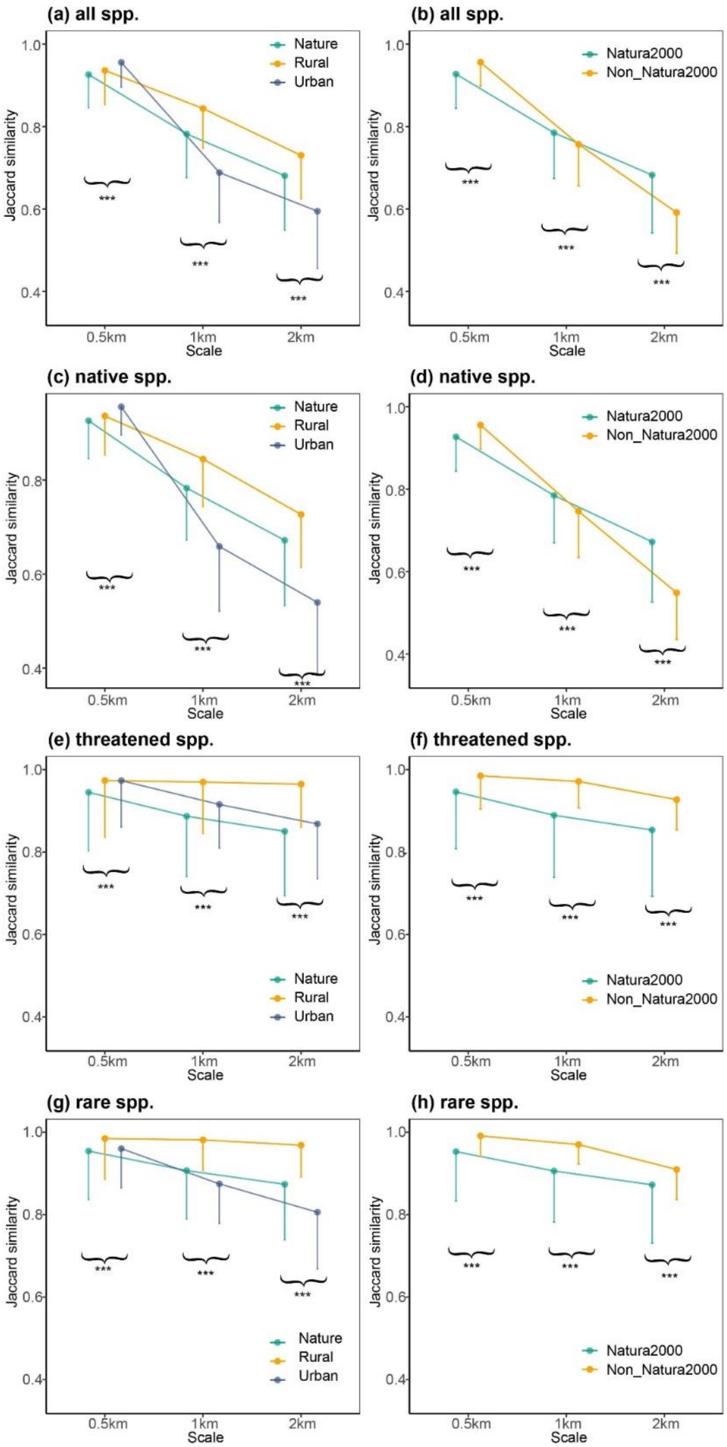

(a) all spp.
(b) all spp.
(c) native spp.
(d) native spp.
(e) threatened spp.
(f) threatened spp.
(g) rare spp.
(h) rare spp.
Nature
Rural
Urban
Natura2000
Non_Natura2000
Jaccard similarity
Scale
0.5km
1km
2km
0.4
0.6
0.8
1.0
***

Figure 4 Species Richness (β-diversity) in different types of habitats or habitats with different protection management. a-b, β-diversity of all species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). c-d, β-diversity of native species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). e-f, β-diversity of threatened species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). g-h, β-diversity of rare species in different habitats (natural, rural, urban habitats; Natura 2000 and non-Natura 2000 habitats). The value is mean ± sd. Significances between groups are indicated by ns (not significantly different) or stars (significantly different). The number of sites across each habitat and mean richness - sd are in Table S3.

Discussion

Plants differ in their ecological preferences, which expresses itself in strong differences in spatial patterns of occurrence and distribution. That this leads to different vegetation types, each with a set of characteristic species is well-known and widely studied. Here the focus is often on the small subset of specialist plants that can be reliably located in the field based on one's knowledge of the vegetation types and thus their typical ecological requirements. However, most plants can be found in a wider range of habitats, but their affiliation with, for example, natural habitats, agricultural land or urban areas is often less studied. Moreover, while the idea of protecting natural areas is to provide long-term viability for plant populations, it is not very clear whether this approach is sufficient for plant conservation. Understanding the above is important for plant conservation and our results contribute to this knowledge.

More Dutch plant species are dependent on natural than on rural and urban habitats

While many (native) species can be found across natural, rural and urban habitats, natural habitats sustain more species in general and more species of conservation concern (rare and threatened) than rural and urban habitats. In addition, many species are found exclusively in urban habitats, which supports previous studies (Schmidt *et al.*, 2014; Ives *et al.*, 2016). It implies that plant species have essential refuges in both natural habitats and urban habitats.

For plant diversity at local scales, all, native and rare species show similar patterns of richness across scales, while threatened species are the only exception. Urban habitats have the highest alpha and beta diversity across all scales if we address all plant species or native species. At the 0.5 km scale, natural habitats harbour more rare species compared to the other land use types, although urban habitats sustain more rare species at larger scales. It means rare species diversities in different habitats are dependent on spatial scale, which has been discussed previously (Faeth *et al.*, 2011). Urban habitats tend to consist of a wide variety of green patches, some natural remnants or (semi-)natural habitats harbouring a high plant diversity, while others support fewer species (Pautasso & McKinney, 2007; Kowarik & Lippe, 2018; Salinitro *et al.*, 2018). Therefore, any given patch at a small scale may have fewer rare species than natural habitats, but these heterogeneous habitats combined at larger scale result in a higher diversity than natural habitats. It implies that the increase in richness of rare species in natural and urban habitats is not simply explained by species-area relationships, but also explained by habitat diversity patterns. However, threatened species show a different pattern, with the highest diversity in natural habitats across scales. This may be because these species are often restricted to their original natural habitats, or because urbanization has a negative influence on threatened species at local scale (Schmidt *et al.*, 2014), although some threatened species are found in urban remnants (Schmidt *et al.*, 2014).

Dutch urban habitats have higher plant richness than rural habitats, like in Germany (Deutschewitz *et al.*, 2003; Kühn *et al.*, 2004; Wania *et al.*, 2006) and the USA (Hope *et al.*, 2003). This is often explained by 1) urban areas being more heterogeneous than rural areas (Wania *et al.*, 2006). A great variety of habitats (e.g. natural remnants, parks, traffic corridors, gardens, etc.) provides a wide range of ecological conditions for different species (Sukopp, 2004); 2) some urban patches being kept in early or mid-successional stage with high species diversity (Grime, 1973; Connell, 1978); 3) rural areas consisting mostly of agricultural land and that is managed intensively (e.g. planting, harvesting, fertilization, usage of herbicide, etc.). The area of (semi-)natural habitats in agriculture is limited, especially in the Netherlands (Manhoudt & Snoo, 2003; Cormont *et al.*, 2016). While urban areas are covered by a larger proportion of green infrastructure (31.4% on average) and (semi-)natural habitats (12.5% on average) (https://www.eea.europa.eu/data-and-maps/dashboards/urban-green-infrastructure-2018).

The disproportionate representation of plant species, particularly threatened species, in nature identified in this study suggests that practitioners should strengthen the protection and restoration of natural habitats to maintain the persistence of plant diversity (Di Marco *et al.*, 2019; Riggio *et al.*, 2020). In addition, it is important to note that cities also contain opportunities for biodiversity conservation. We should act upon species conservation in urban areas by protecting (semi-)natural habitats and increasing connectivity with green corridors (Knapp *et al.*, 2008; Hahs *et al.*, 2009; Faeth *et al.*, 2011), scientific planning (Gordon *et al.*, 2009; Aronson *et al.*, 2017) and nature-positive management of urban nature (e.g. green space along roads, yards and golf courts, green roofs) (Knapp *et al.*, 2008; Faeth *et al.*, 2011; Aronson *et al.*, 2017), construct urban habitats with room for native plant species (Tallamy, 2007; Faeth *et al.*, 2011; Segar *et al.*, 2022), improve the education on the importance of conserving biodiversity (Schwartz *et al.*, 2002; Faeth *et al.*, 2011). However, we have to be aware that some challenges, e.g. how to balance the needs of residents and conservation targets and allocate limited conservation investments, of conserving species in urban areas also need to be addressed (Schwartz *et al.*, 2013; Turo & Gardiner, 2020). Finally, although this study shows that rural habitats have lower potential in sustaining species, we can strengthen species diversity in agriculture by various practices (Tscharntke *et al.*, 2021). This may be a ‘second best’ for some species if the preferred option, extension of natural areas, is not an option.

The importance of protected and unprotected habitats for plant species

Nature conservation areas aim to protect species, habitats and ecosystems against local extinction and degradation. They make up only about 15% of the global land surface, with adequate levels of protection only in a subset of them (Ritchie & Roser, 2021). To what extent protected areas are sufficient for nature protection is not always clear and it has been suggested that terrestrial biodiversity needs more than protected areas alone for their survival (Watson *et al.*, 2014; Rada *et al.*, 2019; Dähler *et al.*, 2019).

We evaluated the effectiveness of Natura 2000 for plants in the Netherlands. While Natura 2000 sites are home to more threatened and rare plant species than non-Natura2000 sites, a larger share of plant species occurs in both types and some exclusively outside Natura2000 sites. The selection of protected areas is commonly dependent on high species richness, endemism and threatened habitats, which is supported by a better performance of protected areas in conserving threatened and rare species in this study. However, although a large percentage of biologically important areas may be protected, it doesn't mean all species are protected (e.g. Duffy *et al.*, 1999; Dimitrakopoulos *et al.*, 2004). In addition, some species are human-tolerant or even dependent on human management and thus have profited from long-term human activities in the Netherlands (Vellak *et al.*, 2009). This has led to the protection of small habitats in unprotected areas with focus on species, particularly threatened species, that are not covered in the protected area network. Small nature reserves have been considered by some to be as important as large protected areas (Higgs & Usher, 1980; Baldwin & Fouch, 2018). Despite the biodiversity found in unprotected habitats, overall, protected areas sustain more species, particularly for threatened and rare species, than unprotected areas. For example, 35%-46% (35% for Natura 2000 and 46% for NNN, Figure 2f; Figure S1c) of threatened species and 48%-56% (48% for Natura 2000 and 56% for NNN, Figure 2h; Figure S1d) of rare species are dependent on protected areas, and 33%-43% of threatened species and 23%-28% of rare species are found in both protected and unprotected areas, adding up to 79% of threatened species and 76%-79% of rare species being conserved by protected areas. These proportions of protected species exceed recommendations by IUCN (Sharrock *et al.*, 2014). However, it is still a concern that not all threatened species are conserved in protected areas.

Surprisingly, the protected areas (both of NNN and Natura 2000) have lower alpha and beta diversity of all species and native species than unprotected areas. It means unprotected areas in the Netherlands are particularly effective in maintaining common plant species, while protected areas are effective in conserving alpha and beta diversity of threatened and rare species, supporting the efforts of establishing protected areas for biodiversity conservation and mitigating the extinction risk of terrestrial biodiversity (Di Marco *et al.*, 2019). Although unprotected areas sustain a higher alpha diversity of rare species at 2 km scale, which is probably because more diverse habitats are included at larger scale in unprotected areas, protected areas have more dissimilar plant communities across sites. Overall, sites from unprotected areas contained more native and exotic species than sites from protected areas. By contrast, protected areas consistently have higher richness of threatened and rare species. However, we admit that it is not clear from our correlative analysis whether the high richness of threatened and rare species is due to protection efforts or high pre-existing plant diversity .

Implications

How can our findings guide conservation investments aimed at plant species? Combining site diversity (α-diversity) with across site similarity (β-diversity) showed that increasing protected areas and natural habitats will lead to the best conservation of plant species, particularly threatened and rare species. The next best option is to increase conservation efforts in urban habitats, taking into account that this also tends to benefit common and exotic species. While much conservation effort is currently geared towards improving agricultural biodiversity, our results suggest that it has only marginal value as rural habitats contain very few unique species and most others benefit (and potentially) more from natural and urban habitats.

References

Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology & Evolution*, **30**, 114–126.

Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., WARREN, P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., Kühn, I., Macgregor-Fors, I., McDonnell, M., Mörtberg, U., Pysek, P., Siebert, S., Sushinsky, J., Werner, P. & Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings. Biological sciences*, **281**, 20133330.

Aronson, M.F.J., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., Nilon, C.H. & Vargo, T. (2017). Biodiversity in the city: key challenges for urban green space management. *Frontiers in Ecology and the Environment*, **15**, 189–196.

Baeten, L., Hermy, M., van Daele, S. & Verheyen, K. (2010). Unexpected understorey community development after 30 years in ancient and post-agricultural forests. *Journal of Ecology*, **98**, 1447–1453.

Baldwin, R. & Fouch, N. (2018). Understanding the Biodiversity Contributions of Small Protected Areas Presents Many Challenges. *Land*, **7**, 123.

Bawa, K.S., Nawn, N., Chellam, R., Krishnaswamy, J., Mathur, V., Olsson, S.B., Pandit, N., Rajagopal, P., Sankaran, M., Shaanker, R.U., Shankar, D., Ramakrishnan, U., Vanak, A.T. & Quader, S. (2020). Opinion: Envisioning a biodiversity science for sustaining human well-being. *Proceedings of the National Academy of Sciences*, **117**, 25951-25955.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Brockington, D. & Wilkie, D. (2015). Protected areas and poverty. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **370**.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–460.

Brooks, T.M., Mittermeier, R.A., Da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006). Global biodiversity conservation priorities. *Science*, **313**, 58–61.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, **1**, e1400253.

Centraal Bureau voor de Statistiek (CBS) (2012). *Bestand Bodemgebruik Productbeschrijving*.

Clark, C.M., Simkin, S.M., Allen, E.B., Bowman, W.D., Belnap, J., Brooks, M.L., Collins, S.L., Geiser, L.H., Gilliam, F.S., Jovan, S.E., Pardo, L.H., Schulz, B.K., Stevens, C.J., Suding, K.N., Throop, H.L. & Waller, D.M. (2019). Potential vulnerability of 348 herbaceous species to atmospheric deposition of nitrogen and sulfur in the United States. *Nature Plants*, **5**, 697–705.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

Cormont, A., Siepel, H., Clement, J., Melman, T., WallisDeVries, M.F., van Turnhout, C., Sparrius, L.B., Reemer, M., Biesmeijer, J.C., Berendse, F. & Snoo, G.R. de (2016). Landscape complexity and farmland biodiversity: Evaluating the CAP target on natural elements. *Journal for Nature Conservation*, **30**, 19–26.

Cusack, D.F., Karpman, J., Ashdown, D., Cao, Q., Ciochina, M., Halterman, S., Lydon, S. & Neupane, A. (2016). Global change effects on humid tropical forests: Evidence for biogeochemical and biodiversity shifts at an ecosystem scale. *Reviews of Geophysics*, **54**, 523–610.

Dähler, N.B., Holderegger, R., FLORA, I. & Bergamini, A. (2019). Effectiveness of Swiss protected areas in maintaining populations of rare vascular plants. *Journal for Nature Conservation*, **52**, 125749.

Daskalova, G.N., Myers-Smith, I.H., Bjorkman, A.D., Blowes, S.A., Supp, S.R., Magurran, A.E. & Dornelas, M. (2020). Landscape-scale forest loss as a catalyst of population and biodiversity change. *Science (New York, N.Y.)*, **368**, 1341–1347.

Dearborn, D.C. & Kark, S. (2010). Motivations for conserving urban biodiversity. *Conservation Biology*, **24**, 432–440.

Desrochers, R.E., Kerr, J.T. & Currie, D.J. (2011). How, and how much, natural cover loss increases species richness. *Global Ecology and Biogeography*, **20**, 857–867.

Deutschewitz, K., Lausch, A., Kühn, I. & Klotz, S. (2003). Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global Ecology and Biogeography*, **12**, 299–311.

Di Marco, M., Ferrier, S., Harwood, T.D., Hoskins, A.J. & Watson, J.E.M. (2019). Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature*, **573**, 582–585.

Díaz, S., Zafra-Calvo, N., Purvis, A., Verburg, P.H., Obura, D., Leadley, P., Chaplin-Kramer, R., Meester, L. de, Dulloo, E., Martín-López, B., Shaw, M.R., Visconti, P., Broadgate, W., Bruford, M.W., Burgess, N.D., Cavender-Bares, J., DeClerck, F., Fernández-Palacios, J.M., Garibaldi, L.A., Hill, S.L.L., Isbell, F., Khoury, C.K., Krug, C.B., Liu, J., Maron, M., McGowan, P.J.K., Pereira, H.M., Reyes-García, V., Rocha, J., Rondinini, C., Shannon, L., Shin, Y.-J., Snelgrove, P.V.R., Spehn, E.M., Strassburg, B., Subramanian, S.M., Tewksbury, J.J., Watson, J.E.M. & Zanne, A.E. (2020). Set ambitious goals for biodiversity and sustainability. *Science*, **370**, 411–413.

Dimitrakopoulos, P.G., Memtsas, D. & Troumbis, A.Y. (2004). Questioning the effectiveness of the Natura 2000 Special Areas of Conservation strategy: the case of Crete. *Global Ecology and Biogeography*, **13**, 199–207.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., Souza, N. de, Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F. & Saleem, M. (2017). An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *BioScience*, **67**, 534–545.

Dinerstein, E., Vynne, C., Sala, E., Joshi, A.R., Fernando, S., Lovejoy, T.E., Mayorga, J., Olson, D., Asner, G.P., Baillie, J.E.M., Burgess, N.D., Burkart, K., Noss, R.F., Zhang, Y.P., Baccini, A., Birch, T., Hahn, N., Joppa, L.N. & Wikramanayake, E. (2019). A Global Deal For Nature: Guiding principles, milestones, and targets. *Science Advances*, **5**, eaaw2869.

Donihue, C.M. & Lambert, M.R. (2015). Adaptive evolution in urban ecosystems. *AMBIO*, **44**, 194–203.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A.E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, **344**, 296–299.

Dornelas, M., Gotelli, N.J., Shimadzu, H., Moyes, F., Magurran, A.E. & McGill, B.J. (2019). A balance of winners and losers in the Anthropocene. *Ecology Letters*, **22**, 847–854.

Duffy, D.C., Boggs, K., Hagenstein, R.H., Lipkin, R. & Michaelson, J.A. (1999). Landscape Assessment of the Degree of Protection of Alaska’s Terrestrial Biodiversity. *Conservation Biology*, **13**, 1332–1343.

Faeth, S.H., Bang, C. & Saari, S. (2011). Urban biodiversity: patterns and mechanisms. *Annals of the New York Academy of Sciences*, **1223**, 69–81.

Fischer, J., Hartel, T. & Kuemmerle, T. (2012). Conservation policy in traditional farming landscapes. *Conservation Letters*, **5**, 167–175.

Gordon, A., Simondson, D., White, M., Moilanen, A. & Bekessy, S.A. (2009). Integrating conservation planning and landuse planning in urban landscapes. *Landscape and Urban Planning*, **91**, 183–194.

Grime, J.P. (1973). Competitive Exclusion in Herbaceous Vegetation. *Nature*, **242**, 344–347.

Hahs, A.K., McDonnell, M.J., McCarthy, M.A., Vesk, P.A., Corlett, R.T., Norton, B.A., Clemants, S.E., Duncan, R.P., Thompson, K., Schwartz, M.W. & Williams, N.S.G. (2009). A global synthesis of plant extinction rates in urban areas. *Ecology Letters*, **12**, 1165–1173.

Hauser, L.T., van der Sluis, T. & Giezen, M. (2016). The Role of Farm Management Characteristics in Understanding the Spatial Distribution of Landscape Elements: A Case Study in the Netherlands. *Rural Landscapes: Society, Environment, History*, **3**, 7.

Higgs, A.J. & Usher, M.B. (1980). Should nature reserves be large or small? *Nature*, **285**, 568–569.

Hirsch, T., Mooney, K. & Cooper, D. (2020). *Global Biodiversity Outlook 5.* Secretariat of the Convention on Biological Diversity.

Hope, D., Gries, C., Zhu, W., Fagan, W.F., Redman, C.L., Grimm, N.B., Nelson, A.L., Martin, C. & Kinzig, A. (2003). Socioeconomics drive urban plant diversity. *Proceedings of the National Academy of Sciences*, **100**, 8788–8792.

Hsieh, T.C., Ma, K.H. & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). *Methods in Ecology and Evolution*, **7**, 1451–1456.

Inter Provinciaal Overleg (2016). *Informatiemodel natuurbeheer (IMNAB): Index Natuur en Landschap*.

IPBES (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services*.

IPBES (2022). *Summary for policymakers of the methodological assessment of the diverse values and valuation of nature of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).* Zenodo, Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Ives, C.D., Lentini, P.E., Threlfall, C.G., Ikin, K., Shanahan, D.F., Garrard, G.E., Bekessy, S.A., Fuller, R.A., Mumaw, L., Rayner, L., Rowe, R., Valentine, L.E. & Kendal, D. (2016). Cities are hotspots for threatened species. *Global Ecology and Biogeography*, **25**, 117–126.

Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L. & Wilmshurst, J.M. (2017). Biodiversity losses and conservation responses in the Anthropocene. *Science*, **356**, 270–275.

Knapp, S., Kühn, I., Mosbrugger, V. & Klotz, S. (2008). Do protected areas in urban and rural landscapes differ in species diversity? *Biodiversity and Conservation*, **17**, 1595–1612.

Kowarik, I. & Lippe, M. von der (2018). Plant population success across urban ecosystems: A framework to inform biodiversity conservation in cities. *Journal of Applied Ecology*, **55**, 2354–2361.

Kühn, I., Brandl, R. & Klotz, S. (2004). The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, **6**, 749–764.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., Palma, A. de, DeClerck, F.A.J., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Humpenöder, F., Jennings, N., Krisztin, T., Mace, G.M., Ohashi, H., Popp, A., Purvis, A., Schipper, A.M., Tabeau, A., Valin, H., van Meijl, H., van Zeist, W.-J., Visconti, P., Alkemade, R., Almond, R., Bunting, G., Burgess, N.D., Cornell, S.E., Di Fulvio, F., Ferrier, S., Fritz, S., Fujimori, S., Grooten, M., Harwood, T., Havlík, P., Herrero, M., Hoskins, A.J., Jung, M., Kram, T., Lotze-Campen, H., Matsui, T., Meyer, C., Nel, D., Newbold, T., Schmidt-Traub, G., Stehfest, E., Strassburg, B.B.N., van Vuuren, D.P., Ware, C., Watson, J.E.M., Wu, W. & Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*.

Li, L., Hu, R., Huang, J., Bürgi, M., Zhu, Z., Zhong, J. & Lü, Z. (2020). A farmland biodiversity strategy is needed for China. *Nature Ecology & Evolution*, **4**, 772–774.

Locke, H. (2013). Nature needs half: A necessary and hopeful new agenda for protected areas. PARKS 19 (2): 13–22. 10.2305/IUCN . CH. 2013. *Parks*, **19**, 13–22.

Lomba, A., Moreira, F., Klimek, S., Jongman, R.H.G., Sullivan, C., Moran, J., Poux, X., Honrado, J.P., Pinto-Correia, T., Plieninger, T. & McCracken, D.I. (2020). Back to the future: rethinking socioecological systems underlying high nature value farmlands. *Frontiers in Ecology and the Environment*, **18**, 36–42.

Magioli, M., Moreira, M.Z., Fonseca, R.C.B., Ribeiro, M.C., Rodrigues, M.G. & Ferraz, K.M.P.M.d.B. (2019). Human-modified landscapes alter mammal resource and habitat use and trophic structure. *Proceedings of the National Academy of Sciences of the United States of America*, **116**, 18466–18472.

Manhoudt, A. & Snoo, G. de (2003). A quantitative survey of semi-natural habitats on Dutch arable farms. *Agriculture, Ecosystems & Environment*, **97**, 235–240.

Marshall, L. (2018). *Wild bee diversity across space and time: the role of land use/land cover and climate,* Presses universitaires de Namur.

Ministerie van Economische Zaken (EZK) (2015). *Basisregistratie Gewaspercelen (BRP).*

Mittermeier, R.A., Mittermeier, C.G., Brooks, T.M., Pilgrim, J.D., Konstant, W.R., Da Fonseca, G.A.B. & Kormos, C. (2003). Wilderness and biodiversity conservation. *Proceedings of the National Academy of Sciences*, **100**, 10309–10313.

Obura, D.O., Katerere, Y., Mayet, M., Kaelo, D., Msweli, S., Mather, K., Harris, J., Louis, M., Kramer, R., Teferi, T., Samoilys, M., Lewis, L., Bennie, A., Kumah, F., Isaacs, M. & Nantongo, P. (2021). Integrate biodiversity targets from local to global levels. *Science*, **373**, 746–748.

Oksanen, J.e.a. (2022). vegan: community ecology package.

Pautasso, M. & McKinney, M.L. (2007). The botanist effect revisited: plant species richness, county area, and human population size in the United States. *Conservation Biology*, **21**, 1333–1340.

Plumptre, A.J., Baisero, D., Belote, R.T., Vázquez-Domínguez, E., Faurby, S., Jędrzejewski, W., Kiara, H., Kühl, H., Benítez-López, A., Luna-Aranguré, C., Voigt, M., Wich, S., Wint, W., Gallego-Zamorano, J. & Boyd, C. (2021). Where Might We Find Ecologically Intact Communities? *Frontiers in Forests and Global Change*, **4**, 26.

R Core Team (2021). R: A language and environment for statistical computing (R Foundation for Statistical Computing, 2019); https://www.R-project.org/.

Rada, S., Schweiger, O., Harpke, A., Kühn, E., Kuras, T., Settele, J. & Musche, M. (2019). Protected areas do not mitigate biodiversity declines: A case study on butterflies. *Diversity and Distributions*, **25**, 217–224.

Ridder, B. (2007). The Naturalness versus Wildness Debate: Ambiguity, Inconsistency, and Unattainable Objectivity. *Restoration Ecology*, **15**, 8–12.

Riggio, J., Baillie, J.E.M., Brumby, S., Ellis, E., Kennedy, C.M., Oakleaf, J.R., Tait, A., Tepe, T., Theobald, D.M., Venter, O., Watson, J.E.M. & Jacobson, A.P. (2020). Global human influence maps reveal clear opportunities in conserving Earth's remaining intact terrestrial ecosystems. *Global Change Biology*, **26**, 4344–4356.

Ritchie, H. & Roser, M. (2021). Biodiversity. *Our World in Data*.

Rivkin, L.R., Santangelo, J.S., Alberti, M., Aronson, M.F.J., Keyzer, C.W. de, Diamond, S.E., Fortin, M.-J., Frazee, L.J., Gorton, A.J., Hendry, A.P., Liu, Y., Losos, J.B., MacIvor, J.S., Martin, R.A., McDonnell, M.J., Miles, L.S., Munshi-South, J., Ness, R.W., Newman, A.E.M., Stothart, M.R., Theodorou, P., Thompson, K.A., Verrelli, B.C., Whitehead, A., Winchell, K.M. & Johnson, M.T.J. (2019). A roadmap for urban evolutionary ecology. *Evolutionary Applications*, **12**, 384–398.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. &

Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Salinitro, M., Alessandrini, A., Zappi, A., Melucci, D. & Tassoni, A. (2018). Floristic diversity in different urban ecological niches of a southern European city. *Scientific Reports*, **8**, 15110.

Schmidt, K.J., Poppendieck, H.-H. & Jensen, K. (2014). Effects of urban structure on plant species richness in a large European city. *Urban Ecosystems*, **17**, 427–444.

Schulte To Bühne, H., Tobias, J.A., Durant, S.M. & Pettorelli, N. (2021). Improving Predictions of Climate Change-Land Use Change Interactions. *Trends in Ecology & Evolution*, **36**, 29–38.

Schwartz, M.W., JURJAVCIC, N.L. & O'BRIEN, J.M. (2002). Conservation's Disenfranchised Urban Poor. *BioScience*, **52**, 601.

Schwartz, M.W., Smith, L.M. & Steel, Z.L. (2013). Conservation investment for rare plants in urban environments. *PLOS ONE*, **8**, e83809.

Segar, J., Callaghan, C.T., Ladouceur, E., Meya, J.N., Pereira, H.M., Perino, A. & Staude, I.R. (2022). Urban conservation gardening in the decade of restoration. *Nature Sustainability*, **5**, 649–656.

Shaffer, H.B. (2018). Urban biodiversity arks. *Nature Sustainability*, **1**, 725–727.

Sharrock, S., Oldfield, S. & Wilson, O. (2014). Plant Conservation Report 2014: A review of progress in implementation of the global strategy for plant conservation 2011–2020. *Secretariat of the convention on biological diversity & botanic gardens conservation international*.

Soanes, K. & Lentini, P.E. (2019). When cities are the last chance for saving species. *Frontiers in Ecology and the Environment*, **17**, 225–231.

Soanes, K., Sievers, M., Chee, Y.E., Williams, N.S.G., Bhardwaj, M., Marshall, A.J. & Parris, K.M. (2019). Correcting common misconceptions to inspire conservation action in urban environments. *Conservation Biology*, **33**, 300–306.

Sparrius, L.B., Odé, B. & Beringen, R. (2014). Basisrapport Rode Lijst Vaatplanten 2012 volgens Nederlandse en IUCN-criteria. *Floron Rapport*, **57**.

Sukopp, H. (2004). Human-caused impact on preserved vegetation. *Landscape and Urban Planning*, **68**, 347–355.

Sundseth, K. & Creed, P. (2008). *Natura 2000. Protecting Europe's biodiversity / Kerstin Sundseth and Peter Creed.* Office for Official Publications of the European Communities, Luxembourg, Oxford.

Sutcliffe, L.M.E., Batáry, P., Kormann, U., Báldi, A., Dicks, L.V., Herzon, I., Kleijn, D., Tryjanowski, P., Apostolova, I., Arlettaz, R., Aunins, A., Aviron, S., Baležentienė, L., Fischer, C., Halada, L., Hartel, T., Helm, A., Hristov, I., Jelaska, S.D., Kaligarič, M., Kamp, J., Klimek, S., Koorberg, P., Kostiuková, J., Kovács-Hostyánszki, A., Kuemmerle, T., Leuschner, C., Lindborg, R., Loos, J., Maccherini, S., Marja, R., Máthé, O., Paulini, I., Proença, V., Rey-Benayas, J., Sans, F.X., Seifert, C., Stalenga, J., Timaeus, J., Török, P., Swaay, C., Viik, E. & Tscharntke, T. (2015). Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity and Distributions*, **21**, 722–730.

Tallamy, D.W. (2007). *Bringing nature home*.

The European environment (2019). *The European environment. State and outlook 2020 : knowledge for transition to a sustainable Europe.* Publications Office of the European Union, Luxembourg.

Trochet, A. & Schmeller, D. (2013). Effectiveness of the Natura 2000 network to cover threatened species. *Nature Conservation*, **4**, 35–53.

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C. & Batáry, P. (2021). Beyond organic farming - harnessing biodiversity-friendly landscapes. *Trends in Ecology & Evolution*, **36**, 919–930.

Turo, K.J. & Gardiner, M.M. (2020). The balancing act of urban conservation. *Nature Communications*, **11**, 3773.

Uchida, K., Blakey, R.V., Burger, J.R., Cooper, D.S., Niesner, C.A. & Blumstein, D.T. (2021). Urban Biodiversity and the Importance of Scale. *Trends in Ecology & Evolution*, **36**, 123–131.

van Strien, A.J., van Swaay, C.A., van Strien-van Liempt, W.T., Poot, M.J. & WallisDeVries, M.F. (2019). Over a century of data reveal more than 80% decline in butterflies in the Netherlands. *Biological Conservation*, **234**, 116–122.

Veach, V., Moilanen, A. & Di Minin, E. (2017). Threats from urban expansion, agricultural transformation and forest loss on global conservation priority areas. *PLOS ONE*, **12**, e0188397.

Vellak, A., Tuvi, E.-L., Reier, Ü., Kalamees, R., Roosaluste, E., Zobel, M. & Pärtel, M. (2009). Past and present effectiveness of protected areas for conservation of naturally and anthropogenically rare plant species. *Conservation Biology*, **23**, 750–757.

Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., Frenne, P. de, Verheyen, K. & Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proceedings of the National Academy of Sciences*, **110**, 19456–19459.

Visconti, P., Butchart, S.H.M., Brooks, T.M., Langhammer, P.F., Marnewick, D., Vergara, S., Yanosky, A. & Watson, J.E.M. (2019). Protected area targets post-2020. *Science*, **364**, 239–241.

Vos, J.M. de, Joppa, L.N., Gittleman, J.L., Stephens, P.R. & Pimm, S.L. (2015). Estimating the normal background rate of species extinction. *Conservation Biology*, **29**, 452–462.

Wania, A., Kühn, I. & Klotz, S. (2006). Plant richness patterns in agricultural and urban landscapes in Central Germany—spatial gradients of species richness. *Landscape and Urban Planning*, **75**, 97–110.

Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, **515**, 67–73.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J. & Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, **2**, 599–610.

Watson, J.E.M., Shanahan, D.F., Di Marco, M., Allan, J., Laurance, W.F., Sanderson, E.W., Mackey, B. & Venter, O. (2016). Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. *Current biology : CB*, **26**, 2929–2934.

Watson, J.E.M. & Venter, O. (2017). Ecology: A global plan for nature conservation. *Nature*, **550**, 48–49.

Wintle, B.A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A., Lentini, P.E., Cadenhead, N.C.R. & Bekessy, S.A. (2019).

Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences*, **116**, 909–914.

Zwaan, D.R. de, Alavi, N., Mitchell, G.W., Lapen, D.R., Duffe, J. & Wilson, S. (2022). Balancing conservation priorities for grassland and forest specialist bird communities in agriculturally dominated landscapes. *Biological Conservation*, **265**, 109402.

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Statement of authorship: G.R. de S., K.B. and K.P. initiated the study. K.B., L.M. and K.P. designed the study. L.M and K.P collated and cleaned the data. K.P. performed the analysis. K.P. wrote the first draft of the manuscript, and all authors contributed substantially to revisions. G.R. de S. and K.B. have jointly supervised the work.

Table S1. Land-use types used in this research.

Rank	Classes in Marshall (2018)	Merged classes in our study
1	Heather	Natural habitat
2	Semi-natural forest	Natural habitat
3	Production forest	Natural habitat
4	Swamp peat	Natural habitat
5	Semi-natural grassland	Natural habitat
6	Dune	Natural habitat
7	River swamp	Natural habitat
8	Crop	Rural habitat
9	Fruit	Rural habitat
10	Pasture	Rural habitat
11	Greenhouse horticulture	Rural habitat
12	Other agricultural uses	Rural habitat
13	Urban green	Urban habitat
14	Urban grey, which include all impervious areas	Urban habitat

Table S2 Alpha diversity shown by mean richness and sd.

Species	Scale	Habitat	N	Richness	sd
all_spp	0.5km	Natural	1836	41	35
all_spp	1km	Natural	1836	180	93
all_spp	2km	Natural	1836	298	125
all_spp	0.5km	Rural	1215	31	24
all_spp	1km	Rural	1215	105	59
all_spp	2km	Rural	1215	206	83
all_spp	0.5km	Urban	502	47	52
all_spp	1km	Urban	502	335	159
all_spp	2km	Urban	502	503	203
all_spp	0.5km	Natura2000	1618	44	38
all_spp	1km	Natura2000	1618	187	101
all_spp	2km	Natura2000	1618	309	133
all_spp	0.5km	Non_Natura2000	8288	45	43
all_spp	1km	Non_Natura2000	8288	258	129
all_spp	2km	Non_Natura2000	8288	506	174
all_spp	0.5km	NNN	2087	43	36
all_spp	1km	NNN	2087	192	100
all_spp	2km	NNN	2087	312	131
all_spp	0.5km	Non_NNN	3931	41	43
all_spp	1km	Non_NNN	3931	216	140
all_spp	2km	Non_NNN	3931	411	186
native_spp	0.5km	Natural	1836	36	32
native_spp	1km	Natural	1836	159	82
native_spp	2km	Natural	1836	259	107
native_spp	0.5km	Rural	1215	28	23
native_spp	1km	Rural	1215	94	54
native_spp	2km	Rural	1215	182	74
native_spp	0.5km	Urban	502	37	45

native_spp	1km	Urban	502	262	116
native_spp	2km	Urban	502	379	135
native_spp	0.5km	Natura2000	1618	38	34
native_spp	1km	Natura2000	1618	165	89
native_spp	2km	Natura2000	1618	269	113
native_spp	0.5km	Non_Natura2000	16576	40	39
native_spp	1km	Non_Natura2000	16576	239	118
native_spp	2km	Non_Natura2000	16576	417	123
native_spp	0.5km	NNN	2087	37	33
native_spp	1km	NNN	2087	169	89
native_spp	2km	NNN	2087	271	112
native_spp	0.5km	Non_NNN	3931	36	37
native_spp	1km	Non_NNN	3931	182	109
native_spp	2km	Non_NNN	3931	336	131
threatened_spp	0.5km	Natural	1836	3	4
threatened_spp	1km	Natural	1836	12	9
threatened_spp	2km	Natural	1836	19	13
threatened_spp	0.5km	Rural	1215	1	1
threatened_spp	1km	Rural	1215	2	2
threatened_spp	2km	Rural	1215	5	5
threatened_spp	0.5km	Urban	502	1	2
threatened_spp	1km	Urban	502	8	7
threatened_spp	2km	Urban	502	15	10
threatened_spp	0.5km	Natura2000	1618	4	4
threatened_spp	1km	Natura2000	1618	12	10
threatened_spp	2km	Natura2000	1618	20	13
threatened_spp	0.5km	Non_Natura2000	8288	2	2
threatened_spp	1km	Non_Natura2000	8288	7	6
threatened_spp	2km	Non_Natura2000	8288	19	12
threatened_spp	0.5km	NNN	2087	3	4

threatened_spp	1km	NNN	2087	12	10
threatened_spp	2km	NNN	2087	19	13
threatened_spp	0.5km	Non_NNN	3931	1	1
threatened_spp	1km	Non_NNN	3931	5	5
threatened_spp	2km	Non_NNN	3931	11	10
native_rare_spp	0.5km	Natural	1836	6	7
native_rare_spp	1km	Natural	1836	22	22
native_rare_spp	2km	Natural	1836	38	34
native_rare_spp	0.5km	Rural	1215	1	2
native_rare_spp	1km	Rural	1215	4	5
native_rare_spp	2km	Rural	1215	11	10
native_rare_spp	0.5km	Urban	502	4	5
native_rare_spp	1km	Urban	502	34	24
native_rare_spp	2km	Urban	502	60	36
native_rare_spp	0.5km	Natura2000	1618	6	8
native_rare_spp	1km	Natura2000	1618	24	23
native_rare_spp	2km	Natura2000	1618	41	35
native_rare_spp	0.5km	Non_Natura2000	16576	3	5
native_rare_spp	1km	Non_Natura2000	16576	19	18
native_rare_spp	2km	Non_Natura2000	16576	68	56

native_rare_spp	0.5km	NNN	2087	6	8
native_rare_spp	1km	NNN	2087	23	23
native_rare_spp	2km	NNN	2087	39	35
native_rare_spp	0.5km	Non_NNN	3931	2	4
native_rare_spp	1km	Non_NNN	3931	15	18
native_rare_spp	2km	Non_NNN	3931	37	33

Table S3 Beta diversity shown by mean Jaccard similarity and sd.

Species	Scale	Habitat	Jaccard_value	Jaccard_value_sd
All_spp	0.5km	Natural	0.93	0.08
All_spp	0.5km	Rural	0.94	0.08
All_spp	0.5km	Urban	0.96	0.06
All_spp	0.5km	Natura2000	0.93	0.08
All_spp	0.5km	Non_Natura2000	0.96	0.06
All_spp	0.5km	NNN	0.93	0.08
All_spp	0.5km	Non_NNN	0.95	0.07
All_spp	1km	Natural	0.78	0.11
All_spp	1km	Rural	0.84	0.1
All_spp	1km	Urban	0.69	0.12
All_spp	1km	Natura2000	0.78	0.11
All_spp	1km	Non_Natura2000	0.76	0.1
All_spp	1km	NNN	0.78	0.11
All_spp	1km	Non_NNN	0.8	0.1
All_spp	2km	Natural	0.68	0.13
All_spp	2km	Rural	0.73	0.11
All_spp	2km	Urban	0.59	0.14
All_spp	2km	Natura2000	0.68	0.14
All_spp	2km	Non_Natura2000	0.59	0.1
All_spp	2km	NNN	0.68	0.13
All_spp	2km	Non_NNN	0.65	0.11
Native_spp	0.5km	Natural	0.93	0.08
Native_spp	0.5km	Rural	0.94	0.08
Native_spp	0.5km	Urban	0.96	0.06
Native_spp	0.5km	Natura2000	0.93	0.08
Native_spp	0.5km	Non_Natura2000	0.96	0.06
Native_spp	0.5km	NNN	0.93	0.08

Native_spp	0.5km	Non_NNN	0.95	0.07
Native_spp	1km	Natural	0.78	0.11
Native_spp	1km	Rural	0.84	0.1
Native_spp	1km	Urban	0.66	0.14
Native_spp	1km	Natura2000	0.79	0.12
Native_spp	1km	Non_Natura2000	0.75	0.11
Native_spp	1km	NNN	0.78	0.11
Native_spp	1km	Non_NNN	0.79	0.12
Native_spp	2km	Natural	0.67	0.14
Native_spp	2km	Rural	0.73	0.11
Native_spp	2km	Urban	0.54	0.15
Native_spp	2km	Natura2000	0.67	0.15
Native_spp	2km	Non_Natura2000	0.55	0.11
Native_spp	2km	NNN	0.67	0.14
Native_spp	2km	Non_NNN	0.62	0.13
Threatened_spp	0.5km	Natural	0.94	0.14
Threatened_spp	0.5km	Rural	0.97	0.14
Threatened_spp	0.5km	Urban	0.97	0.11
Threatened_spp	0.5km	Natura2000	0.95	0.14
Threatened_spp	0.5km	Non_Natura2000	0.98	0.08
Threatened_spp	0.5km	NNN	0.95	0.13
Threatened_spp	0.5km	Non_NNN	0.98	0.1
Threatened_spp	1km	Natural	0.89	0.15
Threatened_spp	1km	Rural	0.97	0.12
Threatened_spp	1km	Urban	0.92	0.11
Threatened_spp	1km	Natura2000	0.89	0.15
Threatened_spp	1km	Non_Natura2000	0.97	0.06
Threatened_spp	1km	NNN	0.9	0.14
Threatened_spp	1km	Non_NNN	0.97	0.08
Threatened_spp	2km	Natural	0.85	0.16

Threatened_spp	2km	Rural	0.96	0.1
Threatened_spp	2km	Urban	0.87	0.13
Threatened_spp	2km	Natura2000	0.85	0.16
Threatened_spp	2km	Non_Natura2000	0.93	0.07
Threatened_spp	2km	NNN	0.86	0.15
Threatened_spp	2km	Non_NNN	0.95	0.08
native_rare_spp	0.5km	Natural	0.95	0.12
native_rare_spp	0.5km	Rural	0.98	0.1
native_rare_spp	0.5km	Urban	0.96	0.1
native_rare_spp	0.5km	Natura2000	0.95	0.12
native_rare_spp	0.5km	Non_Natura2000	0.99	0.05
native_rare_spp	0.5km	NNN	0.96	0.11
native_rare_spp	0.5km	Non_NNN	0.99	0.06
native_rare_spp	1km	Natural	0.91	0.12
native_rare_spp	1km	Rural	0.98	0.07
native_rare_spp	1km	Urban	0.87	0.1
native_rare_spp	1km	Natura2000	0.91	0.12
native_rare_spp	1km	Non_Natura2000	0.97	0.05
native_rare_spp	1km	NNN	0.92	0.11
native_rare_spp	1km	Non_NNN	0.97	0.06
native_rare_spp	2km	Natural	0.87	0.14
native_rare_spp	2km	Rural	0.97	0.08
native_rare_spp	2km	Urban	0.81	0.14
native_rare_spp	2km	Natura2000	0.87	0.14
native_rare_spp	2km	Non_Natura2000	0.91	0.07
native_rare_spp	2km	NNN	0.89	0.13
native_rare_spp	2km	Non_NNN	0.93	0.08

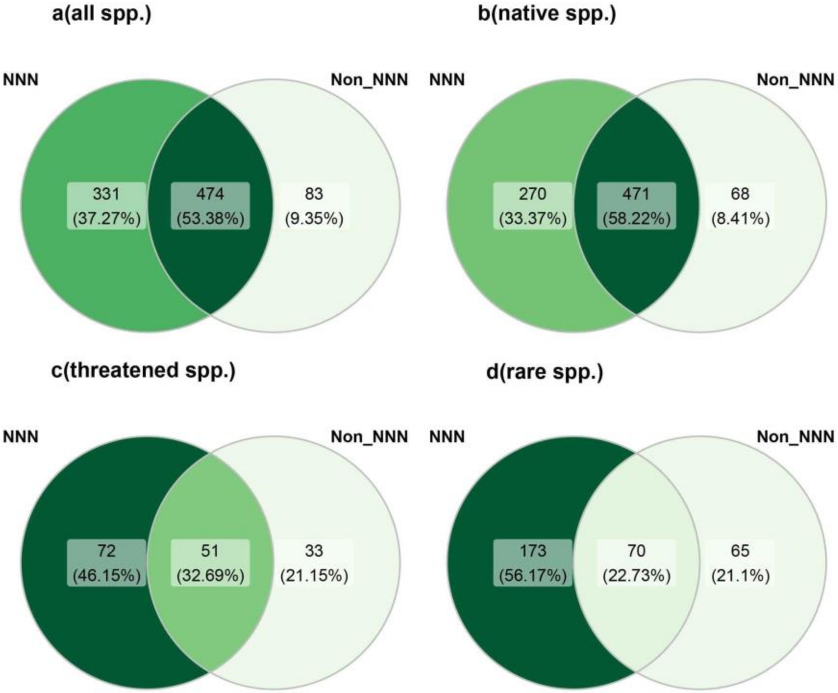

Figure S1 Plant species richness (γ-diversity) in habitats with different protection management (NNN). a-d, all species, native species, threatened species and native rare species.

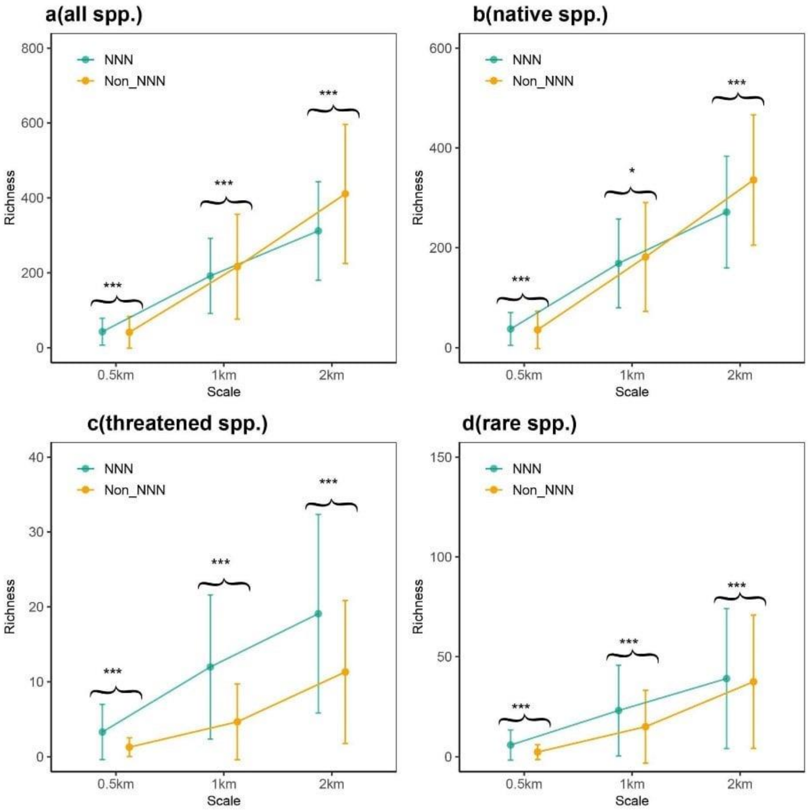

Figure S2 Plant species richness (α-diversity) in habitats with different protection management (NNN). a-d, all species, native species, threatened species and native rare species.

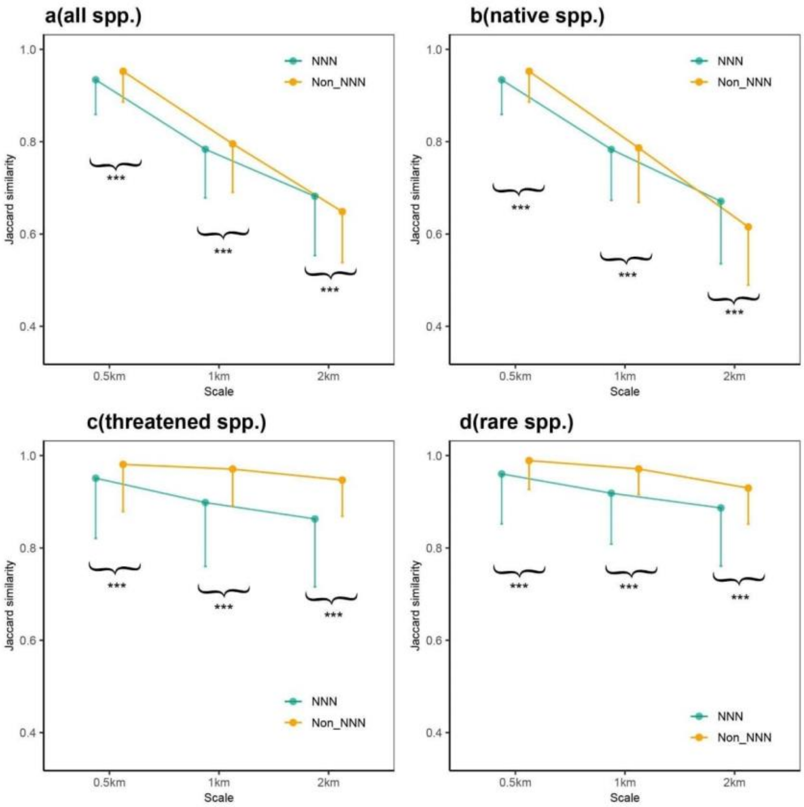

Figure S3 Plant species richness (β-diversity) in habitats with different protection management (NNN). a-d, all species, native species, threatened species and native rare species.

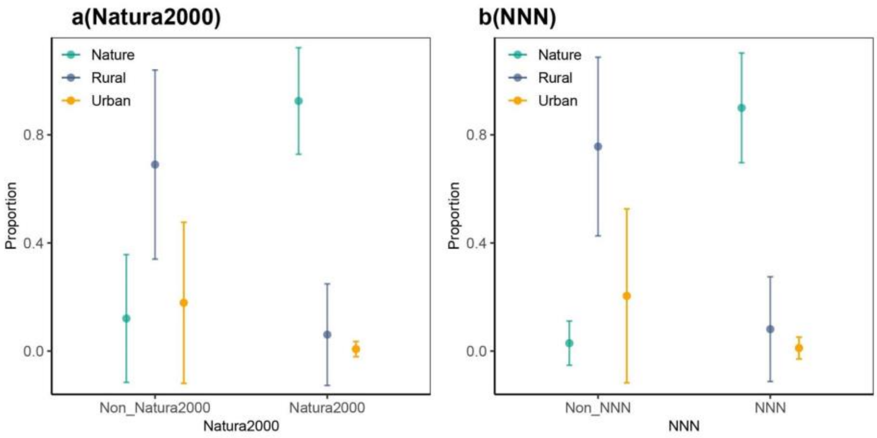

Figure S4 Proportions of land-use types in (a) Natura 2000 and non-Natura 2000, (b) NNN and non-NNN.

Chapter 6

General discussion

Kaixuan Pan

We are currently experiencing what has been termed the sixth mass extinction event, with observed and estimated species extinction rates orders of magnitude larger than long term (geological) background rates, for a wide variety of taxa (Ceballos et al., 2015). Around one million plants and animals are now facing extinction (IPBES, 2019, 2020) and populations of wild animals have plummeted 69% since 1970 (WWF, 2022). Although it has raised concerns and many actions have been attributed to biodiversity conservation, we still fail to halt or even reverse the current trends of species decline (Leclère et al., 2020; Obura et al., 2021). We need to improve our understanding of the patterns, drivers and processes governing wild species populations in the current Anthropocene era. As part of this endeavour, the study of the dynamics of plant occurrence and diversity across space and over time is important as it allows us to predict the occurrence of species and their trends (Schulte To Bühne et al., 2021), which are essential support in making effective guidelines for conservation. A combination of biotic (e.g. pollinator) and abiotic (e.g. land-use and vegetation structure) factors determine the establishment, reproduction and survival of plant species and affect the dynamics of plants (Sala et al., 2000; Ozinga et al., 2009; Schulte To Bühne et al., 2021). Given the continuous threats for plant species and their decline over time, it is urgent to know which are the factors that sustain their populations and what can we do to ensure plant diversity in our ecosystems in the future.

The central aim of this thesis is to improve our understanding of how different plant species respond to biotic and abiotic conditions and how we can improve the conservation effectiveness based on this. Specifically, I focus on the following questions:

1) To what extent is natural land cover important to plant species occurrence?

2) Do plants with biotic and abiotic pollination respond differently to habitat type and vegetation structure?

3) Have insect-pollinated plant species declined more or less than wind-pollinated or selfing species in the Netherlands? and

4) To what extent determine the three main land-use types (nature, rural and urban areas) and the level of nature protection (being part of Netherlands' Nature Network, Nature 2000 or not) the occurrence of different plant species?

In the current chapter, I will synthesise what has been achieved regarding the questions proposed. Then, I'll discuss the available scientific evidence and implications based on our findings. Finally, the outlook of the future study is discussed.

Progress made in answering these questions in this thesis

Question 1: To what extent is natural land cover important to plant species occurrence? (Chapter 2)

The importance of robust (semi-)natural areas for many species is well known. However, in densely-populated areas of the world, which are rapidly expanding, discussion on the need to keep (semi-)natural areas for nature conservation is growing. In fact, in such areas, much effort (and conservation funding) is spent on creating small habitats for protecting species in agricultural and urban landscapes, that's non-(semi-)natural areas. So, understanding exactly whether -and to which extent- (semi-)natural habitat cover affects different species groups remains a central debate.

Chapter 2 aims at understanding the importance of natural land cover to plants. Since different species may respond differently to environmental conditions, with some species preferring nature while others are adaptable to non-nature, I studied the response of each species to natural land cover based on species distribution models. Results show there is a mismatch between the species' preferred landscapes and landscapes available in the Netherlands: most species, particularly threatened species, prefer landscapes with high natural land cover (>= 50%), while most landscapes in the Netherlands have low nature cover (< 25%). Although some patches in non-(semi-)natural areas might be habitats for some species, landscapes with over 50% NLCs are still a hotspot for most species. Accordingly, we should protect those landscapes and improve (semi-)natural areas in disturbed landscapes to avoid species decline. Moreover, landscapes with more than 80% natural land cover are needed to support species of conservation concern.

Question 2: Do plants with biotic and abiotic pollination respond differently to habitat type and vegetation structure?

Plant–animal interactions are fundamentally important in ecosystems, but have often been ignored by studies of land-use change impacts on biodiversity. Chapter 3 presents how the interaction between pollinators and plants affect responses of plants with different pollination types to land-use and vegetation structure. This thesis shows that most woody and herbs in (semi-)natural habitats in the Netherlands are insect-pollinated, with more woody species pollinated by insects in dune, river swamp and swamp peat, more herbs pollinated in dune than in other habitats. Plants with biotic pollination prefer dense cover of herb layer or shrub layer instead of tree layers. However, wind-pollinated woody species prefer high cover of tree layers while grasses prefer open habitats.

Question 3 whether and to what extent insect-pollinated species have declined in our ecosystem at the community level

Related to the third question, this thesis shows that plants pollinated by insects have shown a strong decline over the last 87 years, while wind-pollinated plants have increased over time. This can be explained by the decline in pollination services in the Netherlands. The alarming results inform us that species conservation should also focus on relevant pollinators instead of just plants themselves (Chapter 4).

Question 4 what extent the three main land-use types (nature, rural and urban areas) and the level of nature protection (being part of Netherlands' Nature Network, Nature 2000 or not) contribute to the occurrences of different plant species

Finally, for the last question, I show that protected areas and nature are important habitats as refuges for most species, particularly threatened and rare species. Moreover, protected areas also support high alpha and beta diversity of threatened and rare species, but not of all and native species. Nature is also important to support threatened species and rare species at small scale, but urban areas are important for all and native species (Chapter 5).

Measuring and modelling species occurrence

In the past century, distribution data of plants in the Netherlands has been collected mainly through direct observation in the field either in an opportunistic way, i.e. single records of species, or in more structured surveys, e.g. through species list for a location or vegetation plots. In addition, and starting more recently, these data have become the starting point for large-scale analyses and modelling, e.g. species distribution models (SDM), plant community analysis, and rarefaction and extrapolation. As there are a number of tools available for assessing the occurrence of species, one has to decide which method to select based on the questions. In this thesis I used SDMs, occurrence from plot data, and assessing community aspects using accumulation curves. Below I will shortly reflect on my findings using these methods.

In chapter 2, I used SDMs as I aim to quantify the relationship between environmental conditions and occurrences of each species across space. SDMs have been validated to be an effective method to link environmental variables to species distributions (Laughlin et al., 2020). One of the most powerful algorithms to build SDMs is MaxEnt, which can robustly deal with a variety of presence-only data (Phillips et al., 2006; Phillips and Dudík, 2008; González-Irusta et al., 2015) and often outperforms other SDM modelling applications in dealing with small samples and preventing overfitting (Phillips et al., 2006; Phillips and Dudík, 2008). However, in most cases, SDM is used to predict the habitat suitability of species. In this thesis I show that it can also be used to quantify the relationship between species occurrence and environmental conditions. I show that the responses of different species and species groups (native vs exotic, rare vs common and threatened vs unthreatened) to environmental factors and contributions of different environmental factors to the occurrence of species vary strongly. Understanding these differences better is important to guide conservation strategies and restoration efforts.

Vegetation plot data was used in Chapters 3 and 4 to investigate the correlation between species richness (alpha diversity) over time and environmental conditions across space. A large amount of species occurrence data have been collected in the past decades at either global scale (e.g. GBIF, https://www.gbif.org/), or national scale (e.g. NDFF, https://www.ndff.nl/), and these datasets have contributed to a large amount of studies on species distributions and the development of some macroecological theories (Currie et al., 2004; Pärtel et al., 2016). However, studies on species compositions and richness ideally use a species checklist from a location. Unfortunately, these databases (e.g. sPlot-https://www.idiv.de/en/splot.html, EVA-http://euroveg.org/eva-database and GrassPlot-https://edgg.org/databases/GrassPlot) are still in development and are not unavailable to the public (Bruelheide et al., 2019; Večeřa et al., 2021). LVD is the Dutch Vegetation Database, which provides plant information recorded in each plot in various habitats covering mostly (semi-)natural landscapes in the past 87 years (Hennekens, 2018). This database is made freely available to all researchers and the public. With this database, we can explore the historical changes in species composition and richness of each species group over time. Based on this database, I investigated the temporal trends of different species groups and species richness in relation to habitat and vegetation structure so that I could better understand some of the factors driving species occurrence.

In Chapter 5, I assessed the proportion of different species groups in a community with the assistance of rarefaction and extrapolation methods (see also Carvalheiro et al., 2013).

Plant occurrence data often include different sampling efforts across space, e.g. all species are recorded in some plant communities, while only few species are recorded in other communities. This makes comparison of estimated richness across space difficult (Carvalheiro et al., 2013). Rarefaction and extrapolation methods make richness in different areas comparable (Carvalheiro et al., 2013; Hsieh et al., 2016). In Chapter 5, I estimated the proportion of species that are recorded in a community (sampling effort) by rarefaction and selected those well-sampled cells with the proportion of recorded species above 0.8 to compare richness between cells. Although this method only retains sites that are well-sampled, completed species lists are retained. In contrast, methods estimating richness by either interpolation or extrapolation sampling efforts to the same level will lose species information.

The importance of natural land cover

Whilst there are multiple drivers of contemporary extinctions, natural habitat loss is considered to be the most important driver. With the increase of human activities, many natural habitats are converted to human dominated habitats, e.g. agriculture and urban fabric. Much evidence has revealed the importance of natural habitats to plant species conservation (Brooks et al., 2006; Watson et al., 2016; Veach et al., 2017; Watson et al., 2018; Wintle et al., 2019). This thesis also shows that natural areas are suggested to be important to refuge most species on the checklist in the Netherlands, particularly threatened and rare species. Besides, in a mixed landscape with nature and human-used elements, I find that a higher natural land cover correlates to a higher species occurrence probability, and over 80% natural land cover benefits threatened and rare species the most. These findings reveal that landscapes with very high NLC are particularly valuable for the protection of threatened species. Some other studies also indicate that a relatively high natural land cover is important for sustaining biodiversity (Bascompte and Rodriguez, 2001; Blaser et al., 2018). However, these studies only support the relationship between the overall richness and natural land cover, while different species (groups) may respond differently to natural land cover as they have different adaptation strategies (Laughlin et al., 2020). Some species are extraordinarily dependent on natural habitats, while the others are rapidly adaptable to human dominated habitats (Alberti, 2015; Donihue and Lambert, 2015; Rivkin et al., 2019). Some are even exclusively dependent on agricultural habitats because of food resources provided in these habitats (Magioli et al., 2019). This led to our findings of diversity of different plant groups in urban and rural habitats.

Following natural habitats, urban habitats are the other important habitats for refuging diversity of plants. Urban habitats are also important to support alpha and beta diversity of different taxon groups, particularly for general species but also for a few conservation-relevant species. This result is encouraging because it indicates we can take the chance to create a sustainable ecosystem by conserving species in human dominated habitats.

Turning to other important habitats, rural areas (agriculture), the thesis finds that it sustains fewer species than natural and urban habitats. Given the low plant diversity while over 70% of areas in the Netherlands used agriculture, it is important and urgent to find solutions to improve the quality of agriculture sustaining plant diversity. One of the most important actions is increasing (semi-)natural elements, the effectiveness of which has been discussed by many studies (Manhoudt and Snoo, 2003; Cormont et al., 2016; Tscharntke et al., 2021). A central debate remains how much natural land cover should be maintained in the agricultural landscape. According to Cormont et al. (2016), 3%-7% natural land cover doesn't contribute to the increase of plant diversity, but has an effect on insect species. Other studies suggest that at least 20% natural land cover is the threshold of species conservation in agriculture, but not specifically for plant species (Tscharntke et al., 2021). Although 20% natural land cover will increase the diversity, my results show it is not enough for native species conservation in the Netherlands because 60% natural land cover will support more species. However, given that we have to consider trade-offs between species conservation and crop production, the final suggestion is to keep 20% natural land cover in agricultural areas, but increase natural elements if it is possible.

Overall, natural habitats are important for species conservation, and nature should be brought back to the country, as stated in the new EU nature restoration law. However, the preferences of species for natural land cover is mismatched with the landscapes of the Netherlands, with a large number of species prefer landscapes with over 50% natural land cover while most landscapes in the Netherlands are covered by lower than 25% natural land cover. It implies that species conservation relying on nature is not enough and we need to seek for other conservation opportunities. Although urban communities may be less diverse in threatened species than in natural habitats, they still contain many species of considerable value for conservation. Increasing natural habitats and green infrastructure will contribute to better conservation of these species in urban areas. For agricultural areas, given the lower species richness and (semi)-natural coverage in rural areas than in urban areas, the marginal gain in species conservation, i.e. how many additional species you get for your investment, by increasing (semi-)natural habitats in rural areas is higher than increasing (semi-)natural habitats in urban areas. However, the species that benefit from improving rural areas are rarely restricted to these habitats and thus would also benefit from improving or expanding urban or natural areas. To achieve an effective conservation of species, a 20% threshold of (semi-)natural habitats in agricultural landscapes is recommended. As such, although we may not be able to reverse species extinctions, the trends here presented help justify the continuation of investment in conservation.

Plant-insect interaction

Land use change have been indicated to be the most important drivers of plant biodiversity change, yet most existing studies are limited to the direct effects of land-use on individual species, abundance or richness (Cusser et al., 2016; Mendenhall et al., 2016; Blaser et al., 2018). However, land-use also decreased the availability of some biotic resources (e.g. pollinator and disperser). Comparably few studies take biotic species interaction into consideration when exploring the loss of plant diversity over time, although the importance of biotic factors to the sustaining of plant diversity has been indicated (Blois et al., 2013; Schleuning et al., 2020).

Among all biotic factors, pollinators are shown to be closely related to florastic change (Biesmeijer et al., 2006; Potts et al., 2010). Plant-pollinator interaction is one of the most crucial ecological interactions in terrestrial ecosystems (Ollerton et al., 2011), and pollinator decline reduces plant fitness (Thomann et al., 2013). This thesis demonstrated that natural communities have shifted from insect-pollination to wind-pollination, with declines in insect-pollinated plants and increase of wind-pollinated plants (Chapter 2). Although it remains unknown to what extent the insect-pollinated plants decline is caused by other factors, This thesis convincingly linked the decline of plant species to the decline of corresponding insect pollinators (Chapter 4) as insect-pollinated species didn't show vulnerability to increased nitrogen. In the past decades, accumulating evidence has implied that insect and insect pollinators have shown a strong decline in Europe and all over the world (van Klink et al., 2020; Janzen and Hallwachs, 2021; Hallmann et al., 2021; Warren et al., 2021; Forister et al., 2021) due to environmental changes, with land-use change as the most important driver. With the decline of insect pollinators, the reproductions of many plant species are threatened, which in turn affect ecosystem services. Recent studies show that over 80% of flowering plants are pollinated by insects and over half of them would suffer decline in seed reproduction without pollinators (Ollerton et al., 2011; Rodger et al., 2021). With the failure of plant reproduction, species population will definitely decrease and some will disappear from the local plant community. Compared to results showing decline in insect-pollinated plants at national scale (Biesmeijer et al., 2006), our results demonstrating the loss of insect-pollinated species at community level is alarming. If the insect-pollination continues to decline, plant diversity will be further threatened and over 35% of overall global crop production will be endangered (Tscharntke, 2021). In addition to the decrease of food production, the loss of plant species will definitely affect other ecosystem services, including carbon sequestration, water purification, soil fertility, natural pest regulation, etc (Vos, 2014; Turnbull et al., 2016).

To mitigate the decline of insect-pollinated species, both habitats and vegetation structure are important factors (Chapter 3). In principle, the conversion from (semi-)natural habitat, particularly habitats like dunes and swamp peat, to other land-use types will decline insect-pollinated species (Chapter 3). Natural habitats are considered to have more diverse pollinators, which contribute to the diversity of plant species (Cusser et al., 2016; Bartual et al., 2019). In addition, 3-D vegetation structure change, e.g. habitat becoming too open or covered by shrub or tree layers, will also reduce insect-pollinated plants because habitats that are too open or densely covered have fewer insect pollinator diversity (Rech et al., 2016; Aguirre-Gutiérrez et al., 2017).

Conservation implications and conclusion remarks

Biodiversity conservation tends to focus on intact natural areas without identifying habitat requirements of species or areas with specific species for protection (Dudley, 2008). However, different species often have different responses to environmental conditions due to their varieties of adaptations (Laughlin et al., 2020). Results obtained in this thesis show that formal protected areas are important in conserving different plant species groups, particularly threatened and rare species. Currently, more ambitious targets, including protecting 30% of the planet by 2030 (Dinerstein et al., 2019) and half the terrestrial biosphere by 2050 (Locke, 2013; Dinerstein et al., 2017; Watson and Venter, 2017), have been proposed. However, given the conflict between habitat conservation, food provision and other land uses (Leclère et al., 2020), it is essential to find other conservation strategies. Urban areas are indicated to be emerging conservation hotspots of plant species, particularly for all species and native species. Recently, urban areas as species conservation are increasingly embraced (Dearborn and Kark, 2010; Shaffer, 2018; Soanes and Lentini, 2019; Soanes et al., 2019), even for some threatened species (Ives et al. 2016). Given the expanding urban areas, I suggest strengthening the green facilities in urban areas to achieve a better conservation of species in urban areas. However, the current protected area should still be in central protection. In relation to urban areas, rural areas sustain few species due to intensive human-use (Sala et al., 2000). In this case, increasing natural land cover in agricultural areas will improve the habitat quality and increase species diversity, particularly in areas with low natural land cover (0-50%). To conserve threatened species, natural land cover should be increased to over 75%.

Despite the conservation suggestions provided by this thesis, the first step is to make the goal of conservation clear. Given the urgency of conserving threatened species and the long list of threatened species on the relist in the Netherlands, the conservation priority should be protecting threatened species by paying efforts on protected areas, as well as conserving and recovering natural habitats. Another conservation-relevant species is rare species, which can be conserved in protected areas and natural habitats. In addition, urban habitats should also be maintained because a high rare species richness is found in urban areas. Meanwhile, the common native species can be protected very well in urban areas. Although rural areas also sustain some common species, its conservation effectiveness should be increased by increasing nature and introducing native species. This is also relevant to the recent initiative of nature-inclusive society in the Netherlands (https://en.rli.nl/publications/2022/advice/nature-inclusive-netherlands). This thesis suggests urban areas are acting effectively in supporting common species, but the natural cover and quality in rural areas should be improved, particularly given around 63% of the area in the Netherlands is agriculture. In order to keep a high habitat suitability for native species, 6% natural land cover should be considered.

Additionally, given that the majority of flowering plants, including most crops, are insect-pollinated (Ollerton et al., 2011; Rodger et al., 2021), and that relevant insect pollinators have shown a strong decline in the past decades (Biesmeijer et al., 2006; Hallmann et al., 2021; Warren et al., 2021), which have declined the insect-pollinated plants accordingly, the thesis encourages the conservation of insect pollinators in landscapes. Action can include increasing natural habitats in human-dominated areas, decreasing the use of pesticide, etc (Goulson et al., 2015; Warren et al., 2021). In addition, propriate management actions like managing vegetation structure will also contribute to the increase of pollinators and pollinator-dependent plants (Culley et al. 2002, Chapter 3).

In summary, conservation investments in the Netherlands are suggested to include 1) protecting natural reserves. Some areas with species that are currently not in protected areas should be protected in order to make all species in the Netherlands under protection; 2) strengthen species conservation in urban and rural areas. Strategies include increasing green infrastructure and the coverage of semi-natural elements, and introducing native and threatened species in urban and rural areas, particularly in areas without or with little (semi-)natural coverage; 3) diverging vertical vegetation structure, e.g. mixture of trees and open nature, will benefit species diversity; 4) specific efforts should be given to insect pollinators and insect-pollinated plants.

Although the Netherlands has undertaken a great land use change with decline in many species, currently over 90% of native species and approximately 80% of threatened species are protected in natural reserves due to a lot of conservation efforts. Even in human dominated areas, particularly in cities, there are many species. It may provide some information for other countries, but should be context dependent. The Netherlands experienced a loss of natural areas. The loss of natural areas has been reversed after 1990 and people increase natural elements in urban areas or agriculture. This is a way of land-sharing, which is the fundamental action carried out throughout all of the Europe, e.g. High Nature Value (HNV) farming, which is also partly under protection by Natura 2000, although the percentage of nature in human dominated areas varies across different countries (Benedetti, 2017). Nonetheless, in some countries like China, land-sparing is the main action of species conservation. It means intensified agriculture or urban settlements and wilderness are separate. It provides some wisdom to other countries, for example, China. Although China has paid much effort on species conservation by protecting protected areas. Conservations outside protected areas are still lacking. According to our study and previous studies, scientific planning of land-use, increasing (semi-)natural elements in human dominated areas and diverging vertical vegetation structure are applicable. However, these conservation practices are too dependent on local context. For example, 1.2 million km^2 of farmland has been set up as the redline to ensure food security. These farmlands cannot be transformed into other types of land. In this case, it is not possible to conserve species by increasing large areas of (semi-)natural elements. Instead, increasing the diversity of crops and reducing field size with increasing some natural habitats along field edges may balance the requirements of food supply and species conservation. Slightly increasing some natural elements (e.g. green roof) in urban areas will also benefit biodiversity. In addition, although China has an ambition to achieve ‘Ecological Civilization’ by balancing economic development and nature conservation, China has a growing deficit of conservation research capacity and biodiversity infrastructure. Constructing species monitoring webs will help China to evaluate the status of species and effectiveness of conservation actions.

The findings of this thesis suggest future challenges as in the field of biodiversity conservation and applied ecology. The inclusion of multi-species responses to land use types and protection levels are definitely two with high importance because figuring out the importance of protection managements and land-use types to different species groups will provide a clearer guideline for species conservation. However, with the time on-going, whether and to what extent increased protected areas or natural habitats are important to species? Will protected areas or nature be more important to species or less important to species? The answer to this question will help us to understand the change in species-area relationship, which is an essential guideline for future species conservation.

Moreover, including insect-pollinators and plant species interaction information in the assessment of plant species dynamics is a challenge that deserves much attention given that plant species occurrences and persistence clearly depend on insect pollinators. This is of main concern as most research for biodiversity conservation purposes is carried out with direct responses of species to abiotic factors without considering the effects of abiotic factors. It deserves further exploration in the further studies identifying how the biotic and abiotic factors jointly affect the distributions and occurrences of plant species. In addition, identifying how species with different traits respond to each driver will help us understand the mechanism of species decline.

References

Aguirre-Gutiérrez, J., van Treuren, R., Hoekstra, R., van Hintum, T.J., 2017. Crop wild relatives range shifts and conservation in Europe under climate change. Diversity and Distributions 23, 739–750.

Alberti, M., 2015. Eco-evolutionary dynamics in an urbanizing planet. Trends in Ecology & Evolution 30, 114–126. https://www.sciencedirect.com/science/article/pii/S0169534714002493.

Bartual, A.M., Sutter, L., Bocci, G., Moonen, A.-C., Cresswell, J., Entling, M., Giffard, B., Jacot, K., Jeanneret, P., Holland, J., Pfister, S., Pintér, O., Veromann, E., Winkler, K., Albrecht, M., 2019. The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. Agriculture, Ecosystems & Environment 279, 43–52. https://www.sciencedirect.com/science/article/pii/S0167880919300969.

Bascompte, J., Rodriguez, M.A., 2001. Habitat patchiness and plant species richness. Ecol Letters 4, 417–420.

Benedetti, Y., 2017. Trends in High Nature Value farmland studies: A systematic review. European Journal of Ecology 3, 19–32.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science (New York, N.Y.) 313, 351–354.

Blaser, W.J., Oppong, J., Hart, S.P., Landolt, J., Yeboah, E., Six, J., 2018. Climate-smart sustainable agriculture in low-to-intermediate shade agroforests. Natural Sustainability 1, 234–239. https://www.nature.com/articles/s41893-018-0062-8.

Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C., Finnegan, S., 2013. Climate change and the past, present, and future of biotic interactions. Science (New York, N.Y.) 341, 499–504.

Brooks, T.M., Mittermeier, R.A., Da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L., 2006. Global biodiversity conservation priorities. Science (New York, N.Y.) 313, 58–61.

Bruelheide, H., Dengler, J., Jiménez-Alfaro, B., Purschke, O., Hennekens, S.M., Chytrý, M., Pillar, V.D., Jansen, F., Kattge, J., Sandel, B., Aubin, I., Biurrun, I., Field, R., Haider, S., Jandt, U., Lenoir, J., Peet, R.K., Peyre, G., Sabatini, F.M., Schmidt, M., Schrodt, F., Winter, M., Aćić, S., Agrillo, E., Alvarez, M., Ambarlı, D., Angelini, P., Apostolova, I., Arfin Khan, M.A.S., Arnst, E., Attorre, F., Baraloto, C., Beckmann, M., Berg, C., Bergeron, Y., Bergmeier, E., Bjorkman, A.D., Bondareva, V., Borchardt, P., Botta-Dukát, Z., Boyle, B., Breen, A., Brisse, H., Byun, C., Cabido, M.R., Casella, L., Cayuela, L., Černý, T., Chepinoga, V., Csiky, J., Curran, M., Ćušterevska, R., Dajić Stevanović, Z., Bie, E. de, Ruffray, P. de, Sanctis, M. de, Dimopoulos, P., Dressler, S., Ejrnæs, R., El-Sheikh, M.A.E.-R.M., Enquist, B., Ewald, J., Fagúndez, J., Finckh, M., Font, X., Forey, E., Fotiadis, G., García-Mijangos, I., Gasper, A.L., Golub, V., Gutierrez, A.G., Hatim, M.Z., He, T., Higuchi, P., Holubová, D., Hölzel, N., Homeier, J., Indreica, A., Işık Gürsoy, D., Jansen, S., Janssen, J., Jedrzejek, B., Jiroušek, M., Jürgens, N., Kącki, Z., Kavgacı, A., Kearsley, E., Kessler, M., Knollová, I., Kolomiychuk, V., Korolyuk, A., Kozhevnikova, M., Kozub, Ł., Krstonošić, D., Kühl, H., Kühn, I., Kuzemko, A., Küzmič, F., Landucci, F., Lee, M.T., Levesley, A., Li, C.-F., Liu, H., Lopez-Gonzalez, G., Lysenko, T., Macanović, A., Mahdavi, P., Manning, P., Marcenò, C., Martynenko, V., Mencuccini, M., Minden, V., Moeslund, J.E., Moretti, M., Müller, J.V., Munzinger, J., Niinemets, Ü., Nobis, M., Noroozi, J., Nowak, A., Onyshchenko, V., Overbeck, G.E., Ozinga, W.A., Pauchard, A., Pedashenko, H., Peñuelas, J., Pérez-Haase, A., Peterka, T., Petřík, P., Phillips, O.L., Prokhorov, V., Rašomavičius, V., Revermann, R., Rodwell, J., Ruprecht, E., Rūsiņa, S., Samimi, C., Schaminée, J.H., Schmiedel, U., Šibík, J., Šilc, U., Škvorc, Ž., Smyth, A., Sop, T., Sopotlieva, D., Sparrow, B., Stančić, Z., Svenning, J.-C., Swacha, G., Tang, Z., Tsiripidis, I., Turtureanu, P.D., Uğurlu, E., Uogintas, D., Valachovič, M., Vanselow, K.A., Vashenyak, Y., Vassilev, K., Vélez-Martin, E., Venanzoni, R., Vibrans, A.C., Violle, C., Virtanen, R., Wehrden, H., Wagner, V., Walker, D.A., Wana, D., Weiher, E., Wesche, K., Whitfeld, T., Willner, W., Wiser, S., Wohlgemuth, T., Yamalov, S., Zizka, G., Zverev, A., 2019. sPlot – A new tool for global vegetation analyses. Journal of Vegetation Science 30, 161–186.

Carvalheiro, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R., Groom, Q., Hennekens, S., van Landuyt, W., Maes, D., van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.P.M., Schaminée, J., WallisDeVries, M.F., Biesmeijer, J.C., 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. Ecology Letters 16, 870–878.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: Entering the sixth mass extinction. Science Advances 1, e1400253.

Cormont, A., Siepel, H., Clement, J., Melman, T., WallisDeVries, M.F., van Turnhout, C., Sparrius, L.B., Reemer, M., Biesmeijer, J.C., Berendse, F., Snoo, G.R. de, 2016. Landscape complexity and farmland biodiversity: Evaluating the CAP target on natural elements. Journal for Nature Conservation 30, 19–26. https://www.sciencedirect.com/science/article/pii/s1617138115300388.

Culley, T.M., Weller, S.G., Sakai, A.K., 2002. The evolution of wind pollination in angiosperms. Trends in Ecology & Evolution 17, 361–369. https://www.sciencedirect.com/science/article/pii/S0169534702025405.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E., Turner, J.R.G., 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7, 1121–1134.

Cusser, S., Neff, J.L., Jha, S., 2016. Natural land cover drives pollinator abundance and richness, leading to reductions in pollen limitation in cotton agroecosystems. Agriculture, Ecosystems & Environment 226, 33–42. https://www.sciencedirect.com/science/article/pii/s0167880916302237.

Dearborn, D.C., Kark, S., 2010. Motivations for conserving urban biodiversity. Conservation Biology 24, 432–440.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., Souza, N. de, Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.-P.B., van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. BioScience 67, 534–545.

Dinerstein, E., Vynne, C., Sala, E., Joshi, A.R., Fernando, S., Lovejoy, T.E., Mayorga, J., Olson, D., Asner, G.P., Baillie, J.E.M., Burgess, N.D., Burkart, K., Noss, R.F., Zhang, Y.P., Baccini, A., Birch, T., Hahn, N., Joppa, L.N., Wikramanayake, E., 2019. A Global Deal For Nature: Guiding principles, milestones, and targets. Science Advances 5, eaaw2869.

Donihue, C.M., Lambert, M.R., 2015. Adaptive evolution in urban ecosystems. AMBIO 44, 194–203. https://link.springer.com/article/10.1007/s13280-014-0547-2.

Dudley, N., 2008. Guidelines for applying protected area management categories. IUCN, Gland Switzerland.

Forister, M.L., Halsch, C.A., Nice, C.C., Fordyce, J.A., Dilts, T.E., Oliver, J.C., Prudic, K.L., Shapiro, A.M., Wilson, J.K., Glassberg, J., 2021. Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. Science 371, 1042–1045.

González-Irusta, J.M., González-Porto, M., Sarralde, R., Arrese, B., Almón, B., Martín-Sosa, P., 2015. Comparing species distribution models: a case study of four deep sea urchin species. Hydrobiologia 745, 43–57. https://link.springer.com/article/10.1007/s10750-014-2090-3.

Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347, 1255957.

Hallmann, C.A., Ssymank, A., Sorg, M., Kroon, H. de, Jongejans, E., 2021. Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community. Proceedings of the National Academy of Sciences of the United States of America 118.

Hennekens, S., 2018. Dutch Vegetation Database (LVD). v1.6. Alterra, Wageningen UR. Dataset/Samplingevent.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Methods in Ecology and Evolution 7, 1451–1456.

IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on biodiversity and ecosystem services.

IPBES, 2020. Summary for policymakers of the global assessment report on biodiversity and ecosystem services.

Janzen, D.H., Hallwachs, W., 2021. To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let’s be kind to the survivors. Proceedings of the National Academy of Sciences of the United States of America 118.

Laughlin, D.C., Gremer, J.R., Adler, P.B., Mitchell, R.M., Moore, M.M., 2020. The Net Effect of Functional Traits on Fitness. Trends in Ecology & Evolution, 1037–1047.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., Palma, A. de, DeClerck, F.A.J., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Humpenöder, F., Jennings, N., Krisztin, T., Mace, G.M., Ohashi, H., Popp, A., Purvis, A., Schipper, A.M., Tabeau, A., Valin, H., van Meijl, H., van Zeist, W.-J., Visconti, P., Alkemade, R., Almond, R., Bunting, G., Burgess, N.D., Cornell, S.E., Di Fulvio, F., Ferrier, S., Fritz, S., Fujimori, S., Grooten, M., Harwood, T., Havlík, P., Herrero, M., Hoskins, A.J., Jung, M., Kram, T., Lotze-Campen, H., Matsui, T., Meyer, C., Nel, D., Newbold, T., Schmidt-Traub, G., Stehfest, E., Strassburg, B.B.N., van Vuuren, D.P., Ware, C., Watson, J.E.M., Wu, W., Young, L., 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. Nature.

Locke, H., 2013. Nature needs half: A necessary and hopeful new agenda for protected areas. PARKS 19 (2): 13–22. 10.2305/IUCN . CH. 2013. Parks 19, 13–22. javascript:

Magioli, M., Moreira, M.Z., Fonseca, R.C.B., Ribeiro, M.C., Rodrigues, M.G., Ferraz, K.M.P.M.d.B., 2019. Human-modified landscapes alter mammal resource and habitat use and trophic structure. Proceedings of the National Academy of Sciences of the United States of America 116, 18466–18472.

Manhoudt, A., Snoo, G. de, 2003. A quantitative survey of semi-natural habitats on Dutch arable farms. Agriculture, Ecosystems & Environment 97, 235–240.

Mendenhall, C.D., Shields-Estrada, A., Krishnaswami, A.J., Daily, G.C., 2016. Quantifying and sustaining biodiversity in tropical agricultural landscapes. Proceedings of the National Academy of Sciences of the United States of America 113, 14544–14551.

Obura, D.O., Katerere, Y., Mayet, M., Kaelo, D., Msweli, S., Mather, K., Harris, J., Louis, M., Kramer, R., Teferi, T., Samoilys, M., Lewis, L., Bennie, A., Kumah, F., Isaacs, M., Nantongo, P., 2021. Integrate biodiversity targets from local to global levels. Science (New York, N.Y.) 373, 746–748.

Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? Oikos 120, 321–326.

Ozinga, W.A., Römermann, C., Bekker, R.M., Prinzing, A., Tamis, W.L.M., Schaminée, J.H.J., Hennekens, S.M., Thompson, K., Poschlod, P., Kleyer, M., Bakker, J.P., van Groenendael, J.M., 2009. Dispersal failure contributes to plant losses in NW Europe. Ecology Letters 12, 66–74.

Pärtel, M., Bennett, J.A., Zobel, M., 2016. Macroecology of biodiversity: disentangling local and regional effects. New Phytologist 211, 404–410.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231–259.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25, 345–353. https://www.sciencedirect.com/science/article/pii/s0169534710000364.

Rech, A.R., Dalsgaard, B., Sandel, B., Sonne, J., Svenning, J.-C., Holmes, N., Ollerton, J., 2016. The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. Plant Ecology & Diversity 9, 253–262.

Rivkin, L.R., Santangelo, J.S., Alberti, M., Aronson, M.F.J., Keyzer, C.W. de, Diamond, S.E., Fortin, M.-J., Frazee, L.J., Gorton, A.J., Hendry, A.P., Liu, Y., Losos, J.B., MacIvor, J.S., Martin, R.A., McDonnell, M.J., Miles, L.S., Munshi-South, J., Ness, R.W., Newman, A.E.M., Stothart, M.R., Theodorou, P., Thompson, K.A., Verrelli, B.C., Whitehead, A., Winchell, K.M., Johnson, M.T.J., 2019. A roadmap for urban evolutionary ecology. Evolutionary Applications 12, 384–398. https://onlinelibrary.wiley.com/doi/full/10.1111/eva.12734.

Rodger, J.G., Bennett, J.M., Razanajatovo, M., Knight, T.M., van Kleunen, M., Ashman, T.-L., Steets, J.A., Hui, C., Arceo-Gómez, G., Burd, M., Burkle, L.A., Burns, J.H., Durka, W., Freitas, L., Kemp, J.E., Li, J., Pauw, A., Vamosi, J.C., Wolowski, M., Xia, J., Ellis, A.G., 2021. Widespread vulnerability of flowering plant seed production to pollinator declines. Science Advances 7, eabd3524.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science (New York, N.Y.) 287, 1770–1774.

Schleuning, M., Neuschulz, E.L., Albrecht, J., Bender, I.M.A., Bowler, D.E., Dehling, D.M., Fritz, S.A., Hof, C., Mueller, T., Nowak, L., Sorensen, M.C., Böhning-Gaese, K., Kissling, W.D., 2020. Trait-Based Assessments of Climate-Change Impacts on Interacting Species. Trends in Ecology & Evolution 35, 319–328. https://www.sciencedirect.com/science/article/pii/S0169534719303556.

Schulte To Bühne, H., Tobias, J.A., Durant, S.M., Pettorelli, N., 2021. Improving Predictions of Climate Change-Land Use Change Interactions. Trends in Ecology & Evolution 36, 29–38. https://www.sciencedirect.com/science/article/pii/s0169534720302494.

Shaffer, H.B., 2018. Urban biodiversity arks. Nat Sustain 1, 725–727. https://www.nature.com/articles/s41893-018-0193-y.

Soanes, K., Lentini, P.E., 2019. When cities are the last chance for saving species. Frontiers in Ecology and the Environment 17, 225–231.

Soanes, K., Sievers, M., Chee, Y.E., Williams, N.S.G., Bhardwaj, M., Marshall, A.J., Parris, K.M., 2019. Correcting common misconceptions to inspire conservation action in urban environments. Conservation Biology 33, 300–306.

Thomann, M., Imbert, E., Devaux, C., Cheptou, P.-O., 2013. Flowering plants under global pollinator decline. Trends in Plant Science 18, 353–359.

Tscharntke, T., 2021. Disrupting plant-pollinator systems endangers food security. One Earth 4, 1217–1219. https://www.sciencedirect.com/science/article/pii/s2590332221004802.

Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C., Batáry, P., 2021. Beyond organic farming - harnessing biodiversity-friendly landscapes. Trends in Ecology & Evolution 36, 919–930. https://www.sciencedirect.com/science/article/pii/S016953472100183X.

Turnbull, L.A., Isbell, F., Purves, D.W., Loreau, M., Hector, A., 2016. Understanding the value of plant diversity for ecosystem functioning through niche theory. Proceedings. Biological sciences 283.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Swengel, A.B., Gentile, A., Chase, J.M., 2020. Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. Science 368, 417–420. https://science.sciencemag.org/content/sci/368/6489/417.full.pdf.

Veach, V., Moilanen, A., Di Minin, E., 2017. Threats from urban expansion, agricultural transformation and forest loss on global conservation priority areas. PLOS ONE 12, e0188397.

Večeřa, M., Axmanová, I., Padullés Cubino, J., Lososová, Z., Divíšek, J., Knollová, I., Aćić, S., Biurrun, I., Boch, S., Bonari, G., Campos, J.A., Čarni, A., Carranza, M.L., Casella, L., Chiarucci, A., Ćušterevska, R., Delbosc, P., Dengler, J., Fernández-González, F., Gégout, J.-C., Jandt, U., Jansen, F., Jašková, A., Jiménez-Alfaro, B., Kuzemko, A., Lebedeva, M., Lenoir, J., Lysenko, T., Moeslund, J.E., Pielech, R., Ruprecht, E., Šibík, J., Šilc, U., Škvorc, Ž., Swacha, G., Tatarenko, I., Vassilev, K., Wohlgemuth, T., Yamalov, S., Chytrý, M., 2021. Mapping species richness of plant families in European vegetation. Journal of Vegetation Science 32.

Vos, C., 2014. Biodiversity and ecosystem services. In: Perrings, C. (Ed.), Our uncommon heritage. Biodiversity change, ecosystem services, and human well being / Charles Perrings. Cambridge University Press, Cambridge, pp. 78–118.

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D., Ellis, S., 2021. The decline of butterflies in Europe: Problems, significance, and possible solutions. Proceedings of the National Academy of Sciences of the United States of America 118.

Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J., Lindenmayer, D., 2018. The exceptional value of intact forest ecosystems. Nature Ecology & Evolution 2, 599–610.

Watson, J.E.M., Shanahan, D.F., Di Marco, M., Allan, J., Laurance, W.F., Sanderson, E.W., Mackey, B., Venter, O., 2016. Catastrophic Declines in Wilderness Areas Undermine Global Environment Targets. Current biology : CB 26, 2929–2934.

Watson, J.E.M., Venter, O., 2017. Ecology: A global plan for nature conservation. Nature 550, 48–49.

Wintle, B.A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A., Lentini, P.E., Cadenhead, N.C.R., Bekessy, S.A., 2019. Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. Proceedings of the National Academy of Sciences of the United States of America 116, 909–914.

WWF, 2022. Living Planet Report 2022 – Building a nature- positive society. WWF, Gland, Switzerland.

Summary

Plant diversity is essential for us and our planet as it sustains the stability of our ecosystems, provides vital materials and food to us and supports many ecosystem services. However, plant diversity has shown a strong decline throughout human history, particularly in the past decades. Multiple factors have been and are threatening plant species persistence, particularly climate change and land use change that result from intensive human activities. However, it is well known that different species may respond differently to threats, with some species being vulnerable to environmental change while others are less likely to be threatened. To understand how anthropogenic pressures will affect plant communities and find proper plant conservation strategies, it is important to identify how species change over time and to what extent species differ in their response to environmental pressures.

Among the environmental factors that are driving plant diversity loss, land-cover change, particularly loss of natural habitats, is the most dominant one. Many plant species are likely to depend completely or partially on natural habitats. Consequently, understanding the effect of natural habitat (e.g. size, extent, connectivity) on species is needed to underpin biodiversity conservation strategies. However, whether and to which extent (semi-)natural habitat cover affects individual plant species remains largely unknown. Some studies show that species populations will decline and lose their viability due to (semi-)natural habitat loss. While others show that different species should have different responses to (semi-)natural habitat cover. At the same time, many species can still persist in non-(semi-)natural habitats. Few empirical studies have assessed the importance of natural land cover to plant species' presence for a whole flora. **Chapter 2** is an attempt to achieve that. I assessed the response of 1,132 native and 412 exotic plant species to natural land cover across the Netherlands. This nationwide study, for the first time, showed that most species, particularly threatened species, preferred landscapes with high natural land cover. Natural types (natural forest and open habitat) are also associated with species' presence, and a landscape with a mixture of natural forest and open habitat was better for biodiversity at large than landscapes with completely open or completely forested natural habitats. Threatened species preferred landscapes with higher natural land cover than not threatened species, and native species preferred higher natural land cover than exotic species. This analysis will help inform the long-running debate about the important role of natural land cover in supporting species. It may help government and conservation agencies to better improve conservation guidelines, focus their efforts on (semi-)natural areas and their surroundings and in this way stand a better chance to realise their national and regional biodiversity strategy targets.

In addition to abiotic factors, biotic factors also have substantial effects on plant diversity. Pollination is considered to be one of the most important factors driving plant diversity by limiting or promoting seed production, fruit production and thus affect plant reproductive output. Pollination is one of the most critical events for the reproduction of plants, with insect, wind and selfing as the most common modes. However, few studies have assessed whether the distribution of different pollination modes is related to environmental conditions, e.g. vegetation structure. Even fewer studies have provided an explanation for this. **In chapter 3**, I used distribution records of Dutch plant species to map the composition of pollination modes of different plant groups (woody species, herbs and grasses) across (semi-)natural habitats and assessed whether spatial distributions of different pollination modes are correlated with the 3D vegetation structure. This study showed that insect-pollination is the most common mode across (semi-)natural habitats for woody species and herbs. Woody species pollinated by insects showed an even higher percentage in dune, river swamp and swamp peat habitats than in other habitat types, whereas herbs showed a higher percentage of insect-pollination in dunes than in other habitat types. Grasses were always pollinated by wind or wind and selfing in all habitats. Woody plants pollinated by wind preferred vegetation with height ranging from 2 to 20 m, while woody plants pollinated by insects preferred much lower vegetation with height ranging from 0.5 to 2 m. Grass preferred open habitats instead of covered habitats.

With respect to the importance of pollinated plants, **chapter 4** further investigated plants with different pollination modes in 625,247 Dutch vegetation plots from 1930 to 2017 and confirmed a decline in the proportion of obligately insect-pollinated plants (~10.4%) and a parallel increase in obligately wind-pollinated plants (~9.6%) in natural communities over the last 87 years. The proportional change is explained by both the decline in the richness of insect-pollinated plants and an increase in the richness of wind-pollinated plants. The pattern of temporal changes in pollination mode suggests that natural plant communities are losing insect-pollinated plants and that plant communities are shifting to wind-pollination.

Finally, **chapter 5** reviewed existing strategies of species conservation and assessed the conservation effectiveness of different protection levels (protected areas vs unprotected areas) and land-use types on different species groups. Results showed that protected areas and nature are the most important areas to sustain gamma diversity of different species taxonomic groups, particularly for threatened and rare species. Similarly, protected areas had a higher alpha and beta diversity of threatened and rare species, while unprotected areas had a higher alpha and beta diversity of all and native species. Nature was important in sustaining a high alpha and beta diversity of threatened species at all scales and rare species at 0.5 km scale. However, urban areas sustained the highest alpha and beta diversity of all and native species.

Overall, this thesis reveals the temporal and spatial dynamics of different plant taxonomic groups and provides insights relevant to conserve plant species effectively. Protected areas are very important for species conservation. Nature is suggested to be most important for conservation-relevant species, while urban areas are important to common species. However, increasing natural land cover in a mixed landscape will increase plant diversity in total. Thus, protecting current nature and creating natural patches in intensive human-dominated areas are both essential for future species conservation. Besides, the interaction between plants and insects is a very important factor driving plant species dynamics across space and over time. Protecting insect pollinators will benefit plant species conservation and contribute to the sustaining of human well beings in a great deal.

Samenvatting

Plantendiversiteit is van groot belang voor ons en onze aarde omdat planten de stabiliteit van onze ecosystemen ondersteunen, omdat ze allerlei materialen en voedsel leveren aan de mens en omdat ze veel ecosysteemdiensten leveren. De plantendiversiteit is echter in de loop van de tijd sterk afgenomen, vooral in de afgelopen decennia. Vooral factoren als klimaatverandering en verandering in en intensivering van landgebruik als gevolg van antropogene activiteiten hebben bijgedragen aan de achteruitgang van plantensoorten. Het is echter goed bekend dat soorten zeer verschillend kunnen reageren op dergelijke bedreigingen, waarbij sommige soorten kwetsbaar zijn voor veranderingen in het milieu en andere soorten minder snel worden bedreigd. Om te begrijpen hoe de menselijke invloeden plantengemeenschappen beïnvloeden en hoe we planten beter kunnen beschermen, is het belangrijk om de verandering van verschillende soorten in de tijd te bepalen en te begrijpen in welke mate en hoe verschillende soorten op de omgeving reageren.

Van de omgevingsfactoren die het verlies van plantendiversiteit beïnvloeden, is de verandering van landgebruik door de mens, met name het verlies van natuurgebieden, één van de belangrijkste factoren. Veel planten zijn voor hun voortbestaan geheel of ten dele afhankelijk van natuurlijke habitats. Om planten goed te beschermen moeten we derhalve het effect van habitatverlies op planten goed begrijpen. Dat begrip is nu onvoldoende. Wat we wel weten is dat sommige studies laten zien dat soorten afnemen ten gevolge van (semi-)natuurlijke habitatverlies, terwijl andere studies concluderen dat (andere) soorten geen of nauwelijks effect ondervinden. Tegelijkertijd zien we dat veel soorten voorkomen in niet-(semi-)natuurlijke habitats. Slechts enkele empirische studies wijzen op het belang van natuurlijk landgebruik voor de aanwezigheid van soorten en of de verschillen in response tussen soorten. **Hoofdstuk 2** onderzocht de respons van 1.132 inheemse en 412 exotische plantensoorten op verandering en aanwezigheid van natuurlijke habitats in heel Nederland. Deze studie toont voor het eerst aan dat de meeste soorten, met name bedreigde soorten, de voorkeur geven aan landschappen met een hoge aandeel natuurlijke habitats. Het type natuurlijke habitat (bebost of open terrein) bepaald mede de aanwezigheid van soorten, waarbij een landschap met een mix van natuurlijk bos en open vegetatie beter is voor de plantenrijkdom in het algemeen dan landschappen die volledig open of volledig bebost zijn. Bedreigde soorten gaven de voorkeur aan landschappen met een hoger percentage natuurlijk landgebruik dan niet-bedreigde soorten, en inheemse soorten gaven de voorkeur aan landschappen met een hoger percentage natuurlijke landgebruik dan exotische soorten. Deze analyse draagt bij aan het langlopende debat over het belang van natuurgebieden bij het ondersteunen van soorten. Mijn resultaten kunnen overheden en natuurbeschermingsinstanties helpen om de richtlijnen voor natuurbehoud te verbeteren, hun inspanningen te richten op (semi-)natuurlijke gebieden en hun omgeving en op deze manier een betere kans te geven om hun nationale en regionale doelstellingen voor de biodiversiteitsstrategie te realiseren.

Naast abiotische factoren hebben ook biotische factoren sterke invloed op de plantendiversiteit. Bestuiving wordt beschouwd als een van de belangrijkste factoren die de diversiteit van planten stimuleren door de zaadproductie/plantreproductie te beperken of te bevorderen. Bestuiving is een van de meest kritieke gebeurtenissen bij de reproductie van planten en de meest voorkomende vormen van bestuiving zijn door middel van insecten of de wind en zelfbestuiving. Er zijn echter maar weinig studies die hebben aangetoond dat de verdeling van verschillende bestuivingswijzen verband houdt met omgevingscondities, zoals bijvoorbeeld vegetatiestructuur, en nog minder studies hebben hier een verklaring voor gegeven. In **hoofdstuk 3** gebruik ik waarnemingen van Nederlandse plantensoorten om het voorkomen van de verschillende vormen van bestuiving bij verschillende plantengroepen (houtsoorten, kruiden en grassen) en in verschillende (semi-)natuurlijke habitats in kaart te brengen. Daarnaast gebruik ik gegevens over de 3D-vegetatiestructuur om te beoordelen of de ruimtelijke verdeling van verschillende bestuivingsvormen daarmee verband houdt. Deze studie toont aan dat insectenbestuiving de meest voorkomende vorm van bestuiving is in (semi-)natuurlijke habitats voor houtachtige soorten en kruiden. Door insecten bestoven houtige soorten lieten in duinen, riviermoeras en moerasveen een nog hoger percentage zien dan in andere habitattypen, terwijl kruiden in duingebieden een hoger percentage insectenbestuiving lieten zien dan in andere habitattypen. Grassen werden in alle habitats altijd bestoven door wind of door wind en zelfbestuiving. In alle typen vegetatiestructuur gaven houtige planten die bestoven werden door wind de voorkeur aan dichte vegetatie met een hoogte variërend van 2 tot 20 m, terwijl houtige planten bestoven door insecten meer voorkomen in vegetatie met een hoogte variërend van 0,5 tot 2 m. Grassen gaven de voorkeur aan open habitats.

Over het belang van bestuiving voor planten geeft **hoofdstuk 4** meer inzicht. Daarin is onderzocht hoe planten met verschillende bestuivingsvormen zijn veranderd door de tijd. Mijn analyse van 625.247 Nederlandse vegetatieplots opgenomen tussen 1930 en 2017 laat zien dat er een afname is van het aandeel van obligaat insectbestoven planten (~10,4%) en een toename van de obligaat windbestoven planten (~9,6%) in natuurlijke gemeenschappen in die tijd. De proportionele verandering wordt veroorzaakt door zowel de afname van de soortenrijkdom van door insecten bestoven planten en de toename van de soortenrijkdom van door de wind bestoven planten. Het patroon van temporele veranderingen in de bestuivingsvormen suggereert dat natuurlijke plantengemeenschappen door insecten bestoven planten verliezen en dat planten die windbestuiving gebruiken juist toenemen.

Tenslotte wordt in **hoofdstuk 5** de huidige strategie voor het behoud van soorten (beschermde gebieden versus onbeschermde gebieden) onder de loep genomen. De resultaten laten zien dat beschermde (natuur)gebieden de belangrijkste gebieden zijn om de gammadiversiteit van verschillende soorten en/of taxonomische groepen in stand te houden, met name als het gaat om bedreigde en zeldzame soorten. Daarbij hebben beschermde gebieden een hogere alfa- en bèta-diversiteit van bedreigde en zeldzame soorten, terwijl onbeschermde gebieden een hogere alfa- en bèta-diversiteit van alle soorten en ook van alle inheemse soorten hebben. De natuur is belangrijk bij het in stand houden van een hoge alfa- en bètadiversiteit van bedreigde soorten op zowel kleine als grote schaal en voor zeldzame soorten op een schaal van 0,5 km. Stedelijke gebieden hebben echter de hoogste alfa- en bètadiversiteit van zowel het totaal aantal plantensoorten als alle inheemse soorten.

Dit proefschrift geeft inzicht in de temporele en ruimtelijke dynamiek van verschillende taxonomische groepen van planten en laat zien hoe plantensoorten effectief kunnen worden behouden. Beschermde gebieden zijn zeer belangrijk voor het behoud van soorten, vooral voor de instandhouding van bedreigde en zeldzame soorten, terwijl stedelijke gebieden belangrijk zijn voor algemenere soorten. Het vergroten van natuurgebieden in een gemengd landschap zal zeker de totale plantendiversiteit vergroten. Het beschermen van de huidige natuur samen met het creëren van natuurlijkere habitats in door de mens gedomineerde gebieden is essentieel voor het toekomstige behoud van soorten. Bovendien is de interactie tussen planten en insecten een zeer belangrijke factor die de dynamiek van plantensoorten zowel in ruimte als in tijd stuurt. Het beschermen van bestuivers zal het behoud van plantensoorten ten goede komen en in grote mate bijdragen aan het behoud van het welzijn van de mens.

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Curriculum vitae

Kaixuan Pan was born in Jiangsu Province, China on July 21st, 1992. He attended high school at JiangSu XinHai Senior High School from 2008 to 2011. He then studied ecology at Northeast Normal University in Changchun, Jilin from 2011 to 2015. During the last year of his undergraduate studies, he participated in a group conducting wetland experiments, which sparked his interest in science. After completing his undergraduate studies, Kaixuan pursued a master's degree at Zhejiang University from 2015 to 2018. His thesis focused on constructing micro-refuges for endangered plant species in urban areas. During his master's program, he participated in several projects related to wetland ecology, urban ecology, and ecosystem services. Eventually, he became interested in land-use and plant diversity, which led him to begin his PhD studies at Leiden University in 2018, under the supervision of Prof. Geert de Snoo and Prof. Koos Biesmeijer. He received support from the Chinese Scholarship Council for his PhD project, which aims to investigate the biotic and abiotic effects on the temporal and spatial dynamics of different plant species and contribute to effective plant species conservation. He has presented some of his work at the Netherlands Annual Ecology Meeting (NAEM), the 6th European Congress of Conservation Biology (ECCB), and the NWO Life congress.

Publications

Peer-reviewed journals:

Pan, K., Moens, M., Marshall, L., Cieraad, E., de Snoo, G. R., & Biesmeijer, K. (2021). Importance of natural land cover for plant species' conservation: A nationwide study in The Netherlands. *PloS one*, *16*(11), e0259255.

Pan, K., Marshall, L., Biesmeijer, K., & de Snoo, G. R. (2021). The distributions of insect, wind and self pollination of plants in the Netherlands in relation to habitat types and 3D vegetation structure. *Journal of Pollination Ecology*, *30*, 16-28.

Xu, R., Yue, W., Wei, F., Yang, G., He, T., & Pan, K. (2022). Density pattern of functional facilities and its responses to urban development, especially in polycentric cities. *Sustainable Cities and Society*, *76*, 103526.

Xu, R., Yue, W., Wei, F., Yang, G., Chen, Y., & Pan, K. (2022). Inequality of public facilities between urban and rural areas and its driving factors in ten cities of China. *Scientific Reports*, *12*(1), 1-14.

Chen, Y., Ge, Y., Wu, Z., Ouyang, Y., Yang, G., Du, Y., ... & Chang, J. (2021). Homogenization of tree species diversity in urban green spaces along a temperature gradient in eastern China. *Urban Forestry & Urban Greening*, *66*, 127388.

Chang, J., Ge, Y., Wu, Z., Du, Y., Pan, K., Yang, G., ... & Meyerson, L. A. (2021). Modern cities modelled as "super-cells" rather than multicellular organisms: Implications for industry, goods and services. *BioEssays*, *43*(7), 2100041.

Pan, K., Lu, Y., He, S., Yang, G., Chen, Y. I., Fan, X., ... & Ge, Y. (2019). Urban green spaces as potential habitats for introducing a native endangered plant, Calycanthus chinensis. *Urban Forestry & Urban Greening*, *46*, 126444.

Lu, Y., Ge, Y., Zhang, X., Chang, J., Zhang, P., Yue, C., ... & Li, J. (2019). Potential habitats for introducing an endangered plant Parrotia subaequalis into urban green spaces. *Ekoloji*, *28*(107), 2193-2201.

Du, Y., Ge, Y., Ren, Y., Fan, X., Pan, K., Lin, L., ... & Didham, R. K. (2018). A global strategy to mitigate the environmental impact of China's ruminant consumption boom. *Nature communications*, *9*(1), 1-11.

Du, Y., Pan, K., Yu, C., Luo, B., Gu, W., Sun, H., ... & Chang, J. (2018). Plant diversity decreases net global warming potential integrating multiple functions in microcosms of constructed wetlands. *Journal of Cleaner Production*, *184*, 718-726.

Chang, J., Qu, Z., Xu, R., Pan, K., Xu, B., Min, Y., ... & Ge, Y. (2017). Assessing the ecosystem services provided by urban green spaces along urban center-edge gradients. *Scientific reports*, *7*(1), 1-9.

Ren, Y., Ge, Y., Ma, D., Song, X., Shi, Y., Pan, K., ... & Chang, J. (2017). Enhancing plant diversity and mitigating BVOC emissions of urban green spaces through the introduction of ornamental tree species. *Urban Forestry & Urban Greening*, *27*, 305-313.

Fan, M. Y., Pan, K. X., Han, W. J., Lu, Y. J., Shen, Q., Wang, M., ... & Ge, Y. (2016). A strategy for introducing an endangered plant Mosla hangchowensis to urban areas based on nitrogen preference. *Acta Physiologiae Plantarum*, *38*(11), 1-9.

Conferences:

Oral presentation at the Netherlands Annual Ecology Meeting (NAEM), 20-21 September, 2022. Lunteren, the Netherlands. Session: ‘Biogeography’

Oral presentation at the 6th European Congress of Conservation Biology (ECCB), 22-26 August, 2022. Prague, the Czech Republic. Session: ‘Pollinator conservation’

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Oral presentation at the Netherlands Annual Ecology Meeting (NAEM), 9-10 February, 2022. Online. Session: ‘Conservation Science’