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Research

Urbanization affects oak–pathogen interactions across spatial scales

Laura J. A. van Dijk, Xoaquín Moreira, Anna E. Barr, Luis Abdala-Roberts, Bastien Castagneyrol, Maria Faticov, Bess Hardwick, Jan P. J. G. ten Hoopen, Raúl de la Mata, Ricardo Matheus Pires, Tomas Roslin, Dmitry S. Schigel, Bart G. H. Timmermans and Ayco J. M. Tack

L. J. A. van Dijk (https://orcid.org/0000-0003-1015-8496) ✉ (laura.j.a.vandijk@gmail.com), A. E. Barr (https://orcid.org/0000-0001-6791-4534), M. Faticov (https://orcid.org/0000-0001-8206-9332) and A. J. M. Tack (https://orcid.org/0000-0002-3550-1070), Dept of Ecology, Environment and Plant Sciences, Stockholm Univ., Stockholm, Sweden. – X. Moreira (https://orcid.org/0000-0003-0166-838X), Misión Biológica de Galicia (MBG-CSIC), Pontevedra, Galicia, Spain. – L. Abdala-Roberts (https://orcid.org/0000-0003-1394-3043), Depto de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Univ. Autónoma de Yucatán, Itzimná, Mérida, Yucatán, México. – B. Castagneyrol, BIOGECO, INRA, Univ. Bordeaux, Cestas, France. – B. Hardwick and T. Roslin, Spatial Foodweb Ecology Group, Dept of Agricultural Sciences, Univ. of Helsinki, Helsinki, Finland. TR also at: Spatial Foodweb Ecology Group, Dept of Ecology, Swedish Univ. of Agricultural Sciences, Uppsala, Sweden. – J. P. J. G. ten Hoopen, OneNature Ecology, Arnhem, the Netherlands. – R. de la Mata, Research Inst. of Food Technology and Agriculture-IRTA, Fruit Production Program, Torre Marimon, Caldes de Montbui, Spain. – R. M. Pires, Inst. de Botânica de São Paulo, Núcleo de Pesquisa em Micologia, São Paulo, SP, Brasil. – D. S. Schigel, Faculty of Biological and Environmental Sciences, Univ. of Helsinki, Helsinki, Finland. – B. G. H. Timmermans, Dept of Agriculture, Louis Bolk Inst., Bunnik, the Netherlands.

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The world is rapidly urbanizing, thereby transforming natural landscapes and changing the abundance and distribution of organisms. However, insights into the effects of urbanization on species interactions, and plant–pathogen interactions in particular, are lacking. We investigated the effects of urbanization on powdery mildew infection on *Quercus robur* at continental and within-city scales. At the continental scale, we compared infection levels between urban and rural areas of different-sized cities in Europe, and investigated whether plant traits, climatic variables and CO_2 emissions mediated the effect of urbanization on infection levels. Within one large city (Stockholm, Sweden), we further explored whether local habitat features and spatial connectivity influenced infection levels during multiple years. At the continental scale, infection severity was consistently higher on trees in urban than rural areas, with some indication that temperature mediated this effect. Within Stockholm city, temperature had no effect, while local accumulation of leaf litter negatively affected powdery mildew incidence in one out of three years, and more connected trees had lower infection levels. This study is the first to describe the effects of urbanization on plant–pathogen interactions both within and among cities, and to uncover the potential mechanisms behind the observed patterns at each scale.

Keywords: connectivity, local habitat quality, oak powdery mildew, phenolic compounds, plant–pathogen interactions, *Quercus robur*

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Introduction

The world keeps urbanizing at an unprecedented speed, with over half of the human population currently residing in cities (Richie 2018). This human-driven transformative process leads to dramatic changes in the physical environment and ecological communities, as well as marked and frequently abrupt environmental shifts along urban–rural interfaces (Kareiva et al. 2007, Johnson and Munshi-South 2017). Notably, urbanization alters the temporal and spatial distribution of abiotic and biotic resources needed to support ecological communities (Neil and Wu 2006, Hahs et al. 2009, Williams et al. 2009, Start et al. 2020). While previous work has primarily focused on how urbanization impacts plant and animal community structure (McKinney 2008, Beninde et al. 2015), effects on species interactions and their underlying mechanisms remain largely unexplored (but see Kozlov et al. 2017, Moreira et al. 2019). Specifically, host–pathogen interactions have been largely neglected despite the importance of pathogens in shaping plant and animal abundance and diversity, as well as host-associated food webs (Knapp et al. 2020). Studying host–pathogen interactions within an urban setting is important not only for preventing biodiversity loss due to disease outbreaks (Potter et al. 2011) but also for the protection of pathogens as an intrinsic and functionally valuable part of biodiversity (Dougherty et al. 2016).

Trees in cities are expected to be more susceptible to insect herbivores and diseases than trees in rural or natural systems due to increased plant stress (Dreistadt et al. 1990) and decreased top–down control from natural enemies (Burkman and Gardiner 2014, Turrini et al. 2016). While empirical studies on plant pathogens are lacking, insights can be gained from studies on urban plant–herbivore interactions. These studies have reported contrasting evidence, with either increased (Cuevas-Reyes et al. 2013, Frank 2014) or decreased (Nuckols and Connor 1995, Kozlov et al. 2017, Moreira et al. 2019) herbivory in urban areas compared to rural or natural ecosystems. The impact of urbanization on insect herbivores can partly be explained by their ecology and life cycles; for example, insects with an intimate association with their host plant were found to generally increase with urbanization (Raupp et al. 2010). While there are several studies on the effect of urbanization on plant microbes, these have mainly focused on describing changes in the diversity of fungal and bacterial communities, rather than exploring plant–pathogen interactions (Supporting information). Thus, research is needed to gain insights into plant–pathogen interactions and thereby obtain a more complete view of the impact of urbanization on species interactions.

In order to understand the diverse impacts of urbanization on species interactions, it is essential to investigate the underlying mechanisms that drive these patterns. Urbanization can alter abiotic conditions such as temperature (Oke 1995), water availability (Meineke and Frank 2018), CO_2 concentration (George et al. 2007) and precipitation (Shepherd et al. 2010), which may in turn affect plants, micro-organisms and their interactions. For example, urban areas are notably warmer than surrounding rural areas, which, in combination with water deficits, commonly leads to drought stress in plants (Barta et al. 2011, Moser et al. 2016), thereby increasing a plant's susceptibility to diseases (Porta et al. 2008, Meineke and Frank 2018). Changes in abiotic conditions can also affect plant-associated organisms by modifying primary and secondary plant metabolites (Kumar et al. 2017, Zavala et al. 2017). For example, elevated atmospheric CO_2 concentrations can lead to an increase of salicylic acid-regulated defensive compounds (Zavala et al. 2017), such as flavonoids (Ghasemzadeh et al. 2010), with potential negative consequences for biotrophic pathogens. Notably, these urbanization effects may be stronger in larger cities due to augmented abiotic changes, including higher temperatures (Oke 1973) and CO_2 emissions (Makido et al. 2012), which may in turn determine the magnitude or direction of urbanization effects on species interactions (e.g. plant–herbivore interactions, Kozlov et al. 2017). Researchers recently started to investigate whether abiotic climatic factors and biotic plant traits influence the impact of urbanization on plant-feeding insects (Dale and Frank 2017, Moreira et al. 2019), but for urban pathogens, the impact of these factors remains unexplored. To the best of our knowledge, studies on aboveground plant microbes have focused on small-scale impacts of urbanization for individual cities, whereas broader-scale assessments at regional or continental scales are lacking (Supporting information). This limits the inferences that can be made about the nature and strength of urbanization effects and also prevents identifying commonalities and differences in underlying mechanisms necessary to build a robust framework.

Though biotically impoverished, urban environments are not homogenous; rather, the availability and distribution of abiotic and biotic resources are highly variable across a city (Pincebourde et al. 2016) and may thus affect species distributions and the occurrence and strength of interactions. To obtain insights into the impact of urbanization on species interactions, as well as to further identify potential drivers underlying observed patterns, we need to go beyond comparisons between urban and rural environments; therefore, it is crucial that large-scale studies are complemented by studies at the within-city scale. For example, the diverse set of habitat types represented within a city, such as parks and gardens, contributes to large differences in light availability (Akbari et al. 2001). Increased sunlight exposure, in combination with anthropogenic heat sources (Roth et al. 1989, Oke 1995), creates urban heat islands (Saaroni et al. 2000) and dry surfaces (Miller et al. 2020). Such heterogeneity in sunlight, temperature and humidity may result in varying influences on plant primary and secondary chemistry (Roberts and Paul 2006, Farooq et al. 2009, Wang et al. 2009) as well as pathogen physiology and life cycles (Siebold and von Tiedemann 2012, Sabburg et al. 2015). Local habitats can be further modified by management practices within cities. For example, removal of leaf litter can affect local conditions, as leaf litter provides an insulating layer for ground-dwelling organisms (Suominen et al. 1999, Gessner et al. 2010). Leaf litter may also sustain a reservoir of (overwintering) pathogen

spores close to the host tree (Mmbaga 2000, Sutton et al. 2000). Finally, in addition to changes in local habitat conditions, spatial features within a city may also shape disease dynamics. Urban areas can have reduced but highly variable habitat connectivity (Threlfall et al. 2012), depending on the amount of suitable habitats present and their degree of spatial separation (Scolozzi and Geneletti 2012, Unfried et al. 2013), thus potentially affecting disease spread (Meentemeyer et al. 2012). Although some studies have looked at the effects of local and spatial drivers of plant–insect herbivore interactions within cities (Herrmann et al. 2012, Beninde et al. 2015, Barr et al. 2021), their impact on plant–pathogen interactions remains unknown.

In this study, we investigated the impact of urbanization on plant pathogen infection at the continental and within-city scales, and aimed at uncovering the mechanisms behind the effects of urbanization. First, in order to identify the effect of urbanization (urban vs rural) and city size on plant infection levels at the continental scale, we assessed infection levels of oak powdery mildew (*Erysiphe* spp.) on the pedunculate oak *Quercus robur* across urban and rural environments of small, medium and large cities in six European countries. Second, in order to compare patterns of urban plant–pathogen interactions at the continental scale to patterns at the within-city scale, we further investigated powdery mildew infection levels on oak trees within one large city (Stockholm, Sweden), and explored abiotic, biotic and spatial drivers behind the observed patterns at both scales. Specifically, we aimed at answering the following questions:

1) Do urbanization and city size cause differences in infection incidence and severity at the continental scale? And what is the relative importance of abiotic (i.e. climatic) vs biotic (i.e. plant traits) factors that drive the effect of urbanization on infection levels?
2) How do factors operating within a city, such as local habitat quality (sunlight exposure, leaf litter, temperature, local CO_2 emissions) and spatial connectivity, influence infection incidence and severity among urban trees?

Our detailed hypotheses are presented in the Supporting information.

Material and methods

Study system

Pedunculate oak (*Quercus robur* L.) is a deciduous tree species common throughout Western Europe. Its latitudinal distribution ranges from the Iberian Peninsula up to central Sweden and southern Finland (62°C latitude) (Repo et al. 2008, Eaton et al. 2016). This species has a wide range of potential habitats, with a preference for locations with high light availability (Ellenberg 1988). Pedunculate oaks are commonly found as ornamental trees in cities and urban parks (Willis and Petrokofsky 2017). The growing season of the pedunculate oak varies with latitude, though budburst usually occurs around mid-March to early May (Eaton et al. 2016), and leaf drop starts around late September through November (Ekholm et al. 2019). The pedunculate oak as well as many other oak species are commonly infected by oak powdery mildew, a cryptic fungal pathogen complex in the genus *Erysiphe* (including *E. quercicola*, *E. hypophylla* and *E. alphitoides*). These *Erysiphe* species are specialists on oak species in Europe and are widely distributed across the continent (Desprez-Loustau et al. 2011, 2018, 2019). During the growing season, powdery mildew spreads its asexual spores (conidia) via wind dispersal. Spores germinate best under high relative humidity and high light availability (Pap et al. 2013). Upon germination, feeding organs penetrate epidermal cells while the fungus continues to grow epiphytically. While young oak leaves are particularly susceptible to disease, spores can also infect and cause mildew growth on differentiated leaves (Edwards and Ayres 1981, van Dijk et al. 2020, McClory et al. 2021). At the end of the growing season, sexual fruiting bodies (chasmothecia) are produced and overwinter in the tree bark (Marçais et al. 2009) and in the leaf litter below the tree (Mmbaga 2000). While powdery mildew may impact natural regeneration of oaks (Demeter et al. 2021) and impair radial growth of oaks when infection is severe (Bert et al. 2016), impacts of this disease on short-term oak fitness (e.g. reproduction and survival) tend to be relatively mild (Desprez-Loustau et al. 2011).

The impact of urbanization on pathogen infection levels at the continental scale

To elucidate the impact of urbanization and city size on pathogen infection in oak trees at the continental scale, we selected three cities in six European countries (Spain, France, the Netherlands, Denmark, Sweden and Finland). Within each country, leaves were collected from oak trees in one small (21 000–46 000 inhabitants), one medium-sized (152 000–292 000) and one large city (1 230 000–10 516 000). For each city, trees were sampled in one urban and one rural location. Urban locations were situated inside the city borders, including not only trees surrounded by buildings but also semi-natural environments such as parks and gardens. Rural locations were selected 10–80 km outside the city borders. This hierarchical sampling design resulted in 36 sampling locations (Fig. 1a) and allowed us to tease apart impacts of urbanization from geographic variation in environmental conditions such as climate.

To accommodate substantial differences in climate across sites, we adjusted sampling date to latitude. Northern localities were thus sampled from late August to early September, whereas southern locations were sampled between late September and early October. By this approach, we made sure to sample oaks and mildew at a similar phenological stage across the continent.

At each location targeted, five random mature oak trees were sampled, and from each tree, two low-hanging branches were randomly selected. For each branch sampled, we randomly collected five leaves for infection assessment (n = 10

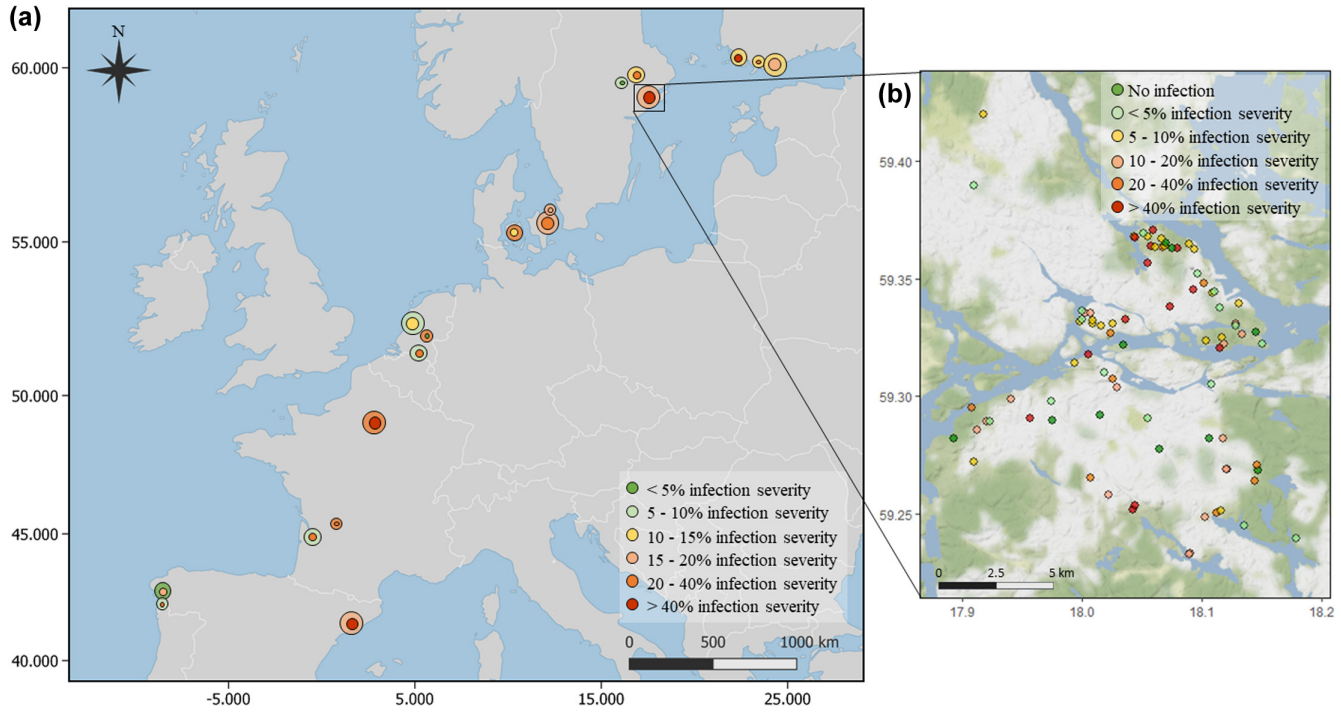


Figure 1. Spatial variation of powdery mildew disease levels in Europe and Stockholm. Panel (a) shows the distribution of powdery mildew in the urban and rural areas of European cities in 2017. City size is visualized by the size of the circle: small (21 000–46 000 inhabitants), medium-sized (152 000–292 000) and large cities (1 230 000–10 516 000 inhabitants). From low to high latitude countries and from small to large cities: Spain (Villagarcía de Arosa, Vigo, Barcelona), France (Perigueux, Bordeaux, Paris), the Netherlands (Wageningen, Eindhoven, Amsterdam), Denmark (Helsingør, Odense, Copenhagen), Sweden (Enköping, Uppsala, Stockholm) and Finland (Lohja, Turku, Helsinki). The average mildew coverage of leaves (conditional on the presence of infection on the leaf) is visualized using an ordinal scale, with urban areas represented as the inner circle and rural areas as the outer circle. Map modified with QGIS v3.10.4, from source: Natural Earth Data. Panel (b) shows the spatial distribution of powdery mildew in Stockholm in 2017. The average mildew coverage for each tree (conditional on the presence of infection on the leaf) is visualized using an ordinal scale, where trees with zero leaves infected are classified as having no infection. In the background map, white areas represent impervious surfaces and green areas show vegetated surfaces. The map was made using the *ggmap* package in R ver. 3.6.3 (Kahle and Wickham 2013).

leaves per tree). To obtain a cumulative estimate of infection by the full set of cryptic powdery mildew species, including all oak flushes and pathogen generations, we collected oak leaves at the end of the growing season in 2017, well before leaves started dropping (Moreira et al. 2018, 2019). This approach of scoring late-season leaf damage as a measure of overall attack rates has been widely adopted in previous studies on insect herbivory (Knepp et al. 2005, Kozlov et al. 2017, Moreira et al. 2019). In the context of pathogens, the approach has rarely been used to measure disease levels – although it provides an attractive solution for estimating total attack levels. For each leaf, we visually scored the incidence of powdery mildew infection (i.e. presence of mycelium and spores on the leaf surface, Madden et al. 2017), as well as the severity of infection (i.e. the percentage of leaf surface covered by mycelium and spores, Madden et al. 2017). The scoring of mildew incidence and severity was conducted by the same person.

For the impact of abiotic variables and leaf chemistry on powdery mildew infection, we adopted measures previously collected for the same set of trees by Moreira et al. (2019). Data on abiotic variables included mean annual temperature (°C), temperature seasonality (expressed as the standard deviation of temperature among months × 100), mean total annual precipitation (mm), precipitation seasonality (coefficient of variation of the daily mean precipitation) and CO_2 emissions in pentagrams of carbon (PgC) (Oda et al. 2018). For leaf chemistry, we included nutrients (nitrogen and phosphorus) and phenolic compounds (flavonoids, lignin, condensed tannins and hydrolysable tannins). For more details, see Supporting information.

Within-city local and spatial drivers of pathogen infection levels

To correlate local and spatial drivers to pathogen infection levels within a city, we observed 84 mature oak trees within Stockholm, Sweden (59°C latitude) (Fig. 1b), independently from the trees sampled for the continental-scale analyses. Trees were selected using Stockholm's Oak Database (Ekdatabasen, Stockholm Stad 2006), in which all 2704 larger and older oak trees (trunk diameter of more than 100 cm) of the city are described. From the database, we selected 84 oak trees for the current study. Details on tree selection are provided in the Supporting information.

We recorded powdery mildew infection on the selected trees in Stockholm in September in 2017 (n = 84), 2018 (n = 50) and 2019 (n = 50). We observed the same set of trees in 2018 and 2019, which was a random subset of the trees sampled in 2017. The climatic conditions during the growing season markedly differed among the sampling years, with the summer of 2018 being extremely dry and hot (Schuldt et al. 2020). The incidence and severity of mildew infection were visually estimated on 15 randomly selected leaves per tree, after having standardized the visual estimation among observers.

For each tree included in the survey, we determined the level of sunlight exposure (freestanding, less than 25% shaded or 25–75% shaded), leaf litter ground coverage (percentage ground covered within a 5 m radius), maximum temperature (on 100 m resolution), CO_2 emissions (on 1 km^2 resolution) and spatial connectivity (calculated as: 1 × (number of trees within 1–50 m) + 0.5 × (number of trees within 51–100 m)). See Supporting information for details on these measures.

Statistical analyses

All statistical analyses were performed in R ver. 3.6.3 (<www.r-project.org>). We used the functions *lmer* and *glmer* in package *lme4* to fit (generalized) linear mixed-effect models (Bates et al. 2015). The Supporting information offers a detailed description of the statistical analyses and it provides an overview of the fitted models linked to each study question, including information on model types, random and fixed effects, distributions and link functions.

The impact of urbanization on pathogen infection levels at the continental scale

To analyse the effect of urbanization on powdery mildew incidence, we modelled the proportion of leaves infected by powdery mildew on each tree as a function of urbanization (urban vs rural) and city size, as well as their interaction (hereafter referred to as the 'urbanization incidence model'). We also tested for the effect of urbanization on the average powdery mildew severity at the tree level, which was calculated based on the subset of infected leaves on each tree (thus excluding zero values of uninfected leaves). We modelled the square root transformed mildew severity of each tree as a function of urbanization and city size, as well as their interaction (hereafter referred to as the 'urbanization severity model'). To account for the hierarchical design of the study, we included the random nested effects of country, city and location in both models.

We further investigated whether the effect of urbanization on mildew incidence and severity was mediated by biotic and abiotic variables. We first explored which plant traits (biotic factors) and climatic variables (abiotic factors) affected mildew incidence and severity. The full model on plant traits included nitrogen, phosphorus, flavonoids, lignin, condensed tannins and hydrolysable tannins. The full model on climatic variables included mean annual temperature, temperature seasonality, mean total annual precipitation, precipitation seasonality and CO_2 emissions (all variables were scaled to zero mean and unit variance). We then used backward model selection, in which we deleted variables that had the highest p-value (and with $p > 0.1$) in a stepwise manner. After backward model selection, we included the biotic and abiotic variables selected as covariates in the above urbanization incidence and severity models that showed a significant effect of urbanization. We reasoned as follows: If the significant effects of urbanization disappeared after including the covariates, then these covariates can be identified as a driver of urbanization effects on infection levels (since the covariates capture the same variation as does urbanization). If the effect of urbanization remained significant after including the covariates, then the covariates cannot be identified as the (sole) driver behind urbanization effects on infections levels. For all predictors, VIF's were lower than 10, indicating that multi-collinearity among predictors was unlikely to have a strong influence on model coefficient parameter estimates (James et al. 2013).

Within-city local and spatial drivers of pathogen infection levels

To analyse the effect of within-city heterogeneity on the incidence and severity of powdery mildew within Stockholm, we modelled the proportion of leaves infected by powdery mildew, as well as the ln-transformed average percentage of mildew coverage on all infected leaves for each tree, as a function of sunlight exposure, leaf litter cover, maximum temperature, CO_2 emissions, ln-transformed connectivity and year. To test whether effects of local habitat factors and connectivity differed among years, we included two-way interactions with year for all model terms. As we detected interactions between local habitat factors and year, and between spatial connectivity and year, we also ran year-specific models, which included the same predictor variables as described above.

Results

The impact of urbanization on pathogen infection levels at the continental scale

At the continental scale, mildew incidence did not differ significantly between urban and rural areas (mean ± SE: 0.48 ± 0.04 and 0.48 ± 0.04, respectively, $\chi^2_1 = 0.002$, $p = 0.96$), city size (from small to large: 0.43 ± 0.05, 0.48 ± 0.05 and 0.53 ± 0.05, $\chi^2_2 = 2.13$, $p = 0.35$) or their interaction ($\chi^2_2 = 3.53$, $p = 0.17$, Fig. 2a, Supporting information). Of the plant traits, mildew incidence was negatively related with leaf phosphorus content ($\chi^2_1 = 6.21$, $p = 0.01$, Fig. 3a). Of the abiotic factors, mildew incidence was positively associated with mean annual temperature ($\chi^2_1 = 5.37$, $p = 0.02$, Fig. 3c) but negatively associated with both mean total annual precipitation and precipitation seasonality ($\chi^2_1 = 9.93$, $p = 0.002$, and $\chi^2_1 = 3.27$, $p = 0.07$, respectively, Fig. 3e, g).

In contrast to mildew incidence, mildew severity was significantly higher in urban than in rural areas (27.3 ± 2.9 and 16.5 ± 2.2, respectively, $\chi^2_1 = 7.19$, $p = 0.01$), whereas city size (from small to large: 17.7 ± 2.6, 23.1 ± 3.5 and

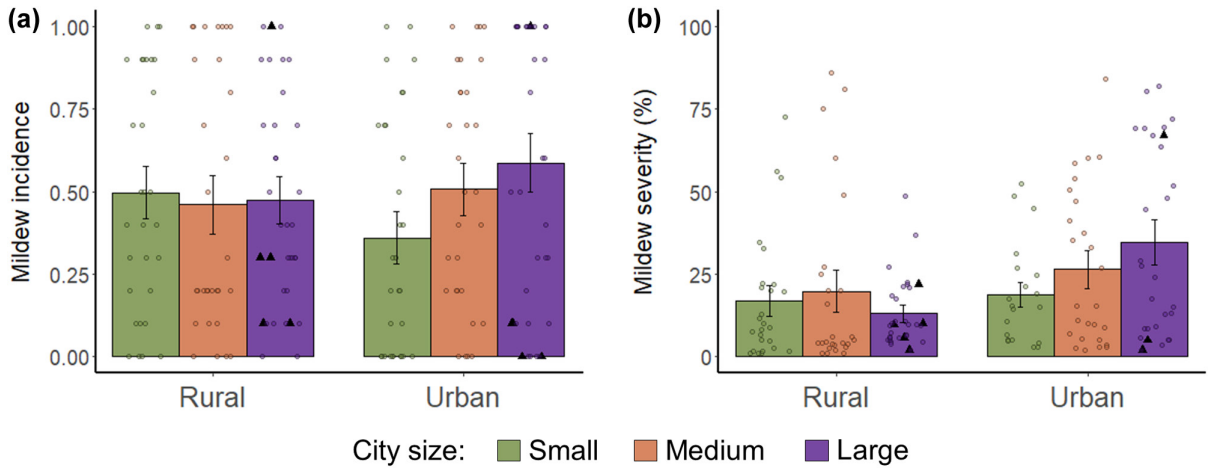


Figure 2. Powdery mildew incidence and severity in rural and urban environments in small (green), medium (orange) and large cities (purple) in 2017. Panel (a) shows the impact of urbanization and city size on mildew incidence, that is, the proportion of infected leaves per tree. Panel (b) shows the impact of urbanization and city size on mildew severity (conditional on presence of infection on the leaf). Shown are means ± SE. Dots represent raw data averaged at tree level (n = 180 trees), with trees from Stockholm marked as solid black triangles.

23.5 ± 3.5, $\chi^2_2 = 0.65$, p = 0.72) and the interaction between urbanization and city size had no statistically detectable effect ($\chi^2_2 = 3.31$, p = 0.19, Fig. 2b, Supporting information). Of the biotic factors, the concentration of flavonoids was negatively associated with mildew severity ($\chi^2_1 = 3.93$, p = 0.05, Fig. 3b), and of the abiotic climatic factors, mean annual temperature and temperature seasonality were positively associated with mildew severity ($\chi^2_1 = 9.77$, p = 0.002 and $\chi^2_1 = 8.81$, p = 0.003 respectively, Fig. 3c–d). After including flavonoids, mean annual temperature and temperature seasonality as covariates in the urbanization severity model, the effect of urbanization on mildew severity became marginally non-significant ($\chi^2_1 = 3.24$, p = 0.07, Supporting information). When removing either temperature seasonality or mean annual temperature from the model, the effect of urbanization became significant again, a pattern suggesting that these temperature factors potentially mediate the impact of urbanization on mildew severity.

Within-city local and spatial drivers of pathogen infection levels

Within the large city of Stockholm, mildew incidence strongly varied among years (Supporting information). Regarding local habitat factors, sunlight exposure did not significantly affect powdery mildew incidence (Supporting information). The influence of leaf litter differed among years: In 2017, leaf litter had a significant negative impact on powdery mildew incidence ($\chi^2 = 6.36$, p = 0.01), whereas there was no effect of leaf litter during 2018 or 2019 (Fig. 4a, Supporting information). Local maximum temperature and CO_2 emissions did not affect powdery mildew incidence during any of the years (Supporting information). Regarding spatial factors, connectivity had a negative overall impact on powdery mildew incidence ($\chi^2 = 4.03$, p = 0.04, Fig. 4b; Supporting information), where trees with higher connectivity had lower mildew incidence.

Mildew severity greatly varied among years (Supporting information) and among trees within a given year (Fig. 1b). Mildew severity was not affected by any of the local habitat factors (sunlight exposure, leaf litter, maximum temperature or CO_2 emissions) during any of the years (Supporting information). Connectivity had a negative effect on mildew severity ($\chi^2 = 6.21$, p = 0.01), though this effect varied among years: In 2017, more connected trees had less severe mildew infections ($F_{1,67} = 11.35$, p = 0.001), whereas during 2018 and 2019, no significant effect of connectivity was detected (Fig. 4c, Supporting information).

Discussion

Our study shows that urbanization increased the severity of powdery mildew infection on oaks at the continental scale, whereas mildew incidence was unaffected. Precipitation, phosphorus and flavonoids had an independent negative influence on mildew infection levels, and we found some evidence that the impact of urbanization on mildew severity was mediated by the differences in temperature between urban and rural areas. At the within-city scale, mildew incidence was negatively influenced by leaf litter during one year. Spatial factors influenced both mildew incidence and severity, where more connected trees had less infected leaves and less severe infection. Overall, our findings illustrate that urbanization can affect plant–pathogen interactions both at the continental and within-city scales and reveal some potential mechanisms at both scales.

The finding that mildew severity increased with urbanization fits with the general expectation that urban trees may be more susceptible to pathogen infections and insect attacks compared to trees in rural or natural systems due to increased physiological stress (Dreistadt et al. 1990, Dale and Frank 2017) or altered morphological traits (e.g. specific leaf area; Bradley et al. 2003, Dong et al. 2019). Besides increased

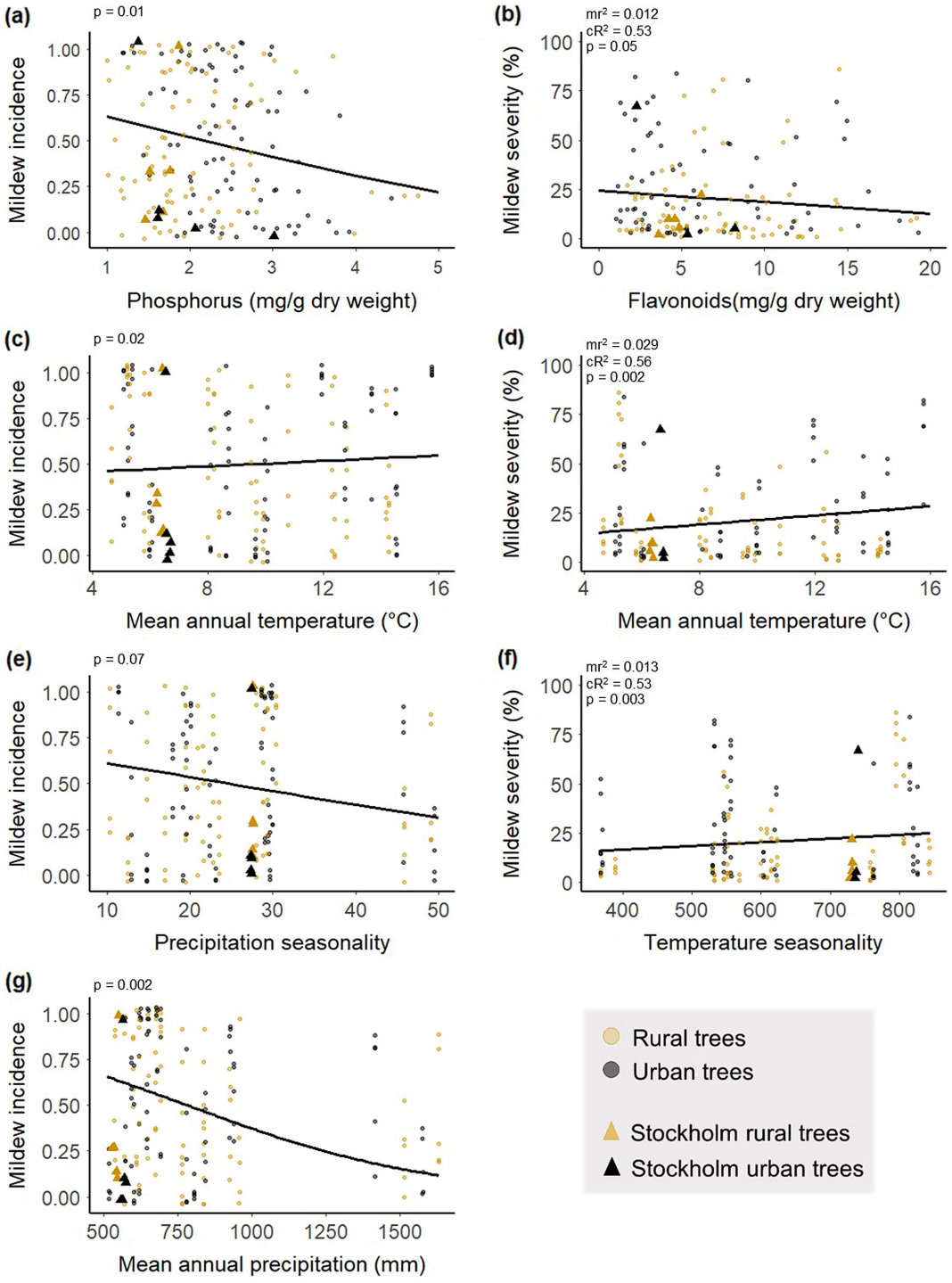


Figure 3. The impact of potential biotic (plant traits) and abiotic (climatic variables) drivers behind urbanization effects on powdery mildew incidence and severity in 2017. Rural areas are indicated in yellow and urban areas in black. Panels on the left show the effect of biotic and abiotic factors on mildew incidence (proportion of infected leaves per tree), and panels on the right show the effect of biotic and abiotic factors on mildew severity (conditional on presence of infection on the leaf). Presented are the effects of (a) phosphorus content, (c) mean annual temperature, (e) precipitation seasonality (coefficient of variation of the daily mean precipitation) and (g) mean total annual precipitation on mildew incidence (the proportion of infected leaves per tree), and the effects of (b) flavonoids, (d) mean annual temperature and (f) temperature seasonality (expressed as the standard deviation of temperature among months × 100) on mildew severity. Solid lines are the predicted relationships from generalized linear mixed-effects models including the fixed effect depicted in the panel as well as the nested random effects (country, city, location). For all these models, p-values are given in the top left corner of the panels, and for the severity models, marginal (simple determination coefficient) and conditional R-squared values (multiple determination coefficient) are also presented. Dots represent raw data averaged at tree level (n = 180 trees), with trees from Stockholm marked as solid triangles in all graphs.

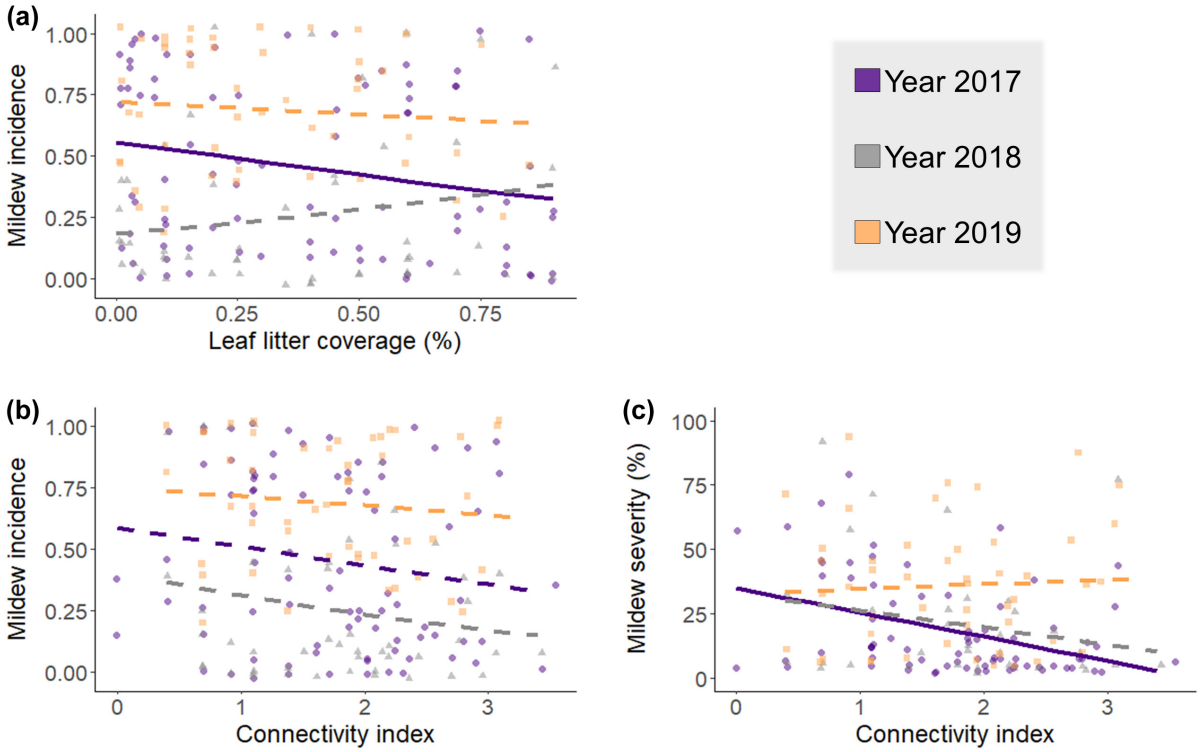


Figure 4. Effect of leaf litter and connectivity on powdery mildew incidence and severity on oaks in Stockholm during 2017, 2018 and 2019. Panel (a) shows the effect of leaf litter coverage underneath a tree on mildew incidence (the proportion of infected leaves per tree). Panel (b) shows the effect of spatial connectivity (ln-transformed) on mildew incidence. Panel (c) shows the effect of spatial connectivity (ln-transformed) on mildew severity (conditional on presence of infection on the leaf). Solid lines are the predicted relationships from generalized linear models including the fixed effect depicted in the panel. Dots represent raw data averaged at tree level. Dashed trend lines are non-significant, solid lines are significant. The relationships between all local habitat and spatial factors and mildew incidence and severity are illustrated in Supporting information, respectively.

physiological stress, the depauperate microbial community of the plant phyllosphere in urban environments (Supporting information) may increase the invasion success of pathogens (Vorholt 2012, Berg et al. 2017). Interestingly, previous research on plant–insect interactions shows that arthropods that are intimately associated with a host plant, including insects that have multiple generations on one host, generally increase in abundance with urbanization (Raupp et al. 2010). We speculate that this general pattern may also be applicable to pathogens: Powdery mildew is a specialist on oak, and the spores of this pathogen are continuously produced throughout the growing season and can reinfect the same oak tree as well as disperse to new oak trees. As severity but not incidence was affected by urbanization, our results suggest that urbanization did not influence the dispersal of mildew spores among leaves and trees but rather promoted the development of mildew colonies on already infected leaves. However, in order to fully understand these dynamics, it would be necessary to follow pathogen generations and oak flushes throughout the growing season. Interestingly, a previous study with the same oak trees (Moreira et al. 2019) found that urbanization significantly reduced leaf chewer damage. While speculative, these contrasting findings could indicate that trees experience a trade-off in defence against herbivores and pathogens (Biere and Bennett 2013, Tack and Dicke 2013). Such inter-kingdom interactions in an urban context could be an interesting topic for future research.

Our results showed that mildew incidence and severity were unaffected by city size, countering our expectation that the impact of urbanization would be more pronounced in larger cities. These findings are in line with those of Moreira et al. (2019), who did not detect any impact of city size on levels of insect leaf herbivory in pedunculate oaks. Yet, they contrast with findings by Kozlov et al. (2017), who found an impact of urbanization on birch tree insect herbivory for large cities but not for medium or small cities. As very few studies have explored whether effects of urbanization on species interactions depend on city size, and none focused on plant pathogens, we cannot yet draw any conclusions about the generality of our findings. Furthermore, as city characteristics are highly variable – even among cities of the same size – we argue it is important to elucidate the underlying factors behind the effects of city size in order to explain discrepancies between studies. Such insights may also be gained by studies at the within-city scale that explore the link between city characteristics and the resulting influences of urbanization on species interactions.

Altered abiotic conditions in urban areas can either directly or indirectly affect species interactions, i.e. by changing local

environments or by influencing plant traits, respectively. Mean annual temperature positively impacted mildew incidence, whereas mean annual total precipitation and precipitation seasonality had a negative impact. Increased temperatures may influence mildew incidence through its positive impacts on spore germination success (Yarwood et al. 1954), whereas increased precipitation may potentially wash spores off the leaves or impair spore germination due to water submergence (Hossain and Manners 1964). Furthermore, we detected a negative effect of phosphorus on mildew incidence. As phosphorus is of nutritional value to plant attackers, this was an unexpected finding. However, phosphorus also improves plant health and can directly promote plant resistance (Orober et al. 2002, Walters and Bingham 2007), thus decreasing plant susceptibility to diseases. As urbanization did not affect mildew incidence, we could not further dissect the influence of abiotic and biotic factors on this relationship. For mildew severity, which was affected by urbanization, we found some evidence that temperature (mean annual temperature and temperature seasonality) may drive the positive impact of urbanization at the continental scale. Previous studies have shown that colder temperatures can slow mildew colony expansion leading to reduced infection severity (Moyer et al. 2010, Uloth et al. 2018). Thus, warmer urban areas may promote infection severity, albeit only to a certain extent, as too high temperatures may again decrease mildew performance (Yarwood et al. 1954). In line with the findings of Moreira et al. (2019) on oak insect herbivory, CO_2 emissions did not affect mildew severity. With regards to the plant traits, we found evidence that flavonoids were negatively associated with mildew severity, as previously reported for powdery mildews on *Cucumis sativus* (Fofana et al. 2002, 2005); however, this defensive compound did not mediate the impact of urbanization on mildew severity.

While our continental-scale analysis sheds light on relevant biotic and abiotic factors potentially underlying urbanization effects at a broad spatial scale, our within-city analysis uncovers that local and spatial urban heterogeneity affects oak–pathogen interactions. While a previous study suggested that powdery mildew thrives best in shady environments (Ekholm et al. 2017), we detected no effects of sunlight exposure on mildew infection within the urban landscape. Notably, and contrary to expectations, leaf litter was found to negatively influence mildew incidence, though this effect was only visible during one of the years. This negative, year-dependent impact contrasts with the positive effects of leaf litter shown for herbivorous insects on urban oaks (Herrmann et al. 2012, Barr et al. 2021), where leaf litter possibly increased overwintering survival by providing an insulative layer. Instead, leaf litter may alter the microclimate of the tree, such as humidity levels, which could impact powdery mildew performance (Sayer 2006), or affect the survival of specialist and opportunistic fungi that attack powdery mildew (Topalidou and Shaw 2016). Since an effect of leaf litter was only detectable in one year, the strength and direction of this effect might be dependent on the specific climatic conditions within a given year. In 2018, when mildew incidence and severity were lowest, the climate was exceptionally dry and hot, which probably led to generally less favourable local habitat conditions. For example, low humidity levels and dry leaf surfaces may have been particularly unsuitable for mildew germination and growth (Guzman-Plazola et al. 2003). Extreme droughts also induce plant stress, potentially leading to higher tree vulnerability to pathogen infection in the following season (Schuldt et al. 2020); in this study, we indeed detected the highest infection levels in 2019. Interestingly, when comparing the influence of abiotic factors measured at both scales, we found that CO_2 levels had no effect on infection levels at either the continental or within-city scales, whereas temperature was a potential driver of mildew infection at the continental scale but did not relate to mildew infection at the within-city scale. Thus, while CO_2-mediated mechanisms appear to be negligible across scales, our results suggest that temperature-related mechanisms of urbanization effects are scale-dependent. However, since our study has no replicates at the level of the continental and within-city scales, we cannot formally compare these scales, and further studies that replicate at multiple scales are needed to disentangle the biotic and abiotic drivers of urbanization across scales.

Species interactions within cities can further be modified by the spatial distribution of the host. Contrary to previous findings on oak powdery mildew within a natural system (Ekholm et al. 2017), our results show that both mildew incidence and severity were lower in more dense oak stands, though this spatial connectivity effect on severity was temporally variable. While one might expect connected oak trees to be more likely to receive spores from neighbouring trees, increased gene flow among connected hosts could also have promoted higher disease resistance (Jousimo et al. 2014). However, this phenomenon has never been studied in an urban setting, and such a scenario may be less likely for long-lived tree species such as oak. Alternatively, decreased mildew incidence and severity among connected oaks may be explained by local environmental features and land-use types possibly associated with connectivity. For example, connectivity could be positively related to the presence of surrounding vegetation and the density of vegetation cover, which may decrease local temperatures and affect airflows (Dimoudi and Nikolopoulou 2003, Fan et al. 2015). Generally, studies on the effect of urbanization on organisms and communities have found the impact of local habitat to be more important than spatial factors (Sattler et al. 2010, Beninde et al. 2015). Here we show that spatial connectivity within the urban landscape may in fact be a determining factor for the abundance of plant diseases and might possibly be even more important than the local habitat. While the current results provide a first indication for within-city drivers of plant–pathogen interactions, future studies including more cities are needed to generalize these patterns.

Conclusions

Our study shows that urbanization can shape plant pathogen dynamics both at the continental and within-city scales, and it identifies some potential drivers of these dynamics at both

scales. To uncover the generality of our findings and to mechanistically determine the drivers behind urbanization effects at each scale, we need more research on a greater array of study systems and at various spatial scales. In doing so, we could further develop a general framework on the impact of urbanization on species interactions. Insights from such a framework, as based on accumulated research, can then be used to inform management strategies both related not only to local management actions but also to spatial design planning of tree species diversity within cities, thereby preventing disease outbreaks of native or non-native pathogens in urban areas.

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Author contributions

Laura van Dijk: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Xoaquín Moreira**: Conceptualization (equal); Investigation (supporting); Methodology (supporting); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Anna Barr**: Investigation (equal); Writing – review and editing (supporting). **Luis Abdala-Roberts**: Investigation (supporting); Writing – review and editing (supporting). **Bastien Castagneyrol**: Investigation (supporting); Writing – review and editing (supporting). **Maria Faticov**: Investigation (supporting); Writing – review and editing (supporting). **Bess Hardwick**: Investigation (supporting); Writing – review and editing (supporting). **Jan ten Hoopen**: Investigation (supporting); Writing – review and editing (supporting). **Raúl de la Mata**: Investigation (supporting); Writing – review and editing (supporting). **Ricardo Pires**: Investigation (supporting); Writing – review and editing (supporting). **Tomas Roslin**: Investigation (supporting); Writing – review and editing (supporting). **Dmitry Schigel**: Investigation (supporting); Writing – review and editing (supporting). **Bart Timmermans**: Conceptualization (supporting); Investigation (supporting); Writing – review and editing (supporting). **Ayco Tack**: Conceptualization (equal); Investigation (supporting); Methodology (supporting); Resources (equal); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0k6djh9zq> (van Dijk et al. 2021).

Supporting information

Any supporting information associated with this article is available from the online version.

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