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1 **Alien plant invasion hotspots and invasion debt in European woodlands**

2
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80

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83

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97

98 **Abstract**

99 **Questions:** European woodlands harbor at least 386 alien plant species but the factors driving
100 local invasions remain unknown. By using a large vegetation-plot database, we asked how
101 local richness and abundance of alien species vary by regions, elevation, climate, soil
102 properties, human disturbance, and habitat types.

103 **Location:** Western, Central and Southern Europe.

104 **Methods:** We linked consolidated data from the European Vegetation Archive (16,211 plots)
105 to a habitat classification scheme, climate, soil properties and human disturbance variables. In
106 addition, we used 250 km × 250 km regional grid cells to test whether local patterns differ
107 among regions. We used generalized additive models (GAMs) and quantile GAMs to explore
108 how relative alien species richness and the sum of alien species covers per plot relate to
109 predictors. Random forest analyses (RFs) were employed to assess the importance of
110 individual predictors that were not multicollinear.

111 **Results:** Relative alien species richness and the sum of alien species covers varied across
112 regions and habitat types, with effects being more pronounced at the maximum rather than
113 average responses. Both response variables decreased with elevation and distance to the
114 nearest road or railroad and increased with the amount of sealed soil. Maxima in fitted
115 functions matched plots from regional invasion hotspots in north-western and central Europe.
116 RFs accounted for 39.6% and 20.9% of the total variation in relative alien species richness
117 and the sum of alien species covers, respectively, with region and habitat as being the most
118 important variables.

119 **Conclusions:** The importance of maximum response quantiles and the prevalence of regional
120 hotspots point to invasion debt in European woodlands. As alien plants expand further, their
121 species richness and abundance in woodlands will be likely driven by the shared effects of the
122 introduction and planting history, differences in the invaded habitat types, and dispersal
123 corridors.

124

125 **Introduction**

126 At least 386 alien plant species have been introduced to European woodlands deliberately or
127 accidentally after the year 1500 (Wagner *et al.*, 2017). While most alien species reach only
128 low abundances and frequencies, some can become invasive by spreading fast. Some few
129 species can even become transformative by changing plant species composition, suppressing
130 native tree regeneration (Langmaier and Lapin, 2020), and altering ecosystem functioning
131 (e.g., Aerts *et al.*, 2017). For example, black locust (*Robinia pseudoacacia*) can homogenize
132 woodland understory composition (Šibíková *et al.*, 2019; Vítková *et al.*, 2020) and trigger soil
133 acidification and nitrification (Lazzaro *et al.*, 2018). Similarly, black cherry (*Prunus serotina*)
134 can change nitrogen, phosphorus, and carbon cycles to its advantage, potentially altering the
135 photosynthetic capacity of the long-lived native broadleaved species (Aerts *et al.*, 2017).

136
137 To decrease possible detrimental effects, the European Union has outlined strategies for the
138 prevention and management of invasive alien species (European Parliament, 2014). However,
139 designing efficient strategies depends on understanding the drivers of local alien plant
140 invasions across European regions. Such knowledge is particularly important for woodlands
141 because they cover a third of the continent's territory and provide essential ecosystem
142 services, including carbon sequestration, water retention, timber production, and biodiversity
143 conservation (Forest Europe, 2015). However, the factors that drive alien plant invasions in
144 European woodlands are not well understood. A recent Europe-wide study has shown that in
145 general, macroclimate is an important abiotic predictor of local plant species richness in
146 woodlands, in congruence with a north-west to south-east continental gradient (Večeřa *et al.*,
147 2019). However, it is not clear whether the same patterns holds true specifically for local alien
148 plant species richness. Macroclimate was not an essential predictor of local alien plant species
149 richness in deciduous woodlands of Catalonia (Gassó *et al.*, 2011) and was just one of several
150 predictors of local alien plant species richness in woodlands of the Czech Republic (Divíšek

151 and Chytrý, 2018). This indicates that other predictors could be more important. For instance,
152 there is strong evidence that the level of invasion generally decreases with elevation, partly
153 due to a drop in human activities and alien plant propagule pressure, which are usually
154 confounded (Alexander *et al.*, 2011; Pyšek *et al.*, 2011). By comparison, the role of abiotic
155 soil conditions in structuring alien plant invasions is less clear. Alien plant invasions are often
156 favored at sites with increased soil nutrient availability (Davis *et al.*, 2000; Gurevitch *et al.*,
157 2008), yet many alien species can grow in low-nutrient ecosystems, likely because of their
158 higher resource use efficiency compared to native species (Funk and Vitousek, 2007). Soil pH
159 explains some variation in local plant species richness in European woodlands (e.g. Večeřa *et*
160 *al.*, 2019) but its importance specifically for local alien plant richness is unknown. Human
161 presence and disturbance at the landscape scale can accelerate alien plant invasions by
162 enhancing propagule pressure and facilitating habitat edge effects (Vilà and Ibáñez, 2011;
163 Conedera *et al.*, 2018). Levels of invasion have been found to increase with landscape
164 fragmentation (Ohlemüller *et al.*, 2006), proportion of urban and industrial land (Chytrý *et al.*,
165 2008a; Liendo *et al.*, 2016), proximity to roads (González-Moreno *et al.*, 2013), and human
166 population density (Pyšek *et al.*, 2010b; Spear *et al.*, 2013; but see Carboni *et al.*, 2010).

167

168 Many studies have revealed marked differences in the level of invasion across habitat types
169 (e.g., Chytrý *et al.*, 2005; 2008b; Campos *et al.*, 2013; González-Moreno *et al.*, 2014; Wagner
170 *et al.*, 2017; Giulio *et al.*, 2020). Habitat types explained more variation (18%) in levels of
171 invasion by neophytes (alien species that arrived in Europe after 1500 AD) than propagule
172 pressure (3.1%) and climate (5.9%) in a study from the Czech Republic (Chytrý *et al.*,
173 2008a). Habitat type was also the strongest predictor of alien plant invasions in Iberian
174 vegetation (González-Moreno *et al.*, 2014). This signal could reflect the integrating role of
175 habitat type as a surrogate capturing the effects of both abiotic and biotic filters but might also

176 reflect a confounding effect of the environmental variables that underlie habitat typologies,
177 like elevation, landscape configuration, soil properties, or biotic interactions.

178

179 Identifying the main factors driving alien plant invasions is complex because invasions are
180 dynamic processes and alien species pools not fully saturated due to dispersal limitation
181 (Brown and Peet, 2003). This could lead to invasion debt, i.e. a time lag between the
182 introduction and spread of alien species (Essl *et al.*, 2011; 2012). At a large scale, this could
183 translate into hotspots of invasion among regions where introduction and spread have been
184 frequent, and invasion debt among regions that are lagging in this respect (Ronk *et al.*, 2017).
185 Hence, an analysis of alien species richness and abundance using quantiles closer to the
186 maximum could provide better insights than the more conventional analysis of the mean
187 response (Brown and Peet, 2003).

188

189 Here, we are building on our previous work on alien plant invasions in European woodlands
190 (Wagner *et al.*, 2017) by analyzing a large dataset of woodland vegetation-plot data stored in
191 the European Vegetation Archive (Chytrý *et al.*, 2016). Whereas our previous study focused
192 on characterizing the alien species pool, this study aims to understand the possible drivers of
193 alien plant invasion in European woodlands. Specifically, we asked: (1) How do relative alien
194 species richness and sum of alien species covers change across regions, habitat types,
195 environmental conditions and human disturbance? (2) What is the importance of these
196 predictors for explaining variation in alien plant invasions?

197

198 **Methods**

199 *Vegetation data*

200 We extracted vegetation-plot data from the European Vegetation Archive (EVA, version 13
201 January 2016, see Online Supplement and Wagner *et al.*, 2017 for details on data

202 preparation). This dataset contained plots from Western, Central and Southern Europe, as well
203 as Lithuania (Fig. 1). For every vascular plant species in a plot, we assigned information on
204 its status in the respective country (native, alien, or uncertain), with alien species defined as
205 those that have been introduced after the year 1500 (i.e. neophytes sensu Thellung, 1915) and
206 Raunkiær's life-form (e.g., hemicryptophytes, phanerophytes, therophytes). The dataset
207 encompassed data for plots surveyed in and after the year 1970 (53% collected after 2000)
208 and was restricted to plots with an area ranging from 100 to 1000 m² (or lacked plot size
209 information, assuming that most of these plots were within this range; 77% of plots had a size
210 of 100–500 m²). We assigned plots to European Nature Information System (EUNIS)
211 woodland habitat types via a custom cross-walk (see Wagner *et al.*, 2017 for details). The
212 used version of the EUNIS habitat classification corresponds to that used in the European Red
213 List of Habitats (Janssen *et al.*, 2016). A crosswalk to the recently revised EUNIS version is
214 provided by Chytrý *et al.* (2020). Only plots unambiguously assigned to a habitat type were
215 included in the analysis.

216

217 Our study focused on the spontaneously established alien vascular plants rather than outcomes
218 of deliberate planting. Hence, we excluded plots with alien tree and shrub species mostly known
219 from planted populations (e.g., *Abies alba* in Belgium, *Pinus strobus* in Slovenia). We also
220 removed plots with alien tree species that are naturalized but widely planted if they covered
221 more than 20% in the tree layer or an unidentified vegetation layer. In addition, we also filtered
222 out plots in which taxa with an uncertain status (native vs. alien) had more than 20% cover (for
223 details, see Wagner *et al.*, 2017).

224

225 *Response variables*

226 For every vegetation plot, we calculated two measures of the level of invasion: (i) relative
227 alien species richness, defined as the percentage of the number of alien vascular plant species

228 among all vascular plant species in a plot, and (ii) absolute sum of alien species covers (in %)
229 in a plot (see Appendix S3, Fig. S3.1 for the frequency distribution of response variables). We
230 chose relative alien species richness instead of the total number of alien species per plot
231 because our dataset included different plot sizes. If an alien species occurred in different
232 layers, we included its absolute sum across layers (alien species occurred in different layers
233 only in 16% of plots). We also considered the presence/absence of any alien species in a plot
234 as a metric but dropped it since subsequent statistical models performed poorly, likely due to
235 the overabundance of absences. In addition, we computed response metrics for five alien
236 species groups: (i) all species; (ii) all species except *Impatiens parviflora*; (iii) phanerophytes;
237 (iv) hemicryptophytes; and (v) therophytes (including *I. parviflora*). We removed *Impatiens*
238 *parviflora* from one subset since it has a much higher frequency in European woodlands than
239 any other alien species (Wagner *et al.*, 2017) and could dominate the results. We focused on
240 phanerophytes, hemicryptophytes, and therophytes because they represent the three most
241 frequent life-forms among alien vascular plant species in European woodlands (Wagner *et al.*,
242 2017).

243

244 *Predictor variables*

245 We considered 75 predictor variables for our analysis: habitat type, region, elevation, six
246 climate variables and two Principal Component (PC) axes based on a PC analysis (PCA) of
247 climate variables, four soil variables and two PC axes based on a PCA of these soil variables,
248 and 50 human disturbance variables (including variables extracted for different spatial
249 buffers) and eight PC axes based on PCAs of these human disturbance variables (two axes for
250 each buffer category of 200m, 500m, 1000m and 2000m) (Table 1). We hypothesized that
251 patterns in our data could vary by region, possibly due to regional differences in alien plant
252 introduction and planting history. To test this hypothesis, we assigned plots to a grid of 250
253 km × 250 km, with grid cell ID as a predictor factor with 41 levels. We chose this specific

254 resolution because it was a compromise between capturing regional effects and limiting the
255 total number of levels in this variable. Information on elevation was derived from the original
256 records or, if missing, extracted with the *raster* package (Hijmans, 2019) in R (R Core Team,
257 2020) following Jarvis *et al.* (2008). We extracted climate variables that could potentially
258 affect alien plant species distribution and abundance (BIO1: Mean annual temperature; BIO4:
259 Temperature seasonality; BIO6: Minimum temperature of the coldest month; BIO10: Mean
260 temperature of the warmest quarter; BIO12: Annual precipitation sum; BIO15: Precipitation
261 seasonality) from the CHELSA dataset, which has a resolution of 30 arc seconds ($\sim 1 \text{ km} \times 1$
262 km at the equator; Karger *et al.*, 2017). Topsoil properties (pH and fraction of sand, organic
263 carbon, and gravel) were retrieved from the Harmonized World Soil Database, which offers
264 data at a 0.05° resolution ($\sim 5.5 \text{ km} \times 3.9 \text{ km}$ at the equator; Wieder *et al.*, 2014).

265
266 We extracted several measures to capture human disturbance. Imperviousness (the percentage
267 of sealed soil, including roads, buildings, parking lots and industry areas) was prepared from a
268 raster dataset of the Copernicus satellite program, which is based on an automatic derivation
269 of calibrated Normalized Difference Vegetation Index (NDVI) in the year 2006 (European
270 Environment Agency, 2013; $100 \text{ m} \times 100 \text{ m}$ resolution). Estimates of human population
271 density were retrieved from a dataset of the GEOSTAT initiative of the European Union
272 (Eurostat, 2012), based on a $1 \text{ km} \times 1 \text{ km}$ grid for the year 2011. We calculated the level of
273 woodland fragmentation and woodland edge complexity based on Copernicus satellite
274 products (European Environment Agency, 2016; original resolution: $20 \text{ m} \times 20 \text{ m}$). To
275 quantify fragmentation, we used the area-weighted average patch size index (S_a ; Turner *et al.*,
276 2001), computed as $S_a = \sum(S_k^2) / \sum(S_k)$, where S_k is the size of the k -th woodland patch
277 within a spatial buffer. The larger the index, the larger the patch sizes within a buffer and the
278 less fragmentation. The complexity of woodland edges was quantified using Patton's
279 diversity index (Patton, 1975), calculated as the perimeter of an individual woodland patch

280 divided by the perimeter of a circle covering the same area as that of the focal patch. Values >
281 1 indicate more complex patch edges and less interior woodland environment compared to the
282 circular patch area. We estimated the proximity to the next propagule dispersal corridor by
283 calculating the distance between plots and the closest road or railroad, respectively, in
284 OpenStreetMap (OpenStreetMap Contributors, 2019). We considered all roads (motorways,
285 trunks, primary, secondary, tertiary roads, residential streets) and all railroads (regular
286 railroads, light rails, monorails, narrow gauges, racks, tram lines). Road density was extracted
287 from global road density raster data (9 km × 9 km resolution; Meijer *et al.*, 2018). We
288 estimated the cover of human-altered landscapes based on CORINE land-cover types
289 (Bossard *et al.*, 2000), which we aggregated into four groups: (i) Intensive agricultural land
290 cover, (ii) Artificial land-cover types I: Artificial land cover potentially related to the spread
291 of alien species, (iii) Artificial land-cover types II: Theoretically the highest affinity to spread
292 of alien species, and (iv) All human-dominated land-cover types combined (see Appendix S2,
293 Table S2.1 for more details). We hypothesized that human disturbance has an effect at the
294 landscape level by influencing the area surrounding a plot. Hence, we used spatial buffers of
295 200 m, 500 m, 1000 m, and 2000 m when extracting mean values for human population
296 density, imperviousness and road density (using QGIS; QGIS Development Team, 2019), and
297 woodland fragmentation, woodland edge complexity, and the cover of human-dominated
298 land-cover types (using ArgGIS; ESRI, 2011). For comparison purposes, we also extracted
299 maximum values for imperviousness, human population density, and road density within the
300 buffers in QGIS.

301 In addition, we constructed simplified and uncorrelated variables for three predictor groups
302 (climate, soil, human disturbance) by calculating two ordination axes using PCA in the *vegan*
303 package (Oksanen *et al.*, 2018) in R (R Core Team, 2020; see details in Appendix S1). These
304 single predictor variables and the PC axes were subsequently used as predictor variables in
305 our bivariate analyses.

306

307 *Data filtering*

308 After preparing our response and predictor variables, we took several data filtering steps.
309 First, we included only plots with geographic coordinates and a location uncertainty of ≤ 1000
310 m (44% of plots in the final dataset had an uncertainty of ≤ 500 m). However, plots that
311 lacked information on location uncertainty but were surveyed after the year 2000 were
312 included (33%), assuming that by that time, global positioning system (GPS) devices or
313 accurate georeferencing were used to record plot locations. We reduced spatial clustering and
314 sampling bias at the landscape and regional scales by randomly resampling up to 10 plots
315 within a combination of $10 \text{ km} \times 10 \text{ km}$ grid cell and habitat type. Next, to balance out
316 regional unevenness, we randomly selected up to 200 plots for a combination of $250 \text{ km} \times$
317 250 km grid cell and habitat type. Regional grid cells with < 100 plots were excluded from
318 the analysis. *Fagus* woodlands on non-acid soils were much more common than other habitat
319 types. To balance out this overrepresentation, we randomly resampled up to 200 plots of this
320 habitat type per country. We finally excluded rare habitat types with < 400 plots in the whole
321 dataset after resampling and deleted outliers (see Appendix S1 in Supplementary
322 Information). The final dataset included 16,211 plots (Fig. 1) and encompassed 15 EUNIS
323 habitat types (see Appendix S2, Tables S2.2, S2.3 and S2.4 for an overview of databases,
324 regions and habitats represented in the final dataset).

325

326 *Bivariate relationships*

327 We fitted standard generalized additive models (GAMs; Wood, 2011) and quantile GAMs
328 (qGAMs; Fasiolo *et al.*, 2017) to bivariate relationships between each of the two studied
329 response variables on the one hand, and predictor variables on the other hand (both model
330 types were run with a Gaussian error family). GAMs and qGAMs allowed us to explore
331 trends using the original, untransformed variables. We used GAMs to inspect trends in

332 average response rate and qGAMs to analyze values closer to the maximum response rates (τ
333 = 0.90, and 0.99). We included the qGAMs approach because our data were zero-inflated
334 (alien plants were present only in 17% of plots), and we hypothesized that signals could be
335 fitted better at higher quantiles rather than as averages. We ran GAMs and qGAMs using the
336 R packages *mgcv* (Wood, 2011) and *qgam* (Fasiolo *et al.*, 2017), respectively. Smoothing
337 parameters were constructed using cubic regression splines with $k = 10$ dimensions and
338 estimated with restricted maximum likelihood estimation.

339

340 *Variable importance*

341 We used Random Forest (RF) analyses in the *randomForest* package (Liaw and Wiener,
342 2002) in R to assess the importance of predictor variables for structuring relative alien species
343 richness and the sum of alien species covers. RF analysis is a machine learning algorithm that
344 averages predictions over several recursively partitioned decision trees based on bootstrapped
345 data (“bagging”), creating a higher accuracy than decision trees. It uses a random subset of
346 predictors for each tree to assess predictor importance in the presence of multicollinearity
347 (Breiman, 2001). Nonetheless, collinearity was present when we included all predictor
348 variables, as suggested by generalized variance inflation factors (GVIF, Appendix S2, Table
349 S2.6), which could bias RF results (Dormann *et al.*, 2013). Hence, we considered all predictor
350 variables but only included those with a GVIF ≤ 2 in the RFs.

351

352 Each RF was based on 10,000 grown trees, with four randomly chosen predictors considered
353 at each split, minimum node sizes of 40 plots, and randomization of cases without
354 replacement. Variable importance was assessed based on out of bag (OOB) data, as the
355 average increase in squared OOB residuals when a variable in the OOB data is permuted
356 (%IncMSE). The latter metric is unbiased compared to the increase in node purity, another
357 metric reported by the package (Grömping, 2009 and references therein). To compare the

358 importance of predictor variables for our two response variables, we normalized %IncMSE
359 values across predictors to sum to 100% (Grömping, 2009).

360

361 **Results**

362 *Bivariate relationships*

363 Both the relative alien species richness and the sum of alien species covers differed by habitat
364 type (Fig. 2). Differences were apparent in GAM estimates but amplified when using qGAMs
365 at the maximum response rates ($\tau = 0.90$ and 0.99). According to GAM estimates, relative
366 alien species richness was highest in temperate and boreal mountain *Betula* and *Populus*
367 *tremula* woodland on mineral soils (G1.9a), acidophilous *Quercus* woodland (G1.8), *Fagus*
368 woodland on acid soils (G1.6b), and temperate and boreal softwood riparian woodland (G1.1)
369 (Fig. 2a). In general, habitats with low relative alien species richness had also low sum of
370 alien species covers. However, the ranking based on the sum cover was more nuanced for
371 habitats with higher relative alien species richness, with Temperate and boreal softwood
372 riparian woodland (G1.1) having the highest sum of alien species covers (Fig. 2b). In general,
373 woodland habitat types at temperate latitudes, such as those listed above, had higher levels of
374 invasion than Mediterranean or montane habitat types like Mediterranean evergreen *Quercus*
375 woodland (G2.1) and Temperate and submediterranean montane *Pinus sylvestris*-*Pinus nigra*
376 woodland (G3.4b).

377

378 The relative alien species richness and the sum of alien species covers differed across regional
379 grid cells (Fig. 3). In general, it was higher in northern than in southern regional grid cells and
380 peaked in north-western and central Europe. These regional patterns were consistent for
381 relative alien species richness and the sum of alien species covers and for responses at the
382 mean and $\tau = 0.99$ quantiles (Fig. 3).

383

384 Relative alien species richness and the sum of alien species covers declined with increasing
385 elevation, distance to the nearest road, and distance to the nearest railroad and increased with
386 maximum imperviousness (percentage of sealed soil cover) in 2000m buffers (Fig. 4).
387 However, these relationships were only pronounced when values closer to the maximum were
388 analyzed ($\tau = 0.99$ and 0.90). None or only weak relationships were found in the analysis of
389 average trends ($\tau = 0.5$; Fig. 4). With respect to elevation, relative alien species richness
390 declined at elevations 0–750 m, whereas the sum of alien species covers showed a slight
391 increase and then a decrease in this elevation range (Fig. 4). Neither the relative alien species
392 richness nor the sum of alien species covers showed a clear trend with climate and soil
393 variables but displayed only local maxima along these gradients (Appendix S3, Figs. S3.2 and
394 S3.3).

395

396 A closer inspection of bivariate relationships between relative alien species richness and the
397 sum of alien species covers on the one hand and elevation, distance to the nearest road,
398 distance to the nearest railroad, and the mean annual temperature on the other, revealed that
399 peaks were driven by regional signals. For all of these predictor variables, most plots that
400 matched the maxima in relative alien species richness at $\tau = 0.99$ and 0.90 quantiles were
401 from the Netherlands, Belgium, Poland and the Czech Republic (Table 2). Plots that were
402 associated with maxima in the sum of alien species covers at these quantiles were from the
403 Czech Republic, the Netherlands, and France (Table 3).

404

405 *Variable importance*

406 The variables that we considered in our RFs models explained together 39.6% of the total
407 variation in relative alien species richness. By comparison, the total amount of variation
408 explained for the sum of alien species covers was only 20.9% (Fig. 5a, b). Habitat type and
409 regional grid cells were the most important predictors ($> 10\%$) for both response variables.

410 Variable importance and percentage of explained variation changed little when we removed
411 *Impatiens parviflora* ($n = 15,214$ plots; Appendix S3, Fig. S3.4a,b) or inspected patterns only
412 among alien phanerophytes (Fig. S3.4c,d). By contrast, when we analyzed only alien
413 hemicryptophytes (Fig. S3.4e,f) or alien therophytes (Fig. S3.4 g,h), the percentage of
414 explained variation decreased.

415

416 **Discussion**

417 Several key findings suggest that European woodlands display regional hotspots of local alien
418 plant invasion and that woodlands in some regions might not be fully saturated with alien
419 species but rather experience invasion debt (Brown and Peet, 2003; Essl *et al.*, 2012). First,
420 although macroclimate is an important predictor of local plant species richness in European
421 woodlands (Večeřa *et al.*, 2019), it did not emerge as a significant driver of local relative alien
422 species richness across European woodlands. Second, local levels of alien plant invasions
423 differed strongly by region, with regional hotspots in north-western and central Europe. Third,
424 for continuous predictors that showed relationships with relative alien species richness and
425 the sum of alien species covers (i.e. elevation, distance to the nearest road or nearest railroad,
426 imperviousness), effects were only pronounced at higher quantiles and non-detectable at the
427 average response of our response variables. When we looked closer at peaks in these
428 relationships, the signal at the maximum quantiles was driven by vegetation plots located
429 within regional invasion hotspots.

430

431 Interestingly, the regional hotspots that we detected broadly match hotspots of regional alien
432 species richness described by Ronk *et al.* (2017). In contrast to our work, this study assessed
433 richness at a coarser spatial resolution, based on species lists for $50 \text{ km} \times 50 \text{ km}$ grid cells in
434 Europe. This may imply that the magnitude of alien plant invasions at the local scale in
435 European woodlands is influenced by regional differences in alien species pool size. In

436 theory, the high estimates for the Czech Republic and France could be due to more intense
437 sampling in these regions (% of plots in the final dataset: 15.1%, 12.1%, respectively). Plots
438 in the Netherlands and Belgium made up only 5.9% and 2.2% of the final dataset,
439 respectively (Appendix S2, Table S2.3), albeit these countries are also smaller. Here, the high
440 levels of invasion could also reflect the region's legacy as an invasion hub, especially the long
441 history of international trade at its seaports and high density of traffic corridors (Eurostat,
442 2018). Another explanation is the lower richness in the native woodland flora in north-
443 western Europe (Večeřa *et al.*, 2019). Since we used a relative measure of alien species
444 richness (to account for different plot sizes), calculated as the number of alien species divided
445 by all species in a plot, naturally species-poor forests could appear to be relatively more
446 invaded. The lower magnitude of alien plant invasions in southern Europe is in line with
447 patterns observed at the higher spatial scale by Ronk *et al.* (2017). The prevalence of summer
448 drought in this region could make its woodlands more resistant to invasion. Alternatively,
449 given the high rates of alien plant invasions in other regions with summer drought, like
450 California (van Kleunen *et al.*, 2015), our results could also imply that invasion debt is more
451 prominent in southern European woodlands (Rouget *et al.*, 2016). These hypotheses deserve
452 more attention by researchers in the future. Furthermore, our study did not cover all of Europe
453 and might have missed other regional patterns of local alien plant invasions in European
454 woodlands.

455

456 Our results also join an increasing number of studies that found habitat type to be an
457 important predictor of the magnitude of invasions (Chytrý *et al.*, 2008a; Pyšek *et al.*, 2010a;
458 Pyšek and Chytrý, 2014; Dyderski and Jagodziński, 2019). Our study encompassed a smaller
459 set of habitat types than Wagner *et al.* (2017) due to stronger data filtering. However, the
460 trends in mean relative alien species richness among habitat types were broadly similar. For
461 instance, the three highest-ranked habitats according to the mean (G1.1, G1.8, G1.9a), as

462 shown by GAMs, were among the five highest-ranked habitat types in Wagner *et al.* (2017).
463 The high levels of invasion in temperate and boreal softwood riparian woodlands are well
464 known (Schnitzler *et al.*, 2007). They can be linked to several habitat characteristics,
465 including a high propagule pressure at low elevations, their role as dispersal corridors and
466 intersections by roads and railroads, and their exposure to nutrient pulses, frequent
467 disturbance, and light gaps due to flooding. The high rankings for Acidophilous *Quercus*
468 woodland and Temperate and boreal mountain *Betula* and *Populus tremula* woodland on
469 mineral soils are more surprising. In theory, they could be explained by native species
470 richness per plot, which tends to be low in these habitat types (Wagner *et al.*, 2017, their
471 Appendix S5). However, in general, we did not find a correlation between mean alien species
472 richness and mean native species richness per habitat type (Pearson's $r = -0.41$, $d.f. = 13$, $p =$
473 0.126 ; calculated for the most frequent plot size of 100 m^2). In addition, the high levels of
474 invasion in these habitat types may be due to their relatively open canopy cover, occurrence
475 in regional invasion hotspots, higher local disturbance through management, and the ability of
476 frequent alien species to colonize acidic soils and forest gaps, as displayed for example by
477 *Prunus serotina* (Godefroid *et al.*, 2005) or *Impatiens parviflora* (Chmura *et al.*, 2007).
478
479 The magnitude of alien plant invasions in European woodlands decreased with increasing
480 elevation. Similar signals at the local scale have been explained by declining propagule
481 pressure or directional filtering. The latter process refers to an overrepresentation of taxa with
482 a niche optimum at lower elevations, within the low elevation species pool (e.g., Alexander *et*
483 *al.*, 2011; Pyšek *et al.*, 2011). However, in our study, the decline of the levels of alien plant
484 invasions with elevation could also be partly due to the confounding effect of region, with
485 maxima reported from regional hotspots at low elevations, like the Netherlands.
486

487 Distances to the nearest road and railroad and cover of impervious surfaces were the only
488 clear indicators of human-induced disturbance associated with the magnitude of alien plant
489 invasions in European woodlands. In general, the decline of alien species richness and cover
490 with increasing distances from these corridors supports the role of road and railroad traffic as
491 a pathway for alien plant invasions (von der Lippe and Kowarik, 2008). Imperviousness
492 showed a positive relationship with our response variable, but only when we extracted
493 maximum imperviousness values in a 2000-m buffer around the plot. This could reflect the
494 importance of urban areas as propagule sources and as dispersal corridors (Klotz and Kühn,
495 2010) in the wider perimeter of woodlands. In our study, the effect of distances to the nearest
496 road and railroad, and imperviousness, may also reflect a confounding effect with region.
497 North-western Europe, where the magnitude of invasion was particularly high, has one of the
498 highest road and imperviousness densities in Europe (Eurostat, 2018; European
499 Environmental Agency, 2021).

500

501 Surprisingly, our study did not detect a link between alien plant invasions and other human
502 disturbance predictors, including population density, woodland fragmentation and edge
503 complexity, and the cover of human-dominated land. We hypothesize that other factors, like
504 introduction and planting history, could over-ride the importance of human disturbance at the
505 landscape scale. For instance, given that trees and shrubs are over-represented in the
506 European alien woodland flora compared to natives (Wagner *et al.*, 2017), our finding could
507 echo the large-scale planting of this group in the mid-18th to early 20th century (Bucharová
508 and van Kleunen, 2009; Nyssen *et al.*, 2016). Well-known examples are the planting of
509 *Prunus serotina* (Schrader and Starfinger, 2009; Nyssen *et al.*, 2016) and *Robinia*
510 *pseudoacacia* (Vítková *et al.*, 2017) in north-western and central Europe. This hypothesis is
511 supported by Bucharová and van Kleunen (2009) and Pyšek *et al.* (2009), who found planting
512 frequency to be the most important predictor of the success of alien trees in Europe. Planting

513 could have removed landscape filters and facilitated the spread of alien phanerophytes into
514 European woodlands. Furthermore, our proxies of human disturbance at the continental scale
515 were available only at the turn of the 21st century, roughly when 50% of our vegetation plots
516 have been sampled. However, invasions may be the result of much earlier human disturbance
517 activities. Linking our data to historic disturbance and planting data could have explained
518 more variation, but such data are more difficult to gather at the European extent.

519

520 Soil properties explained only a small amount of variation in our data. It is possible that their
521 spatial resolution ($\sim 5.5 \times 3.9$ km) was too coarse to detect any signal in the data. Linking our
522 data to soil information at a finer spatial resolution might have improved models, but such
523 data were not available and are generally underrepresented or recorded inconsistently in
524 vegetation databases. Future studies that couple vegetation surveys with detailed analyses of
525 soil abiotic and biotic properties could shed more light in this respect.

526

527 RFs predicted 39.6% and 20.9% of the variation in relative alien species richness and the sum
528 of alien species covers, respectively. The lower variance explained in the latter response
529 variable is likely due a higher imprecision in cover estimates compared to species richness
530 estimates, and to a stronger influence of effects not captured in our models, such as local
531 disturbance (Chabrierie *et al.*, 2008). In addition, we considered only single effects in driving
532 alien plant invasions. However, invasion patterns are driven by interactions of multiple effects
533 (Thuiller *et al.* 2006; Pyšek *et al.*, 2015). An analysis of interactions between habitat type and
534 human disturbance, in particular, could reveal whether some habitat types are more prone to
535 invasions under increased human disturbance.

536

537 **Conclusions**

538 European woodlands show clear signs of invasion debt for alien plants, with regional hotspots
539 of invasions, links to predictors representing propagule pathways, and the strongest
540 environmental predictions for maximum levels of invasion. Looking into the future, our
541 results imply that alien plant invasions will continue to expand in European woodlands, likely
542 driven by the complex effects of regional introduction history, factors associated with
543 differences between habitat types, and the prevalence of dispersal corridors and urban areas.
544 A challenge for future research is to clarify the role of local and historic factors as drivers of
545 alien plant invasions. Avoidance strategies, such as regulations of alien plant introductions
546 and plantings (Brundu and Richardson, 2017; Pötzelsberger et al. 2020), must be key
547 components for the protection of European woodlands from future invasions. Given that alien
548 plant invasions are dynamic processes and will likely proceed further, we advocate for
549 continuous surveys in European woodlands at the local and regional scales.

550

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562

563 **Author contributions**

564 VW and MC conceived the idea and developed the study design. VW and MV prepared the
565 data. VW carried out the statistical analysis, with feedback from co-authors, and led the
566 writing. All co-authors supplied data, species status and life-form assignments, and helped
567 develop the manuscript.

568

569 **Data availability statement**

570 Vegetation-plot data used in this study are stored in European Vegetation Archive with
571 reference to project no. 1 (2014-05-31). Accompanying data and R scripts can be accessed at
572 [10.6084/m9.figshare.13697329](https://doi.org/10.6084/m9.figshare.13697329).

573

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833

834 SUPPORTING INFORMATION

835 Additional supporting information may be found online in the Supporting Information
836 section.

837 **Appendix S1.** Methods supplement

838 **Appendix S2.** Supplementary tables

839 **Appendix S3.** Supplementary figures

840 **Table 1.** Overview of predictor variables. EEA = European Environment Agency, T =
841 Temperature, Min = Minimum, SD = standard deviation, CV = coefficient of variation. See
842 **Appendix S1.** Methods supplement for more details on data extractions.

	Source	Data type
Habitat type , Appendix S2.4, Table S2.1	Custom assignment based on Schaminée <i>et al.</i> (2014) and Janssen <i>et al.</i> (2016), see Wagner <i>et al.</i> (2017) for details	Categorical, 15 levels
Region (regional grid cells)	Custom calculation	Categorical, 41 levels (250 km × 250 km cells)
Environmental variables		
Elevation [m]	Original plot data, Jarvis <i>et al.</i> (2008)	Continuous. Original entry or extracted from a raster of 90 m × 90 m resolution*)
BIO1: Mean annual T × 10 (°C)	Karger <i>et al.</i> (2017)	Continuous. Extracted from a raster of 30 arcsec (~1 km × 1 km*) resolution
BIO4: T seasonality (SD × 100)	"	"
BIO6: Min. T of coldest month × 10 (°C)	"	"
BIO10: Mean T of warmest quarter × 10 (°C)	"	"
BIO12: Annual precipitation sum (mm)	"	"
BIO15: Precipitation seasonality (CV)	"	"
Topsoil pH	Wieder <i>et al.</i> (2014)	Continuous, extracted from raster of 0.05° (~5.5 km × 5.5 km*) resolution
Topsoil sand fraction (% weight)	"	Percentage, extracted from a raster of 0.05° resolution
Topsoil organic carbon (% weight)	"	"
Topsoil gravel fraction (% weight)	"	"
Degree of human disturbance		
Imperviousness % (year 2006) = percentage of sealed soil	Copernicus (Geoland-2), EEA (2013)	Percentage, extracted from a raster of 100 m × 100 m resolution (mean, max in buffer**)
Human population density	Eurostat 2012 (year 2011)	Count, extracted from grid polygons of 1 km × 1 km**

Degree of woodland fragmentation (m)	Custom calculation based on Copernicus (EEA 2016)	resolution (mean, max in buffer**) Continuous, extracted from a raster of XX m XX m (mean in buffer**)
Woodland edge complexity	"	Continuous, extracted from a raster of XX m XX m resolution (mean in buffer**)
Distance to the nearest road (km)	OpenStreetMap Contributors (2019)	Polyline vector
Distance to the nearest railroad (km)	"	"
Road density	Meijer <i>et al.</i> (2018)	Continuous, extracted from a raster of 5 arc minutes (~9 × 9 km*) resolution (mean, max in buffer**)
Cover of human-dominated land types %, four different variables, Appendix S2, Table S2.1	Aggregated CORINE land-cover types; Bossard <i>et al.</i> (2000)	Continuous, extracted from a raster of 500 m × 500 m** resolution (mean in buffer**)

843 * at equator

844 ** extracted within 200, 500, 1000 and 2000 m buffer circles around plots

845 **Table 2.** Regional origin of plots associated with peaks in 99% and 90% quantiles of relative
846 alien species richness along selected predictor variables; peaks were defined as plots falling
847 into the range of a predictor variable and the response quantile, as inspected for a bivariate
848 relationship; *n* = no. of plots and % = percentage of plots in the peak; displayed are only the
849 three regions with the highest plot numbers.
850

≥ 99% quantile			≥ 90% quantile		
region	<i>n</i>	%	region	<i>n</i>	%
Elevation: 0-500 m			Elevation: 0-500 m		
Netherlands	72	42.6	Netherlands	344	22.2
Belgium	45	26.6	Czech Republic	269	17.4
Poland	13	7.7	Belgium	165	10.6
Distance to nearest road: 0-2 km			Distance to nearest road: 0-2 km		
Netherlands	70	40.5	Netherlands	338	25.3
Belgium	45	26.0	Czech Republic	290	18.0
Poland	13	7.5	Belgium	165	10.2
Distance to nearest railroad: 0-10 km			Distance to nearest railroad: 0-10 km		
Netherlands	70	41.4	Netherlands	329	21.4
Belgium	42	24.9	Czech Republic	290	18.8
Poland	13	7.7	Belgium	159	10.3
Mean annual temperature: 8-12°C			Mean annual temperature: 8-12°C		
Netherlands	72	43.6	Netherlands	344	24.7
Belgium	45	27.3	Czech Republic	259	18.6
Poland	13	7.9	Belgium	165	11.8

851

852

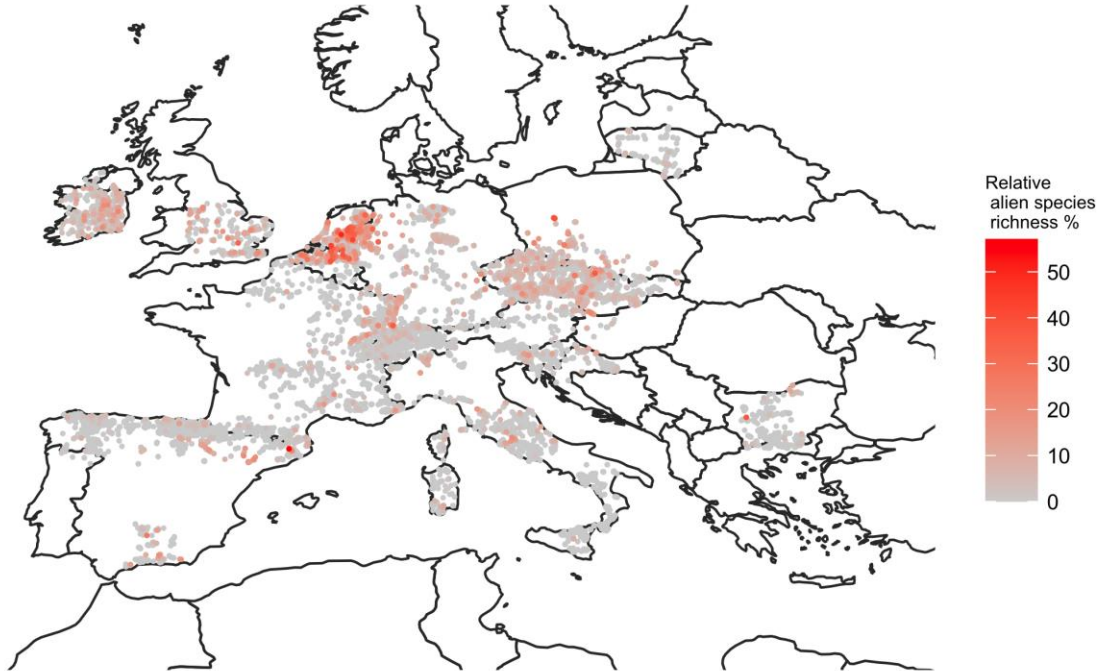
853 **Table 3.** Regional origin of plots associated with peaks in 99% and 90% quantiles of the sum
854 of alien species covers along selected predictor variables; peaks were defined as plots falling
855 into the range of a predictor variable and the response quantile; n = no. of plots and % =
856 percentage of plots; displayed are only the three regions with the highest plot numbers.
857

$\geq 99\%$ quantile			$\geq 90\%$ quantile		
region	n	%	region	n	%
Elevation: 0-500 m			Elevation: 0-500 m		
France	32	20.4	Czech Republic	341	16.8
Belgium	25	15.9	Netherlands	322	15.3
Czech Republic	23	14.6	France	152	14.6
Distance to nearest road: 0-2 km			Distance to nearest: 0-2 km		
France	32	19.5	Czech Republic	365	22.1
Czech Republic	28	17.1	Netherlands	317	20.8
Belgium	25	15.2	France	159	11.2
Distance to nearest railroad: 0-10 km			Distance to nearest railroad: 0-10 km		
France	31	19.9	Czech Republic	367	23.6
Czech Republic	27	17.3	Netherlands	312	20.0
Belgium	25	16.0	France	156	10.0
Mean annual temperature: 8-12°C			Mean annual temperature: 8-12°C		
France	30	20.3	Czech Republic	329	23.6
Belgium	25	16.9	Netherlands	322	23.1
Czech Republic	24	16.2	France	147	10.5

858

859 **Fig. 1.** Location and relative alien species richness of vegetation plots included in the final
860 dataset ($n = 16,211$ plots).

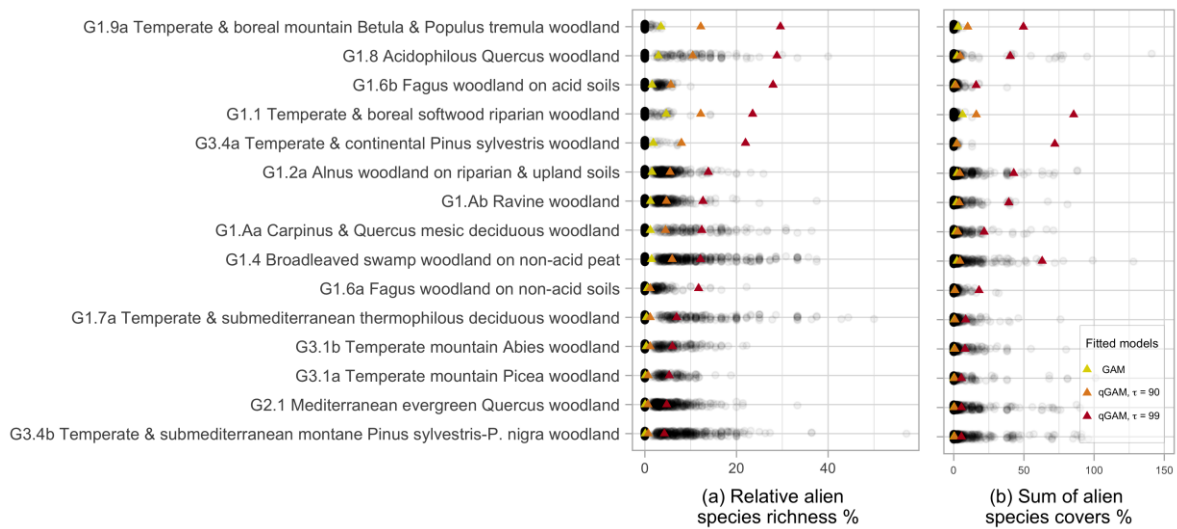
861



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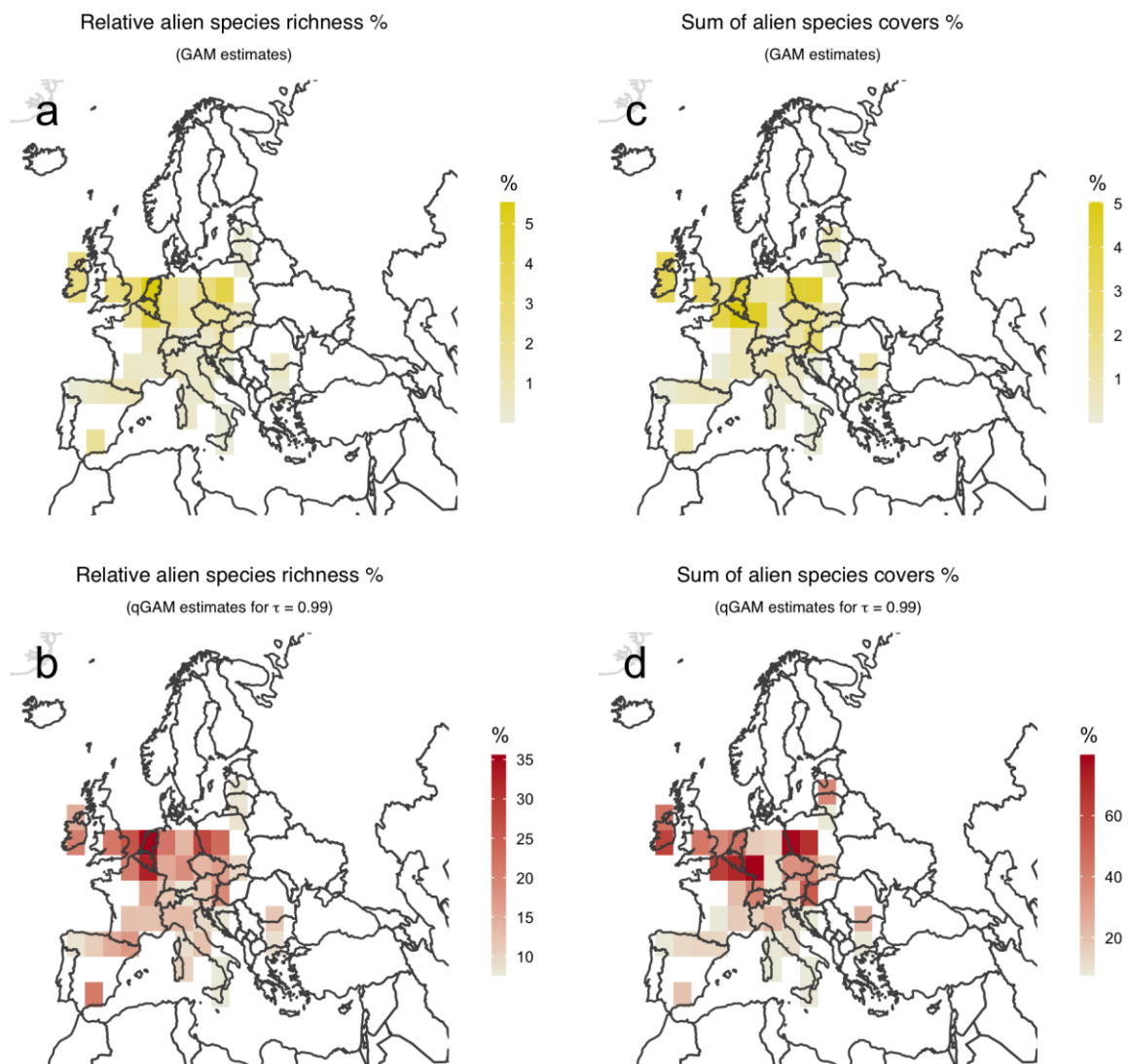
863

864 **Fig. 2.** Differences in (a) the relative alien species richness and (b) the sum of alien species
 865 covers among EUNIS habitat types of European woodlands. Colored symbols are group
 866 estimates as fitted by generalized additive models (GAMs) and quantile GAMs (qGAMs) for
 867 quantiles $\tau = 0.90$ and 0.99 . In both figures, the habitat types are sorted in decreasing order
 868 according to coefficient estimates from qGAMs of relative alien species richness at $\tau = 0.99$
 869 (panel figure a).



870

871 **Fig. 3.** Differences in relative alien species richness (a, b) and the sum of alien species covers
872 (c, d) among regional grid cells. Colored cells are estimates fitted by quantile generalized
873 additive models (qGAMs) at quantile $\tau = 0.99$ with the factor variable “region” ($n = 41$
874 levels) used as the only predictor variable. Areas in white were not included due to
875 insufficient data availability. Results for qGAMs at quantile $\tau = 0.90$ are not displayed since
876 models failed to converge.



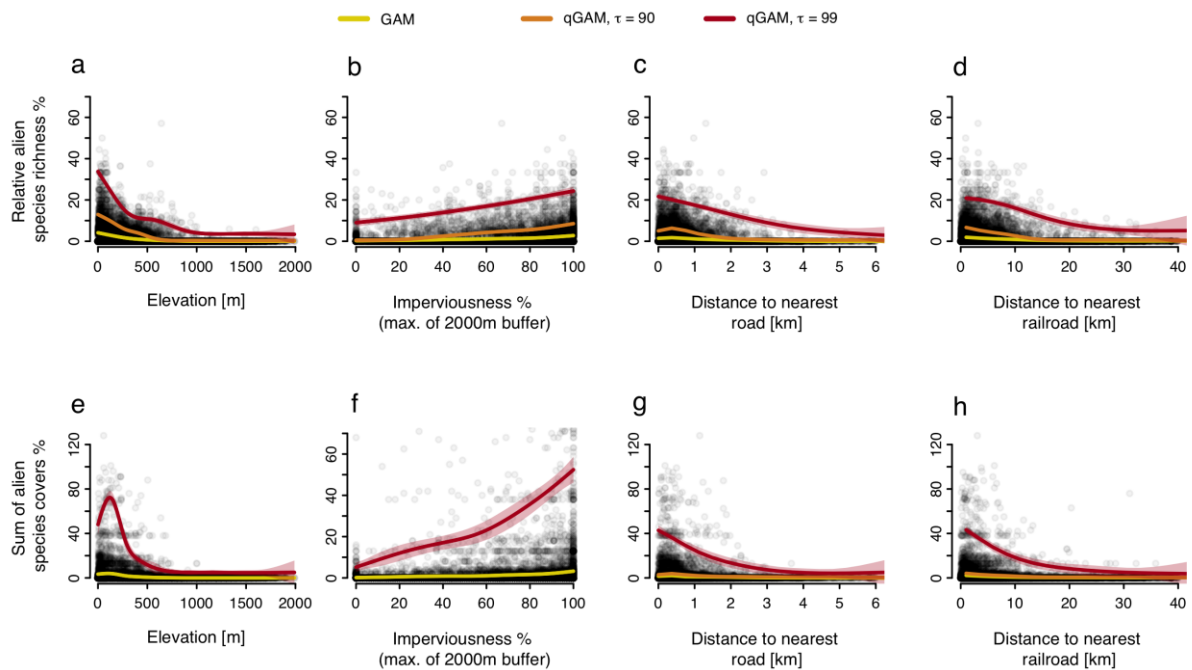
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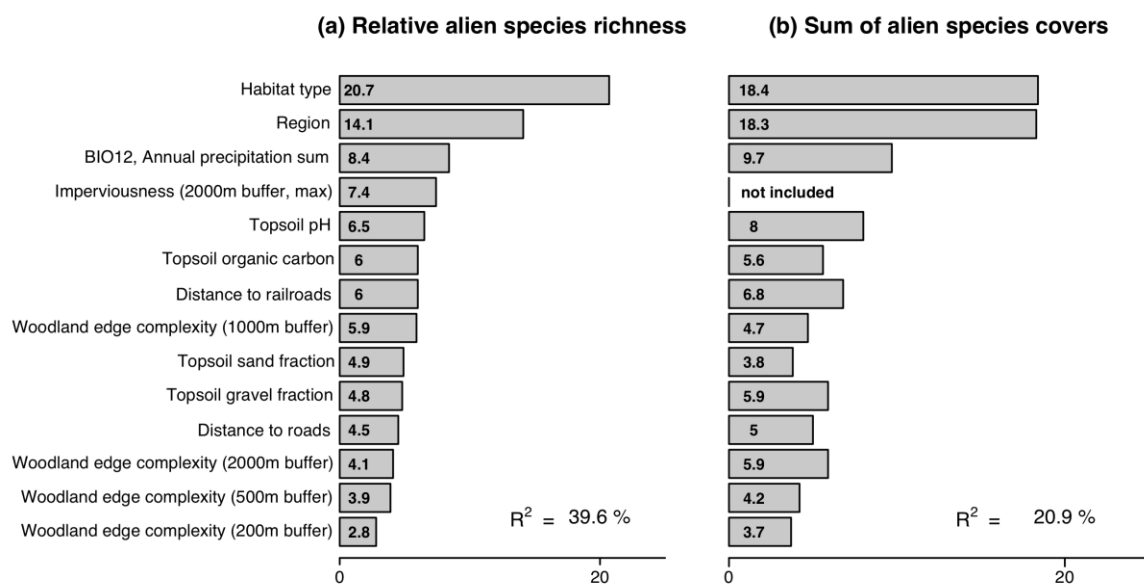
880 **Fig. 4.** Bivariate relationships between (a-d) relative alien species richness and (e-h) sum of
881 alien species covers with elevation, imperviousness (max. of 2000m buffer), distance to the
882 nearest road, and distance to the nearest railroad. Lines were fitted using generalized additive
883 models (GAMs) and quantile generalized additive models (qGAMs), with a 95% confidence
884 interval. Only fits of converged models are shown. See Appendix S3, Figs S3.2 and S3.3 for
885 relationships with all continuous predictors.

886



887

888 **Fig. 5.** Importance of predictors for explaining (a) relative alien species richness and (b) sum
 889 of alien species covers when all aliens are included, assessed by Random Forest analyses.
 890 Bars show an average increase in the mean standard error (MSE), normalized across
 891 predictors to sum to 100%. Only predictors with a generalized variance inflation factor ≤ 2
 892 were included to avoid multicollinearity. See Appendix S3, Fig. S3.4 for importance values
 893 for other alien groups.
 894



895