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Analyzing remotely sensed structural and chemical canopy traits of a forest invaded by *Prunus serotina* over multiple spatial scales

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Abstract Non-native invasive plant species can influence ecosystem functioning over broad spatial scales, but most research on ecosystem impacts has focused on the plot level covering sampling units of only a few square meters or less. We used a multi-scale approach to analyze structural and leaf chemical vegetation traits depending on the presence of non-native American black cherry (*Prunus serotina*) in a mixed deciduous forest at the plot level and at the forest stand level. Trait data were derived from remotely sensed maps of leaf area index (LAI), wood volume as well as canopy leaf nitrogen concentration (N_{mass}), phosphorous concentration (P_{mass}), and N:P ratio. Differences in these traits were compared between invaded and non-invaded areas at the plot level using 264 sampling units with a size of 25 m × 25 m and in 4119 forest management units (mean area: 7.6 ± 5.1 ha). Observed patterns between invaded and non-invaded areas were similar at both spatial scales. Invaded areas were characterized by less wood volume, indicating that lower standing biomass promotes the occurrence of *P. serotina*. In contrast, LAI did not differ between invaded and non-invaded areas. Furthermore, the presence of *P.*

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serotina trees had an impact on the chemical composition of the forest canopy by decreasing leaf N:P. While for P_{mass}, we found no differences in between invaded and non-invaded areas, for N_{mass} we observed an invasion effect, though only at the plot level. Using remotely sensed trait data proved valuable to evaluate the spatial relevance of invasion impacts over large areas.

Keywords Alien plants · Foliar stoichiometry · Hyperspectral · Imaging spectroscopy · LiDAR

Introduction

Non-native invasive plant species can have manifold impacts on ecosystems, by changing biotic or abiotic conditions through many different pathways (Ehrenfeld 2010; Weidenhamer and Callaway 2010; Gaertner et al. 2014). Due to effective spreading and fast growth they are often found to build up dense populations and can thus change the composition of native plant communities and locally decrease biodiversity (Powell et al. 2011; Vilà et al. 2011; Pyšek et al. 2012). Besides altering community composition, invasive plant species can also influence ecosystem properties or processes (Stricker et al. 2015). For instance, the presence of non-native invasive plant species has often been associated with an increase in above-ground biomass, above ground nutrient stocks, and nutrient concentrations in the topsoil (Liao et al.

2008; Dassonville et al. 2008; Weidenhamer and Callaway 2010; Vilà et al. 2011).

Changes in ecosystem properties are often related to increased primary production (Vilà et al. 2011) that can be attributed to the fast growing character of many invasive plant species (Van Kleunen et al. 2010). Fast growth is generally related to low investments of carbon in leafs associated with higher leaf nitrogen (N) and phosphorous (P) concentrations (Wright et al. 2004). Hence, many invasive plant species are characterized by higher leaf N and P concentrations (e.g. Thorpe et al. 2006; Kurokawa et al. 2010; Jäger et al. 2013) or increased total N and P uptake (e.g. Windham and Ehrenfeld 2003; Chapuis-Lardy et al. 2006; Aguilera et al. 2010) compared to co-occurring native species. Changes in community level above-ground nutrient contents can be caused by direct or indirect effects. An direct effect can be for example an increase of community level above-ground nitrogen, due to high uptake by an invasive species. Indirect effects can include increased nitrogen or phosphorous concentrations in the leaves of co-occurring native species due to nutrient mobilization (Fisher et al. 2006; Kurten et al. 2008). However, invasive plants can also reduce nutrient concentrations in the leaves of co-occurring species (Aerts et al. 2017), presumably as an effect of resource competition (Vilà and Weiner 2004).

The majority of studies dealing with ecosystem impacts of invasive plants have been limited to plot based observations or experiments, in which each sampling unit is covering areas of only few square meters (Parker et al. 1999; Stricker et al. 2015). While this is a valid approach to understand effects of

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invasion processes it provides little information about the spatial relevance of such impacts. Besides the per capita or per biomass impact of an invasive species, its broad scale ecosystem impact depends on its range size and its occurrence prevalence within the area of interest (Parker et al. 1999; Thiele et al. 2009). Moreover, the spatial distribution patters of invasive plant species can differ across spatial scales, and similarly also their ecological effects (Pauchard and Shea 2006). Plot level studies of invasion effects thus provide only part of the information needed to evaluate its overall ecosystem impact. Evaluating the impact of an invader at multiple spatial scales will provide a more comprehensive picture of its impact (Parker et al. 1999; Pauchard and Shea 2006), and therefore also valuable information for prioritizing management actions.

Remote sensing offers great opportunities to support ecological research addressing multiple spatial scales by providing spatial explicit projections of vegetation traits. Such projections include structural vegetation traits such as biomass or LAI (Zheng and Moskal 2009; Fassnacht et al. 2014; Kumar et al. 2015), chemical leaf traits such as chlorophyll or N concentration (Asner et al. 2015; Singh et al. 2015) and plant functional types (Ustin and Gamon 2010; Kattenborn et al. 2017). Applications of remote sensing in invasion ecology have mainly focused on mapping and monitoring the distribution of invasive plant species (Bradley 2014) holding potential to detect early invasion stages (Rocchini et al. 2015; Skowronek et al. 2016). However, remote sensing data can also be used to detect invasion impacts on ecosystem functioning over large areas in a spatially continuous manner (Asner and Vitousek 2005; Vicente et al. 2013).

In this study, we applied a multi-scale approach to investigate the impact of an invasive tree species on structural and chemical vegetation traits in a mixed deciduous forest using sampling units of different size. Impacts were analyzed at the plot level and at the level of forest management units, hereafter referred to as stand level.

Our target species was *Prunus serotina*, an alien invasive tree species in Western and Central Europe. In its non-native range *P. serotina* mainly occurs on nutrient poor acidic soils within oak and pine forests (Starfinger et al. 2003; Closset-Kopp et al. 2010) and is promoted by high light availability in canopy gaps or

in forests characterized by sparse canopies (Vanhellemont et al. 2008; Terwei et al. 2013). Reported impacts of *P. serotina* outside of its native range include changes of soil conditions and understory plant communities in forest ecosystems (Halarewicz and Pruchniewicz 2015). Especially as a shrub, *P. serotina* can form very dense populations and dramatically reduce understory light availability (Starfinger et al. 2003). *P. serotina* is characterized by higher leaf N and P concentrations than most of the co-occurring native tree species (Aerts et al. 2017), thereby showing potential to alter nutrient cycling in forest ecosystems. At the plot level *P. serotina* has been found to decrease leaf N of co-occurring European beech (*Fagus sylvatica*) and to increase leaf P of co-occurring Scots pine (*Pinus sylvestris*) (Aerts et al. 2017).

Differences in structural and chemical traits were analyzed dependent on stand type, stand age, soil pH and the presence of *P. serotina* in the tree layer at the plot level and at the forest stand level. Using this multi scale approach we aimed to get a more comprehensive picture of ecosystem changes caused by *P. serotina*.

Materials and methods

Study area

The forest of Compiègne (northern France, coordinates: N 49.370, W 2.886), covering an area of 144.2 km², is located in the oceanic climate zone with a mean annual temperature of 10.3 °C and a mean annual precipitation of 677 mm. Soils are formed of nutrient-poor sandy substrate in the northern part of the forest and nutrient rich calcareous substrate in the southern part (Chabrerie et al. 2008). The forest is mainly managed as even-aged stands of beech (*Fagus sylvatica*), oaks (*Quercus robur*, *Quercus petrea*) and pine (*Pinus sylvestris*), which often also occur in mixed stands. These stands are frequently intermingled with European hornbeam (*Carpinus betulus*) and ash (*Fraxinius excelsior*). Stands can reach ages of more than 200 years (Chabrerie et al. 2008). *P. serotina* was introduced to the area around 1850 and has since then spread across a substantial part of the forest (Fig. 1) (Chabrerie et al. 2008). Although *P. serotina* is affected by frequent thinning, it is often highly abundant in the shrub layer and can locally

become the dominant tree species within the forest canopy.

Data

Spatial forest stand information

We used forest inventory maps from the year 2009, providing polygons with information on stand age (9 different classes ranging from "0–20 years" to "older than 200 years") and up to four dominant tree species for each of the 2846 forest management units (Table 1, Fig. S1, Online Resource 1). We classified stand types according to the most dominant tree species of each forest stand. Stands consisting of three or more tree species exceeding 20% of total canopy cover were classified as mixed stands.

Soil pH map

Information on soil pH was obtained from a soil pH map at 25 m × 25 m resolution covering the entire study area (Table 1, Fig. S1, Online Resource 1). This map was generated through regression-kriging using 161 point measurements of topsoil pH and including soil type, elevation, slope, bedrock geology and a litter quality index as predictors (for more information see Hattab et al. 2017).

Data on *P. serotina* presence

For the analysis of differences between invaded and non-invaded parts of the forest at the plot level we sampled information on presence-absence of *P. serotina* in the tree canopy within 336 field plots with a size of 25 m × 25 m (Table 1, Fig. 1). Presence-absence data were recorded between July and October 2015 throughout the whole forest area combining random sampling with an environmental systematic mapping (Hattab et al. 2017).

For the stand level we used 6432 polygons with information on the occurrence of *P. serotina* in the tree layer in 6 discrete classes ranging from 0 to 5 (0: no *P. serotina*, 1: isolated individuals, 2: scattered aggregates of individuals, 3: fragmented populations, 4:

Fig. 1 Study area with forest management units and presence-absence locations used for analyses at the stand and plot level respectively. Colors indicate estimated frequency of *P. serotina* trees within the management units. (Reproduced with permission from Chabrerie et al. 2007)
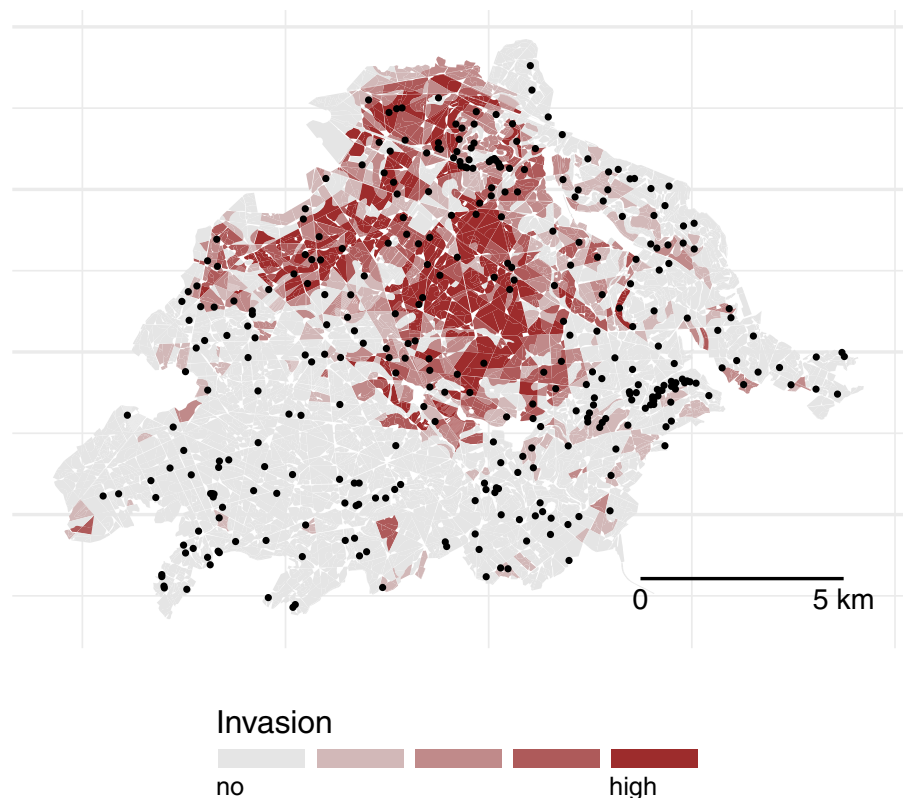
Table 1 Overview of data used as basis for response and predictor variables

Variable	Data type	Variable type	Data source
Response			
LAI	Raster	Continuous	Combination of high resolution remote sensing and field data
Wood volume	Raster	Continuous	Combination of high resolution remote sensing and field data
N_{mass}	Raster	Continuous	Combination of high resolution remote sensing and field data
P_{mass}	Raster	Continuous	Combination of high resolution remote sensing and field data
Predictors			
Soil pH	Raster	Continuous	Hattab et al. (2017)
P. serotina presence[a]	Point	Factor (2 levels)	Field acquisition
P. serotina presence[b]	Polygon	Factor (5 levels)	Chabrerie et al. (2007)
Stand type	Polygon	Factor (4 levels)	Forest inventory data
Stand age	Polygon	Factor (9 levels)	Forest inventory data

[a] Only used for analyses at the plot level

[b] Only used for analyses at the stand level

large, continuous population, 5: dominant canopy tree species over the entire stand) based on field sampling between the years 2003 and 2004 (Chabrerie et al. 2007). Because of its low sample size, class 5 was merged with class 4. In order to join information on stand type/age and occurrence of *P. serotina* trees we calculated a spatial overlay of the two polygon maps.

Remotely sensed maps of structural and chemical traits

To compare structural and chemical vegetation traits within invaded and non-invaded parts of the forests we used maps for leaf area index (LAI), wood volume, canopy nitrogen content (N_{mass}), canopy phosphorous content (P_{mass}), and canopy N:P ratio, based on a combination of field derived trait and remote sensing data (Table 1). Remote sensing data consisted of airborne imaging spectroscopy data (248 bands, 380–2500 nm) acquired in July 2014 by the Airborne Prism Experiment (APEX) spectrometer (Schaepman et al. 2015) with a spatial resolution of 3 m × 3 m, and airborne discrete return LiDAR data with an average point density of 23 points m^{-2} (for detailed information on remote sensing data, and its processing see Online Resource 2).

For mapping LAI, wood volume, N_{mass}, P_{mass} and N:P, we used partial least squares regression models that were calibrated by field-derived trait data (Fig. 2, for more information see Online Resource 2). In order

to get more robust predictions, model calculations were embedded in a repeated data splitting procedure with 200 repetitions. For each iteration a random set of 10 out of 50 field plots was not included in model calibration. Predictive models resulted in mean Pearson r^2 values of 0.48, 0.72, 0.41, 0.63 and 0.61 in leave-one-out cross-validation for LAI, wood volume, N_{mass}, P_{mass} and N:P respectively. Spectral bands and LiDAR-derived variables were used to predict 200 maps for LAI, wood volume, N_{mass}, P_{mass} and N:P from the resulting models of each data split. Finally, for each trait, we calculated median maps representing the median value for each pixel from those 200 prediction maps (Fig. S2, Online Resource 1).

Data processing

We created two different datasets: one for the analysis of impacts by *P. serotina* at the plot level and one for the analyses at the stand level (Fig. 2). For both datasets we extracted information on stand type, stand age, soil pH, LAI, wood volume, N_{mass}, P_{mass} and N:P from the available set of maps. Information from raster maps (pH, LAI, wood volume, N_{mass}, P_{mass}, N:P) was extracted for all pixels intersecting with an square of 25 m × 25 m around the presence-absence locations and all pixels intersecting with the polygons representing forest stands, respectively. For soil pH we calculated median values for each location and forest
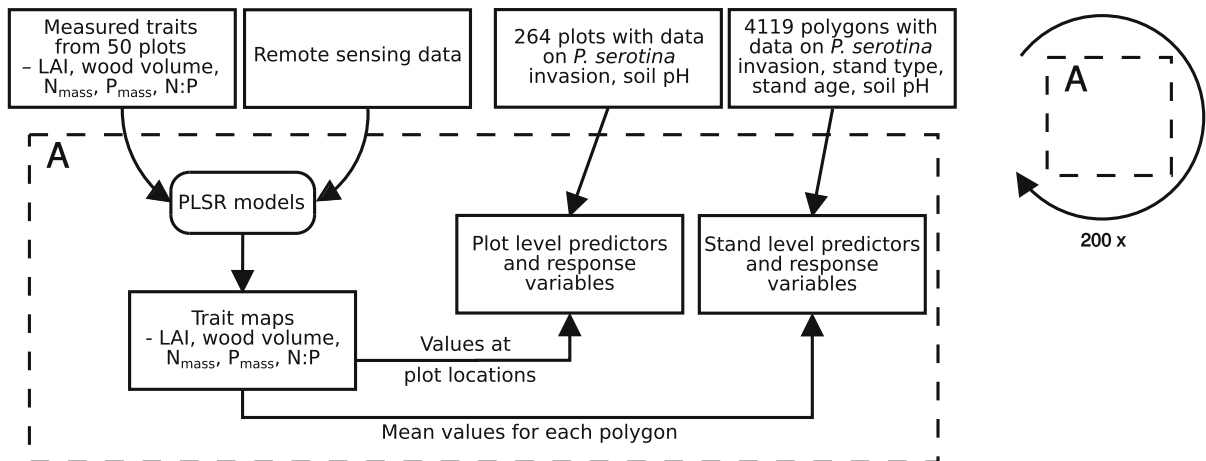
Fig. 2 Work-flow illustrating the retrieval of response and predictor datasets at the plot and at the stand level (for more information on used variables see Table 1). Trait maps were generated using predictions from partial least squares regression (PLSR) models

stand. Extracted pixel values of the remaining variables were averaged. For LAI, wood volume, N_{mass}, P_{mass} and N:P this procedure was repeated for each of the 200 predicted maps and the median map.

We only considered mixed stands and stands dominated by *F. sylvatica*, *Q. robur* or *P. sylvestris* for the subsequent analyses. Mixed stands were usually only represented by broadleaved tree species. Other stand types were excluded from the analyses because of their small sample size. Furthermore, for the analyses at the stand level polygons smaller than 0.5 ha were not considered as stands and thus discarded from the data set. This resulted in 264 samples for analyses at the plot level and 4119 polygons (mean area: 7.6 ha, maximum area: 34.5 ha, standard error: $\pm$ 5.1 ha) for analyses at the stand level.

Statistical analyses

We aimed to analyze the four vegetation traits (LAI, wood volume, N_{mass}, P_{mass}) in depending on *P. serotina* presence (plot level) or invasion degree (stand level) and stand type (Table 1), considering the confounding effects of soil pH and stand age. Both plot and stand level data was analyzed using the same procedure (Fig. 3). We ran mixed effects models using each of the four studied vegetation traits as response variables, whereas stand type, soil pH and invasion by *P. serotina* were used as fixed effects and stand age

class was integrated as a grouping factor. In a first step we built preliminary models for each response variable using values extracted from the median prediction maps. These models were used to select an appropriate model type (model family) and link function by visual examination of quantile–quantile plots. Additionally, preliminary models were used to test for spatial autocorrelation (SAC) in the residuals. For this purpose we calculated the centroids of polygons representing forest stands. SAC was tested calculating the Moran's I value between residuals ordered by distance in uniformly distributed distance classes. Class width was 200 m for plot level models and 50 m for stand level models. For all response variables we observed considerable SAC.

We chose linear mixed effects models with identity link and a Gaussian error distribution (LMM) as quantile–quantile plots suggested this for all variables at the plot level as well as for LAI, wood volume and N_{mass} and N:P ratio at the stand level. We accounted for SAC by integrating a correlation function into the model (Dormann et al. 2007). For all response variables an exponential correlation function was chosen based on visual examination of the residual's correlogram (Dormann et al. 2007).

To select the best set of predictors we successively calculated five candidate models. Each candidate model included different predictor variable combinations (see Table 2, Fig. 3) for each of the four response variables. This procedure was repeated 200 times for each dataset resulting from the 200 prediction maps
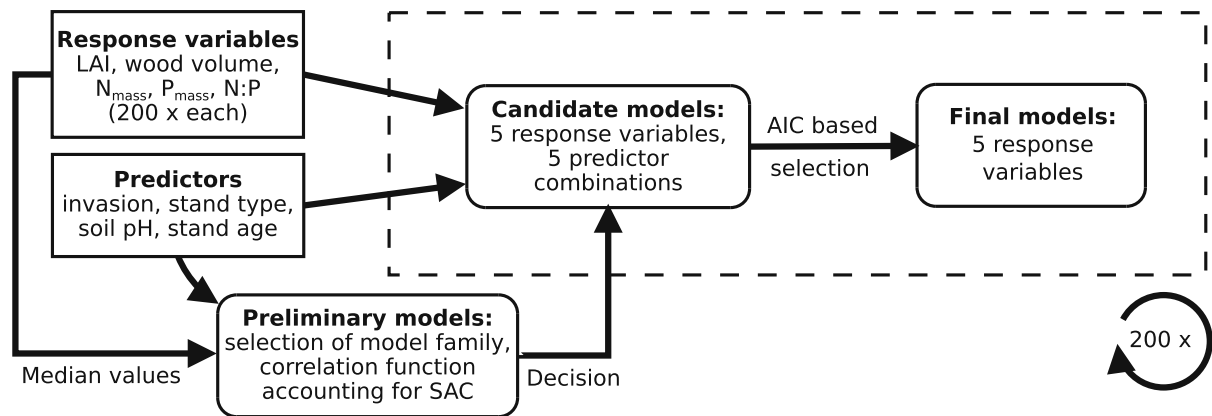
Fig. 3 Work-flow illustrating the steps of statistical analyses of structural and chemical canopy traits depending on the presence of *P. serotina*, stand type and soil pH and stand age (for more information on response and predictor variables see Table 1). The presented procedure was used for analyses at both the plot and stand level. SAC: Spatial autocorrelation

respectively. For each of the response variables, we selected the final conceptual model according to lowest median AIC values resulting from 200 model repetitions (Table 2).

To test for differences between included fixed effects we extracted parameter coefficients and calculated the differences between the coefficients of all possible factor combinations for each of the 200 calculated models. In a second step we checked if these differences were significantly different from zero by calculating the 95% confidence intervals.

Data processing and statistical analyses were performed using R 3.3.1 (R Core Team 2016). SAC was tested using the package ncf 1.1 (Bjornstad 2016) and LMMs were calculated using the package nlme 3.1 (Pinheiro et al. 2016).

Results

In all LMMs stand type was included as predictor variable, irrespective of the response variable for both plot and stand level (Table 2). This indicated a high influence of species-specific differences in the variation of observed canopy traits, LAI, wood volume, N_{mass} and P_{mass} and N:P ratio. Best models after AIC-based model selection also included invasion by *P. serotina* for wood volume, N:P and N_{mass} (see Table 2). However, for N_{mass} an influence of *P. serotina* was only apparent at plot level and not at the stand level. Furthermore, for N:P models at the stand level, integration of *P. serotina* invasion reduced AIC

values only moderately (16,751.1 vs. 16,750.7). LAI and P_{mass} did not differ between invaded and non-invaded parts of the forest, irrespective of the spatial scale. Final models resulted in mean Pearson r^2 values between 0.26 and 0.52 at the plot level and between 0.29 and 0.39 at the stand level (see Table 1).

While the presence of *P. serotina* in the tree layer was connected to lower wood volume at the stand level for all forest types, we observed no clear trend at the plot level (Figs. 4, 5). Here, wood volume was higher at sites with *P. serotina* trees in *Q. robur* and mixed stands, whereas it was lower in *F. sylvatica* and *P. sylvestris* stands, though not significant for the latter two. At the plot level, presence of *P. seronita* trees was connected to significantly lower N_{mass} in mixed deciduous stands and higher N_{mass} in *P. sylvestris* stands (see Fig. 5). Canopy N:P ratios observed at the plot level were lower in *F. sylvatica* and mixed deciduous stands when *P. serotina* trees were present. When looking at the stand level, *P. serotina* presence was related to decreased N:P ratios for all stand types, but only for invasion classes 3 and 4, representing large fragmented up to continuous populations of *P. serotina* trees (see Fig. 4).

Stand type specific differences of canopy traits were similar across fine and coarse spatial scales for LAI, N_{mass}, P_{mass} and N:P ratio (Figs. 6, 7). Most apparent was a lower LAI and lower N_{mass} in pine stands, depicting the functional differences between broadleaved tree species and the coniferous *P. sylvestris*. Despite the observation of lowest P_{mass} and highest N:P values in beech dominated stands,

Table 2 Median AIC and Pearson r^2 values of the five candidate linear mixed effect models for LAI, wood volume, N_{mass}, P_{mass} and N:P

Response	Model	Fixed effects	Grouping factor	r^2 plot	r^2 stand	AIC plot	AIC stand
LAI	M1	pH	stand.age	0.41	0.24	711.2	6843
	M2	invasion.tree + pH	stand.age	0.41	0.24	714.7	6845
	M3	stand.type + pH	stand.age	0.52	0.39	**675.4**	**6430**
	M4	invasion.tree + stand.type + pH	stand.age	0.52	0.40	679.3	6447
	M5	invasion.tree + stand.type + invasion.tree:stand.type + pH	stand.age	0.53	0.40	681.1	6479
Wood volume	M1	pH	stand.age	0.22	0.27	2159	29,314
	M2	invasion.tree + pH	stand.age	0.23	0.29	2155	29,286
	M3	stand.type + pH	stand.age	0.23	0.30	2150	29,257
	M4	invasion.tree + stand.type + pH	stand.age	0.24	0.32	2145	29,226
	M5	invasion.tree + stand.type + invasion.tree:stand.type + pH	stand.age	0.26	0.32	**2131**	**29,187**
N_{mass}	M1	pH	stand.age	0.18	0.04	1132	13,223
	M2	invasion.tree + pH	stand.age	0.19	0.08	1129	13,225
	M3	stand.type + pH	stand.age	0.32	0.33	1088	**12,534**
	M4	invasion.tree + stand.type + pH	stand.age	0.33	0.34	1088	12,543
	M5	invasion.tree + stand.type + invasion.tree:stand.type + pH	stand.age	0.35	0.34	**1082**	12,569
P_{mass}	M1	pH	stand.age	0.22	0.22	− 122.0	− 6349
	M2	invasion.tree + pH	stand.age	0.23	0.24	− 119.3	− 6343
	M3	stand.type + pH	stand.age	0.33	0.29	**− 139.4**	**− 6499**
	M4	invasion.tree + stand.type + pH	stand.age	0.34	0.30	− 132.8	− 6477
	M5	invasion.tree + stand.type + invasion.tree:stand.type + pH	stand.age	0.34	0.29	− 121.0	− 6414
N:P	M1	pH	stand.age	0.12	0.03	1388	17,335
	M2	invasion.tree + pH	stand.age	0.15	0.07	1380	17,351
	M3	stand.type + pH	stand.age	0.37	0.33	1306	16,751
	M4	invasion.tree + stand.type + pH	stand.age	0.39	0.34	1302	**16,751**
	M5	invasion.tree + stand.type + invasion.tree:stand.type + pH	stand.age	0.40	0.33	**1296**	16,760

Results are presented for analyses at the plot level and the forest stand level. Bold values indicate lowest AIC values. pH: soil pH, stand.type: forest stand type defined by dominating tree species, stand.age: stand age comprising 9 age classes, invasion.tree: Invasion of *P. serotina* in the layer (presence-absence for plot level data and five classes for stand level data)

differences between broadleaved forest stands were low. For wood volume we observed no consistent pattern between the stand types, when comparing plant and stand level results (see Fig. 6).

Discussion

Influences of *P. serotina* on canopy chemical traits

Regarding leaf N:P, our results suggest that *P. serotina* has the potential to alter forest canopy chemical stoichiometry across scales. While previous field studies found evidence for ecosystem impacts of *P. serotina* at the plot level (Halarewicz and Pruchniewicz 2015; Aerts et al. 2017) we could now demonstrate the relevance of impacts on forest ecosystems also at larger scales.

Observed differences in leaf chemical composition between invaded and non-invaded areas can be explained by direct and indirect effects of *P. serotina*. We can assume that *P. serotina* directly influenced canopy N:P due to its leaf chemical stoichiometry differing from the resident species (Aerts et al. 2017). This also conforms to the results of a recent meta-study by Lee et al. (2017), which showed that impacts
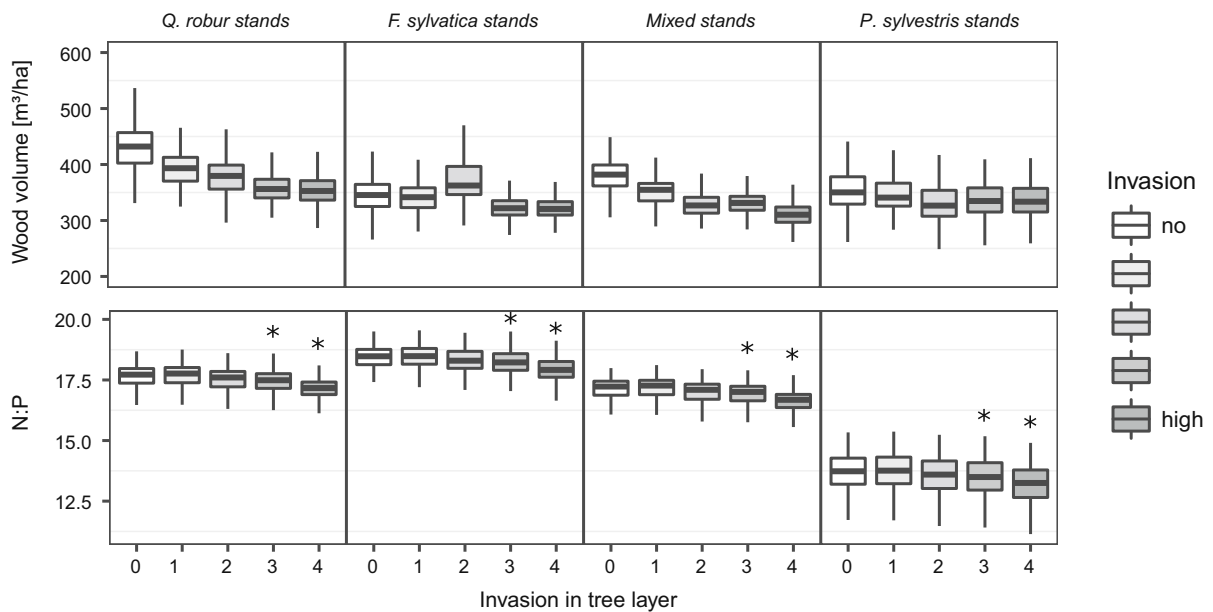
Fig. 4 Predicted values of 200 repeated model calculations for wood volume and canopy N:P depending on the occurrence of *P. serotina* trees at the stand level for different stand types characterized by the dominant tree species. *P. serotina* occurrence is grouped into 5 classes (0: no *P. serotina*, 1: isolated individuals, 2: scattered aggregates of individuals, 3: fragmented populations, 4: large, continuous population). Asterisks indicate significant differences from areas without presence of *P. serotina* trees resulting from a comparison of model coefficients from 200 model repetitions. Results are displayed for stands with an age of 90–100 years and a soil pH value of 5.96

of invasive plant species on N cycling were mainly driven by trait differences between invaders and native plant communities.

An indirect way of altering canopy chemistry would presuppose that *P. serotina* was able to influence leaf chemical traits of the co-occurring resident tree species. In fact, Aerts et al. (2017) observed that *P. serotina* increased P_{mass} of co-occuring *P. sylvestris* and decreased N_{mass} of co-occuring *F. sylvatica*. One possible driver is resource competition causing reduced soil nutrient availability for the resident species and consequently also reduced leaf nutrient contents. This is one possible reason for the reduced N_{mass} in invaded areas at the plot level and for reduced N:P ratios observed at the stand level. Another possible pathway is improved soil nutrient availability through alterations of litter chemical composition. Early successional fast-growing tree species like *P. serotina* are often characterized by lower resorption rates of leaf nutrients from senescent leaves (Sardans and Peñuelas 2015) that are also depicted in higher litter nutrient contents (Richardson et al. 2005) accelerating litter decomposition. Likewise, *P. serotina* has been found to accelerate litter

decomposition (Aerts et al. 2017) which may have increased nutrient availability in the topsoil resulting in higher N_{mass} of the co-occurring trees species, like observed in invaded *P. sylvestris* stands.

The leaf N:P ratio can be used as an indicator for plant nutrient status giving information on productivity and tree vitality (Güsewell 2004). In the last decades leaf N:P ratios have increased across European forests presumably resulting from high N deposition (Jonard et al. 2015; Talkner et al. 2015; Sardans et al. 2016). Mean observed N:P ratios in our study area (20.5, 18.3 and 11.7 in the leaves of *F. sylvatica*, *Q. robur* and *P. sylvestris* respectively), already exceeded the tolerable ranges suggested by Mellert and Göttlein (2012), indicating P deficiency. In that respect, a potential reduction of leaf N:P ratios by *P. serotina* can be rather considered positive.

Structural differences between invaded an non-invaded areas

Invaded mixed deciduous and *Q. robur* stands were characterized by less wood volume than non-invaded ones. In contrast, invaded *P. sylvestris* stands showed
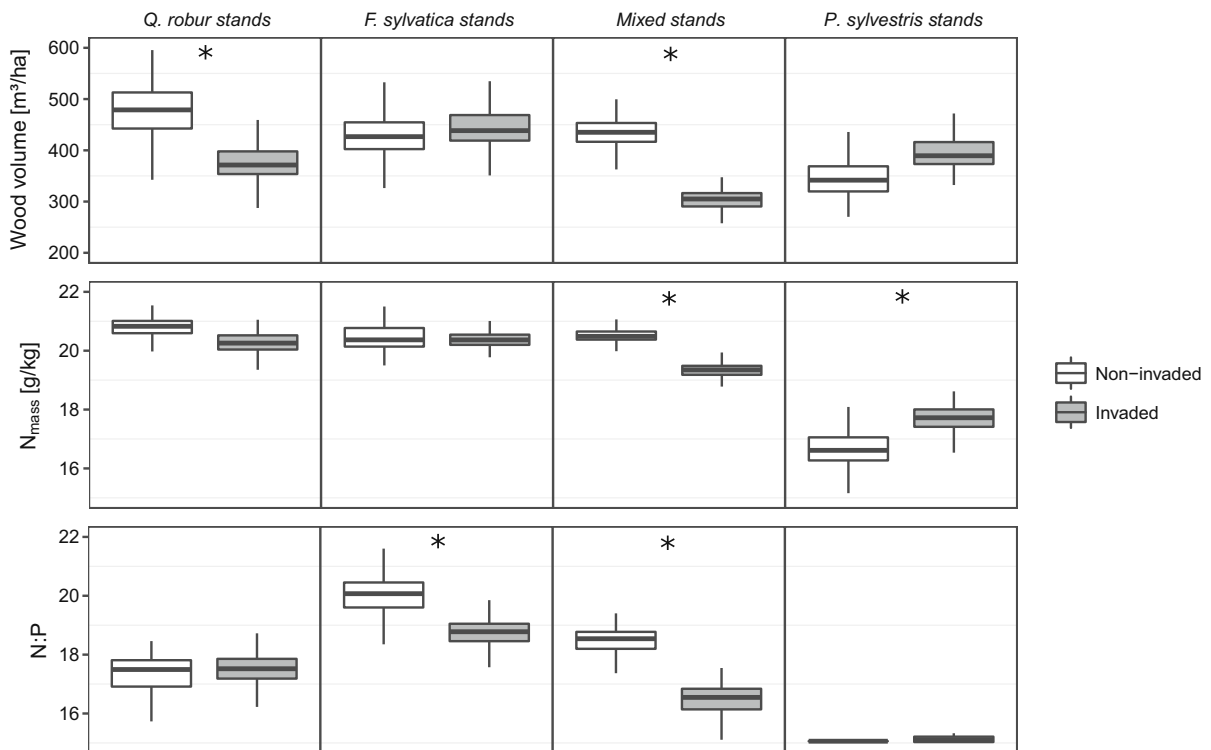
Fig. 5 Predicted values of 200 repeated model calculations for wood volume, N_{mass} and N:P depending on the presence of *P. serotina* trees at the plot level (based on presence-absence locations) for different stand types characterized by the dominant tree species. Soil pH was kept constant. Asterisks indicate significant differences between invaded and non-invaded sites resulting from a comparison of model coefficients from 200 model repetitions. Results are displayed for stands with an age of 90–100 years and a soil pH value of 5.96

slightly higher wood volume at the plot level, though not significant. This pattern can be attributed to the strong demand for light of *P. serotina* (Vanhellemont et al. 2008; Terwei et al. 2013) and different light conditions in broad-leaved and pine stands. Broad-leaved stands in our study area were characterized by lower light availability at the forest floor compared to pine stands (see Fig. 6). Therefore, in broadleaved stands *P. serotina* establishment is constrained to canopy gaps caused by natural and anthropogenic disturbances (Chabrerie et al. 2008; Closset-Kopp et al. 2010). As a result, stands with less wood volume were characterized by a higher infestation of *P. serotina*. In pine stands, light availability at forest floor is usually sufficient for *P. serotina* establishment and therefore we did not observed significant differences between invaded and non-invaded stands.

Contrary to differences in wood volume, we found no differences in LAI between invaded and non-invaded areas. As discussed above, *P. serotina*

establishment is promoted by high light availability which is related to lower LAI values. Our finding suggests that *P. serotina* is able to quickly compensate lower LAI needed for its establishment by its own biomass. This agrees with previous studies reporting dense cover of *P. serotina* in the shrub layer and reduced light availability at the forest floor. The latter is regarded as most influential factor for inhibiting natural forest regeneration (Starfinger et al. 2003; Halarewicz and Pruchniewicz 2015).

Evaluating invasion impacts across scales

We found general agreement between patterns observed at the plot and the stand level. Most important, we found evidence for invasion effects on canopy nutrient-contents caused by *P. serotina* also when taking larger areas into account. Due to the fact, that in many cases it is unknown how invasion effects on biogeochemical cycles scale up (Weidenhamer and
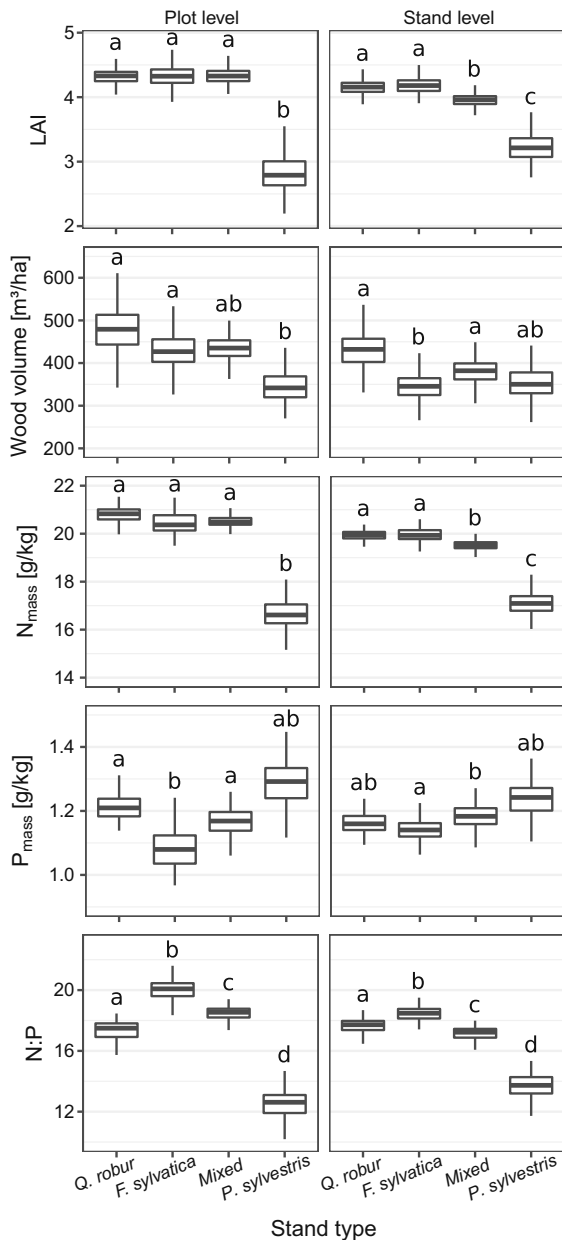
Fig. 6 Predicted values of 200 repeated model calculations for LAI, wood volume, canopy N_{mass}, P_{mass} and N:P depending on stand types characterized by the dominant tree species. Predictions from plot level models are displayed on the left, predictions from stand level models on the right. Characters indicate significant differences between stand types resulting from a comparison of model coefficients from 200 model repetitions. Results are displayed for non-invaded stands with an age of 90–100 years and a soil pH value of 5.96

Callaway 2010), such information is very valuable for evaluating plant invasion impacts. Additionally it may

be important for evaluation of invasion effects on ecosystem services, which are usually accounted for at larger spatial scales (Eviner et al. 2012).

Previous studies assessing plant invasion impacts over multiple scales almost solely focused on effects on plant community composition. The results of these studies underline the importance of mulit-scale assessments (Fridley et al. 2007). While plant invasions generally tend to decrease local biodiversity when looking at the fine scale, this effect is smaller or even opposed at broader spatial scales (Gaertner et al. 2009; Powell et al. 2011, 2013).

Besides the evidence for spatial relevance, also the observation that invasion impacts were dependent from the occurrence frequency of *P. serotina* delivered valuable information. This result suggests that *P. serotina* can influence leaf nutrient stoichiometry already when forest stands are affected by fragmented populations of individuals present in the tree layer. Interpreting this results it is important to consider that at the moment single individuals reach the tree layer, there is usually already subsequent recruitment present in the shrub layer, that may also influence canopy nutrient stoichiometry indirectly. Our results confirm that consideration of the spatial distribution patterns of species abundances or prevalences are an important aspect for the evaluate invasion impacts (Thiele et al. 2009).

Contrary to leaf N:P ratio, for N_{mass} we found an invasion effect only at the plot, but not at the forest stand level. This finding indicates, that the influence of *P. serotina* of canopy leaf N contents alone is less substantial than its influence on N:P ratios. The interpretation of differences between scales is strongly limited due to the high temporal mismatch between *P. serotina* occurrence data used for the plot and the stand level analysis. Since 2004 *P. serotina* further spread within the forest area, but was also partly removed in some management units in the course of thinning activities. Apart from the temporal mismatch in used data, differing results between the two scales, may be also caused by strongly decreased variability at the stand level, by calculation mean values. This may have lead to smaller differences between invaded and non invaded ares compared to the plot level (Wiens 1989). This effect at least can be observed when comparing differences between stand types at the plot and the stand level (see Fig. 6).
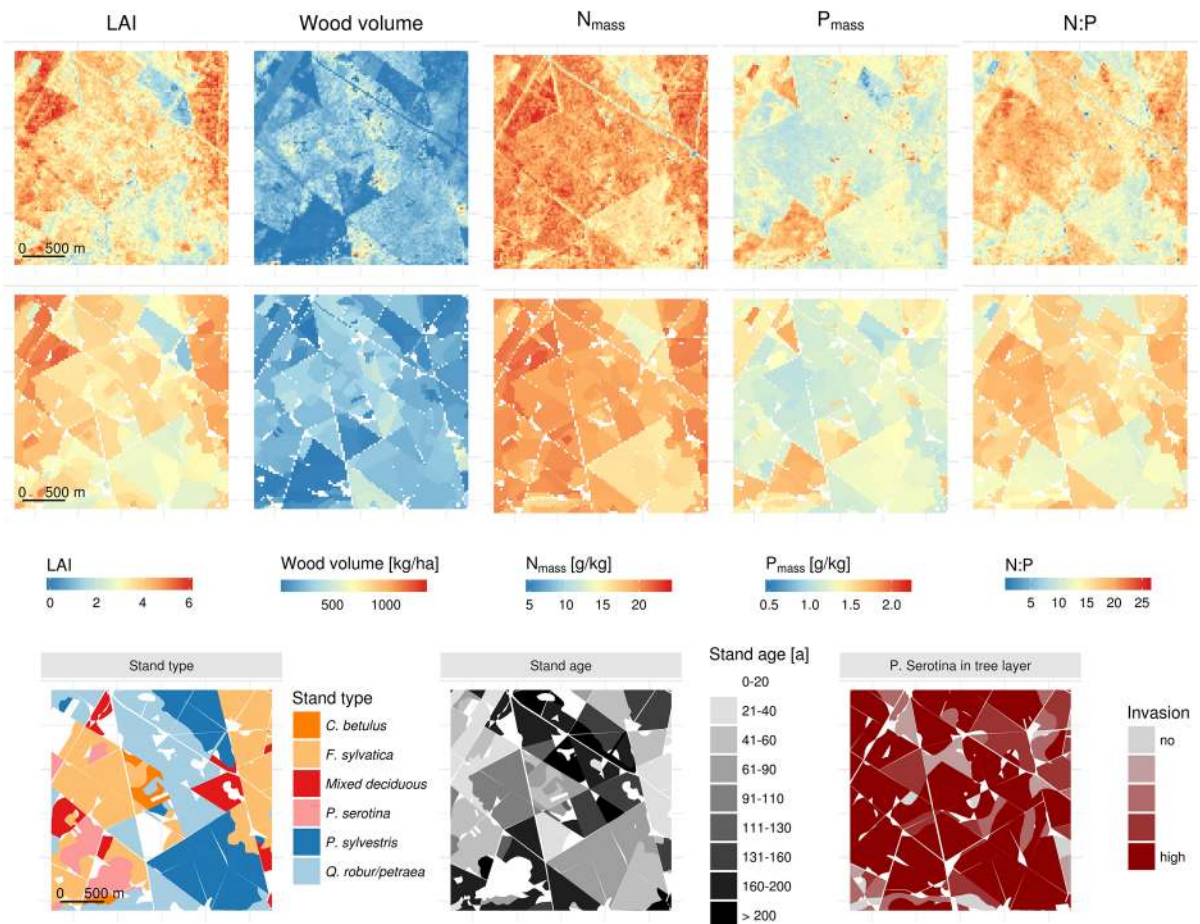
Fig. 7 Map segments showing trait values derived from remote sensing at the original resolution with 24 m pixel size (above) and aggregated to the single forest management units as used for the analyses at the stand level (center). Polygon maps at the bottom display stand-level information on stand type, stand age and *P. serotina* occurrence

Remote sensing data proved useful to characterize differences between invaded and non invaded areas beyond the plot level, thereby highlighting its potential for quantification of invasion impacts across scales. This includes impacts on vegetation or ecosystem properties that otherwise are only hard to obtain across large areas. It is important to note that many plant functional traits, like N_{mass} and P_{mass} are not directly represented in the spectral signal of plant canopies (Ollinger 2011). Thus, relationships between such traits and canopy reflectance can be established only via empirical models, which have to be calibrated with field data (Verrelst et al. 2015). Limitations of empirical relationships arise from their strong site specificity making predictions of traits under novel environmental conditions difficult (Ollinger 2011).

Apart from providing maps of vegetation traits, applications of remote sensing in invasion ecology most commonly relate to mapping distributions of invasive plant species (Huang and Asner 2009). Resulting maps can be used to study spatial distribution patterns of invasive plant species across scales and thus provide valuable information for the management of invasive species. Similar to traits, transferring models for mapping species distributions to other study areas is challenging, but feasible when focusing on distinct habitat types (Skowronek et al. 2018). Such model transfer is an important prerequisite for efficient early detection of invasive plant species. One major limitation for the use of remote sensing in invasion ecology evolves from the trade-off between resolution and coverage. Depending on the size of the target species, monitoring plant

invasions requires fine resolution remote sensing particularly for the purpose of early detection (Bradley 2014). Such fine resolution data have become readily available by the use of sensors mounted on unmanned areal vehicles (UAV), but usually only over limited spatial extents.

Conclusion

We assessed differences in structural and biochemical forest canopy traits between invaded and non-invaded areas at the plot and the forest stand level. Using this multi-scale approach provided a more comprehensive picture on patterns and impacts of *P. serotina* invasions. Particularly, the assessment of invasion impacts over larger areas beyond the plot level provided valuable additional information on the spatial relevance of invasion impacts. Such information can help to prioritize management actions, by focusing on species that affect ecosystems over large areas. For the evaluation of potential impacts of plant invasions we thus recommend observations at a coarser spatial grain to supplement plot-level observations. Remotely sensed vegetation trait maps proved useful for this kind of multi-scale assessments.

Compliance with ethical standards

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

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