1   Small scale variability in soil moisture drives infection of vulnerable juniper populations by

2   invasive forest pathogen

3

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13 **Abstract**

14

15 The oomycete plant pathogen, *Phytophthora austrocedri*, is an aggressive killer of cypress

16 trees causing severe mortality of Chilean cedar (*Austrocedrus chilensis*) in Argentina since

17 the 1940s and now common juniper (*Juniperus communis* s.l.) in the UK. Rapid mortality of

18 key UK juniper populations was first observed in the early 2000s; the causal agent of mortality

19 was confirmed as *P. austrocedri* in 2012 and the pathogen has now been widely detected -

20 but is not ubiquitous - in juniper populations across Scotland and England. Although juniper

21 has a broad distribution across the northern hemisphere, the UK incidence of *P. austrocedri*

22 remains the only confirmed infection of juniper populations globally. Juniper is an important

23 species for biodiversity, so it is imperative to understand the abiotic and biotic drivers of

24 emergent *P. austrocedri* infection to inform detection, containment and conservation strategies

25 to manage juniper populations across the full extent of its range.

26

27 As management of UK juniper populations is primarily conducted at a local level, we

28 investigated field scale drivers of disease – in three, geographically separate populations with

29 different infection histories. Variation in the proportion of juniper showing symptoms -

30 discoloured or dead foliage – was measured using stratified sampling across along key

31 environmental gradients within each 100-hectare population, including juniper density

32 identified from aerial imagery. Potential predictors of infection included altitude, slope,

33 distance to nearest watercourse, soil moisture (mean percentage volumetric water content),

34 area of red deer browsing damage and area of commonly associated vascular plant species.

35 We assessed support in the data for alternative models explaining the spatial distribution of

36 *P. austrocedri* symptoms using full subset covariate selection and Deviance Information

37 Criteria (DIC). Despite differences in environmental gradients and infection histories between

38 populations, area of juniper symptomatic for *P. austrocedri* increased with waterlogging,

39 increasing with soil moisture in sites where soils had higher peat or clay contents, and

40 decreasing with proximity to watercourses where sites had shallower, sandier soils. These

41   results are consistent with key drivers identified at both local and landscape scale in Chilean

42   cedar. Our approach enables identification of site-specific disease management strategies

43   including prioritisation of inspections in microsites with high soil moisture and promoting

44   conservation measures such as creation of sites for natural regeneration in drier microsites to

45   minimise pathogen spread and maximise the resilience of existing juniper populations.

46

47   **1.0 Introduction**

48

49   The frequency of plant pathogen introductions outside their native ranges is increasing as

50   global trade networks expand (Chapman et al., 2017). Successful establishment of pathogens

51   in these new environments is increasingly being facilitated by degradation of the receiving

52   communities through habitat fragmentation, species turnover and land use change (Chapman

53   et al., 2016; Meentemeyer et al., 2011). Economic losses from plant diseases in the natural

54   environment can result directly from drastic reductions in the extent and viability of host

55   species, increased cost of detection and containment measures, or from indirect losses such

56   as destablisiation of ecosystem functioning from loss of biodiversity or negative visual impacts

57   detering tourists, driving down house prices and increasing local crime rates (Boyd et al., 2013;

58   Kovacs et al., 2011; Mills et al., 2011; Troy et al., 2012). While it is appealing to act immediately

59   to try to control disease outbreaks, the effectiveness of these actions improves as more

60   information on the processes governing spread becomes available, often relying on

61   information that does not exist prior to pathogen introduction (Thompson et al., 2018).

62   Understanding the subset of abiotic and biotic conditions in the invaded range under which

63   introduced pathogens are likely to infect susceptible host populations can improve targeting

64   of such interventions and highlight risk factors for outbreaks in uninvaded locations (Cunniffe

65   et al., 2016).

66

67   The oomycete genus *Phytophthora* contains many pathogenic species that adversely impact

68   plant health, forestry and agriculture, necessitating expensive, long-term, landscape scale

69   management. Between 1970 and 1989, 11 *Phytophthora* species were introduced to China,

70   12 to the UK and 16 to the USA (Barwell et al., in review). In the two decades following, the

71   number of additional species introduced at least doubled in China (20) and the UK (29) and

72   increased five-fold in the USA (54). While not all of these species established, some of them

73   have caused serious tree mortality with dramatic landscape and economic consequences. In

74   Western Australia 282 000 ha of Jarrah (*Eucalyptus marinata*) have been lost to *P. cinnamomi*

75   (Boyd et al., 2013), while trade of Port Orford cedar (*Chamaecyparis lawsoniana*) in the north-

76   western United States was almost eliminated by *P. lateralis* (Hansen, 2015). Meanwhile,

77   millions of coast live oak (*Quercus agrifolia*) and tanoak (*Notholithocarpus densiflorus*) trees

78   in California and Oregon, and 18 000 ha of Japanese larch (*Larix kaempferi*) in the UK and

79   Ireland have been killed by *P. ramorum* (Meentemeyer et al., 2011; O'Hanlon et al., 2018;

80   Peterson et al., 2014).

81

82   First described in 2007, *Phytophthora austrocedri* Gresl. & E. M. Hansen has caused

83   widespread mortality of Chilean cedar (*Austrocedrus chilensis*) in Argentina since the 1940s

84   (Greslebin et al., 2007; Greslebin and Hansen, 2010). The pathogen is homothallic and is

85   potentially spread by both asexual, motile zoospores dispersed through any form of moving

86   water, and sexually produced, thick-walled oospores that can remain viable for extended

87   periods of time and be translocated in soil (Green et al., 2015; Henricot et al., 2017a). Infection

88   usually starts in the roots before spreading into the cambium and phloem, creating necrotic

89   lesions that can extend to the full width of each layer, starving whole branches, trunks or trees

90   of water and nutrients causing rapid defoliation and mortality (Green et al., 2015).

91

92   Symptoms were first brought to the attention of UK plant pathologists in the mid-2000s, when

93   significant numbers of symptomatic juniper (*Juniperus communis* L. s. l.) could be observed

94   in two of the larger populations (Glenartney and Haweswater), but *P. austrocedri* was not

95   confirmed as the causal agent of mortality until 2012 following isolation and confirmation of

96   Koch's postulates (Green et al., 2012). In the UK the pathogen is present as a single genetic

97   lineage exhibiting no diversity in nucleic and mitochondrial loci, suggesting introduction and

98   spread of a single clonal strain (Henricot et al., 2017a). The extent of juniper decline varies,

99   with some populations showing wholesale dieback of bushes compared to others with only

100   localised patches of symptoms, suggesting populations have been infected at different times

101   and/or different site conditions promote different rates of spread.

102

103   Although interceptions of infected cypress and juniper trees in Scotland, England and

104   Germany confirm that infected material is being traded (Green et al., 2015; Werres et al.,

105   2014) the outbreak in British juniper populations in the wider environment remains the only

106   detected infection of a natural host population outside Argentina (Green et al., 2012). Globally,

107   juniper has a large, circumboreal distribution extending across the northern hemisphere but

108   as no investigation of environmental drivers of infection has been undertaken, the proportion

109   of juniper vulnerable to *P. austrocedri* infection is unclear.

110

111   In the UK, juniper has a wide but discontinuous distribution occupying much of Scotland and

112   northern England and remaining as scattered populations in southern England, Wales and

113   Northern Ireland (Fig. 1). Populations are undergoing long term declines in most areas as a

114   result of burning, afforestation, over-grazing, under-grazing, increased levels of diffuse

115   pollution (particularly nitrogen) and poor germination following warmer winter temperatures

116   (Broome and Holl, 2017; Clifton et al., 1997; Long and Williams, 2007; Sullivan, 2003;

117   Verheyen et al., 2009; Walker et al., 2017; Ward and Shellswell, 2017). It is difficult to estimate

118   the area of juniper lost specifically to disease but infected populations are widespread across

119   Scotland and England, where juniper occupancy of 10 x 10 km cells reportedly declined by 23

120   % and 44 % respectively between 2000 and 2016 (Plantlife, 2015).

121

122   The societal and environmental value of woodlands was recognised in the 2014 Tree Health

123   Management Plan for England as several times higher than the commercial value of forestry

124   (Department for Environment Food & Rural Affairs, 2014a) and the Scottish Plant Health

125   strategy identifies plant health in the natural environment as integral to the £1.8 billion rural

126   economy (The Scottish Government, 2016). Loss of UK juniper populations to *P. austrocedri*

127   could be significant as the species is highly ecologically important as a dominant component

128   of many habitats including woodland, scrub, heath, dune and calcareous grassland, as a nurse

129   species ameliorating environmental conditions and protecting other seedlings from herbivory,

130   a rare source of winter food and nesting habitat for birds, and a host of many specialist fungi

131   and insects (Thomas et al., 2007; Ward and Shellswell, 2017; Wilkins and Duckworth, 2011).

132

133   As juniper occupies such a broad variety of habitats, trees are subject to different

134   environmental conditions and land uses that may alter their susceptibility to disease.

135   Epidemics occur across a range of spatial scales, arising first as microscopic infections that

136   can spread to whole plants, populations and landscapes (Gilligan and Van Den Bosch, 2008).

137   Successful disease control requires matching of the scale of management to the inherent

138   scale of spread as mediated by host population connectivity and pathogen dispersal distances

139   (Cunniffe et al., 2016). Transmission of soil borne pathogens is likely to occur across short

140   distances resulting in highly aggregated infection prevalence and spatially variable exposure

141   to pathogens within host populations (Penczykowski et al., 2018). However, very few studies

142   of soil borne Phytophthoras investigate spread at field scale and those that do use small (<

143   20) sample sizes (La Manna and Matteucci, 2012; La Manna and Rajchenberg, 2004a; Nagle

144   et al., 2010; Tippett et al., 1989).

145

146   We measured juniper symptoms in 147 quadrats across three, geographically separate juniper

147   populations with contrasting infection intensities and analysed the data using Generalised

148   Linear Mixed Models (GLMMs) to compare drivers of spatial variation in symptoms at field

149   scale. Correlative approaches, such as GLMMs, are appropriate tools to perform such

150   exploratory analyses as they can accommodate a broad range of potential covariates as is

151   necessary when drivers of pathogen dispersal and spread in the invaded range are poorly

152   understood (Purse and Rogers, 2009).

153

154   We expected *P. austrocedri* infection of juniper would exhibit similar responses to

155   environmental covariates as infected Chilean cedar, which occupies a similarly diverse range

156   of ecotypes. Population level studies in Argentina found area of foliage symptoms increased

157   in microsites situated at low altitude with poor soil drainage, flat slopes, close proximity to

158   watercourses and fine soil textures, with greater infection of female cedars because they

159   typically occupy wetter microsites (Baccalá et al., 1998; V. a El Mujtar et al., 2012; La Manna

160   et al., 2008; L. La Manna and Rajchenberg, 2004; Ludmila La Manna and Rajchenberg, 2004).

161

162   In addition, we expected that the area of symptoms in juniper would increase with i) increasing

163   host density, as inoculum production is likely to increase with availability of host tissue and

164   dispersal distances between roots will be reduced (Anderson and May, 1986; Dillon et al.,

165   2014); and ii) increased ungulate herbivory, and proximity to deer and sheep tracks and lie-

166   ups, as evidence for increased exposure to inoculum transported in soil on herbivore hooves

167   (Jules et al., 2002; La Manna et al., 2013).

168

169   Given the contrast in abiotic and biotic conditions occupied by each population, we further

170   expected that the relative importance of the investigated covariates would vary between

171   locations and require site specific strategies to manage individual juniper populations.

172 **2.0 Methods**

173

174 **2.1 Study Areas**

175

176 Three infected juniper populations from where *P. austrocedri* had previously been isolated

177 (Henricot et al., 2017) were selected to best represent the diversity of climatic, topographic

178 and edaphic conditions occupied by juniper. Two populations are located in Scotland: one in

179 Perthshire (P) and one in the Cairngorms (C), and one population is situated in the Lake

180 District (LD) in the north of England. In all three locations, the juniper population is a

181 component feature of a Special Area of Conservation designated habitat and a qualifying

182 interest of a Site of Special Scientific Interest (SSSI; Fig. 1).

183
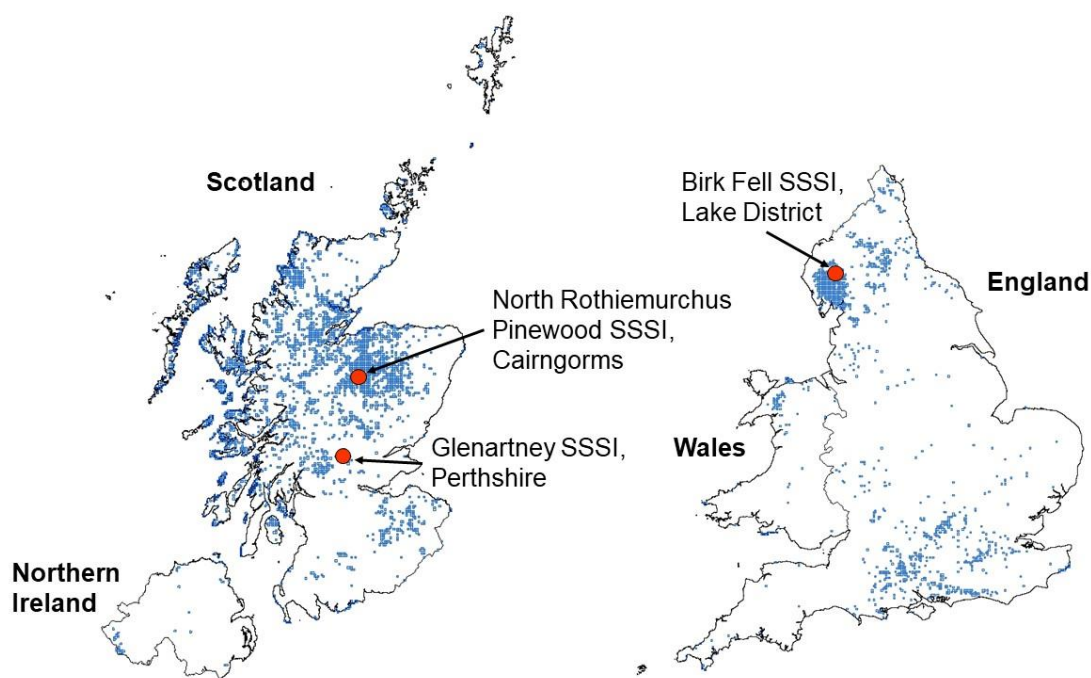
184

185 **Figure 1.** SSSI name and location of the three juniper study populations mapped against the

186 distribution of UK juniper (*Juniperus communis* s. l.) at 2 x 2 km resolution (shown in blue)

187 recorded during the period 2000 – 2017 (Botanical Society of Britain and Ireland, 2017).

188

189   Each population contained 100 – 130 hectares of continuous juniper cover. The greatest area

190   of mortality was observed in the Perthshire population; symptoms were first reported in 2004

191   and represented a 20% decline in area of live juniper trees compared to a 1983 baseline

192   survey (Tene et al., 2007). The precise duration of infection in the Lake District and

193   Cairngorms populations is unknown, but *P. austrocedri* symptoms were first noted after 2010,

194   and a lower proportion of symptomatic juniper was observed at both sites potentially

195   consistent with a more recent introduction.

196

197   **2.2 Quadrat stratification**

198

199   Juniper was sampled using 10 x 10 m quadrats from pre-selected locations stratified according

200   to the area and density of juniper, altitude, slope and distance to watercourses. A 2010

201   distribution map of the Perthshire juniper population derived from 15 cm full colour (RGB) and

202   false colour infrared (CIR) imagery was provided by Scottish Natural Heritage (Whittome,

203   2010) and distribution maps of the remaining two populations were classified from 25 cm RGB

204   imagery supplied for 2010 by NeXTPerspectives™. The classification methods are described

205   in Appendix A.

206

207   To capture differences in juniper abundance and density, the area of juniper predicted by the

208   image classifications was measured in 10 x 10 grid cells using landscape class statistical

209   functions in the SDMTools package (Van der Wal et al., 2014) implemented in R v. 3.4.2 (R

210   Core Team, 2017). To understand if each 10 x 10 m cell was isolated from other juniper stands

211   or part of a larger stand, the area of juniper in 30 x 30 m including each 10 x 10 m grid cell

212   was also calculated, producing distributions of juniper % cover at each scale for each study

213   population (Fig. 2). These distributions were used to devise eight categories to describe

214   juniper abundance that could be easily identified in the field. Each 10 x 10 m cell containing

215   juniper was assigned to one of four categories describing juniper % cover in 10 x 10 m (≤ 10,

216   11-25, 26-50, > 51 %) and to one of two categories characterising the area of juniper

217   surrounding the 10 x 10 m cell as isolated from (< 20 %), or contiguous with (> 21 %), juniper

218   growing in the wider 30 x 30 m.

219
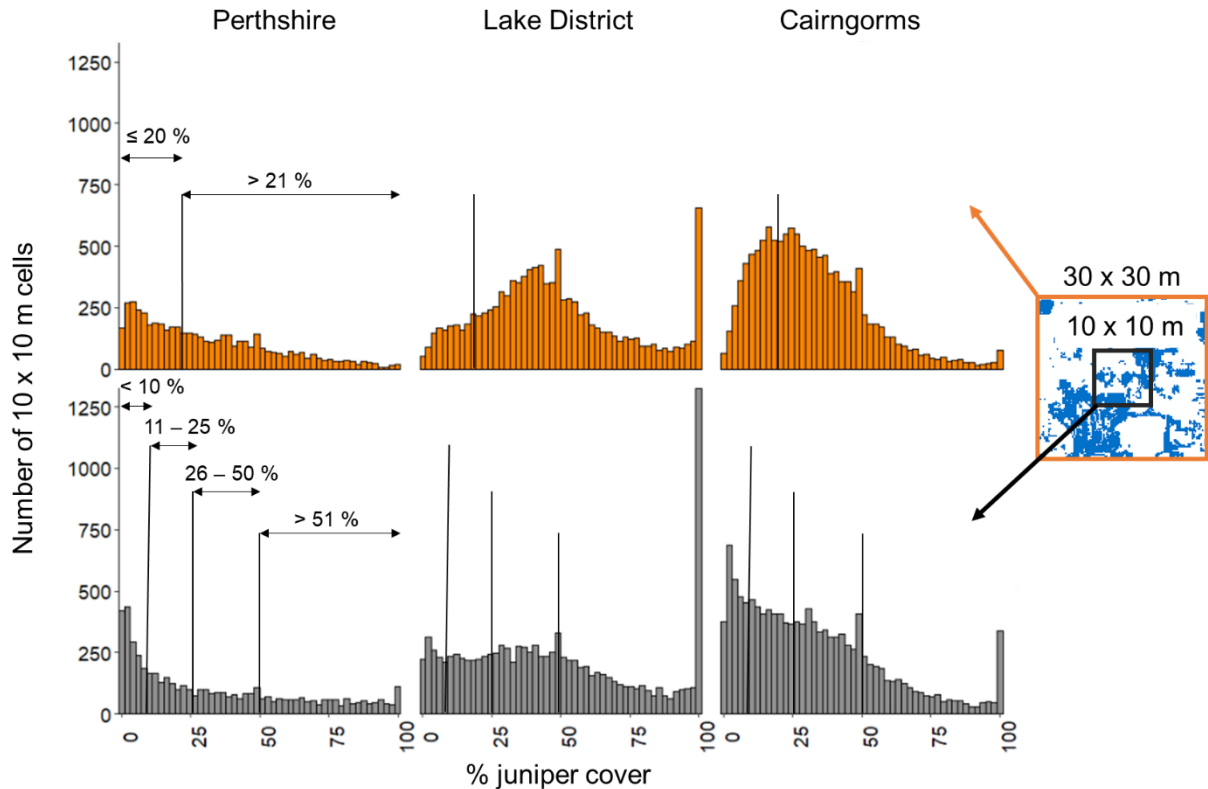
220

221   **Figure 2.** Number of 10 x 10 m cells per study population with estimated % cover of juniper

222   (shown in blue) across 10 x 10 m (grey) cells and the surrounding 30 x 30 m (orange).

223   Thresholds used to divide juniper % cover into categories at each scale are marked with

224   black lines.

225

226   Layers of slope and aspect were calculated from the resampled NeXTPerspectives™ 10 m

227   DEM using the *terrain* function in the raster package (Hijmans, 2016). Slope, aspect and

228   altitude were then extracted to the centroid of each 10 x 10 m grid cell containing juniper.

229   Euclidean distance (m) from the nearest watercourse to each 10 m grid cell centroid was

230   measured from a rasterised version of the 50 m digital rivers network (Moore et al., 2000).

231

232   Fifty 10 x 10 m cells per study population were randomly selected for sampling in proportion

233   to the total number of cells assigned to each abundance category. This was repeated five

234   times for each population. After each run, selected cells were plotted across the altitudinal,

235   slope and watercourse proximity gradients occupied by juniper at each location and the

236   selection that captured the widest distribution of samples along each of the three gradients

237   was chosen as sampling locations.

238

239   **2.3 Survey of spatial patterns in juniper symptoms**

240

241   Quadrat sampling was carried out over five days at each location in October 2017. Quadrats

242   were geo-located using ArcPad v. 10.2 on a Panasonic FZ-GI tablet with GPS accuracy to 3

243   m. To minimise transference of inoculum across populations, areas of high and low infection

244   were visited on different days and all equipment breaking the soil surface (e.g. marker poles,

245   soil moisture probes) was disinfected between quadrats. All other equipment was thoroughly

246   disinfected between study populations.

247

248   Juniper quadrats were placed as close to pre-selected locations as was possible to meet the

249   abundance criteria by estimating the area of juniper in 10 x 10 m and scoring abundance in

250   30 x 30 m as a binary measure of more or less than 20 %. The area of symptomatic juniper

251   was measured as a fraction of the total area of juniper present in each quadrat, where

252   symptoms constituted foliage discolouration and dead needles (retained or dropped) that

253   extended to a minimum of a whole branch and did not result from either browsing or

254   mechanical damage. Where a distinctive phloem lesion typical of *P. austrocedri* could be

255   found, a 500 mg tissue sample was collected from one representative symptomatic tree per

256   quadrat. The sampled tissue was stored at - 20 °C until quantitative real-time PCR (qPCR)

257   could be carried out following the protocol described in Mulholland et al. (2013) to verify the

258   consistent presence of *P. austrocedri* across each population.

259

260   **2.4 Abiotic and biotic predictors**

261

262   We measured a suite of potential abiotic and biotic predictors of spatial patterns in

263   *P. austrocedri* symptoms and included these in statistical models for each population (Table

264   1).

265

266   The following predictors were measured in each field quadrat. The binary observation of ≤ 20

267   % or > 21 % juniper cover across 30 x 30 m to distinguish between quadrats situated in

268   isolated or contiguous juniper stands was included in the model as juniper "density". The area

269   of juniper bearing berries was used to estimate the area of female juniper. Area of herbivore

270   damage was measured as the area of bark stripping plus any resulting dead branches / stems

271   (i.e. mechanical breakage from wind or snow damage was excluded). This metric was not

272   included in Cairngorm models as herbivory was only detected in nine quadrats, encompassing

273   an area greater than 10 cm^2 in only three quadrats.

274

275   Soil moisture was measured as % volumetric water content (VWC) using a FieldScout TDR

276   300 probe. Shallow soil and surface rock only permitted measurements using the 3.8 cm depth

277   setting across the Lake District population, whereas measurements were collected at 20 cm

278   depth in Perthshire and the Cairngorms. Measurements were collected from i) areas within

279   each quadrat where juniper was absent, ii) under asymptomatic juniper and iii) under

280   symptomatic juniper. An equal number of measurements (minimum four) was collected from

281   each category present, resulting in eight to twelve point sample measurements from which

282   mean soil moisture was calculated (% VWC).

283

284   Area of vascular plant taxa present in each quadrat was recorded according to a target list

285   (Appendix B) of taxa chosen to indicate placement of microsites along soil moisture, nitrogen

286   and pH gradients.

287

288   Mapping in the field was carried out using the tracking function in ARCpad, to record any

289   watercourses additional to the 50 m digital rivers network (Moore et al., 2000). These were

290   merged with the original dataset and used to recalculate the watercourse proximity (m) metric

291   for each quadrat. Clearly visible deer and sheep tracks were also mapped and proximity to

292   sampled quadrat centroids measured as an alternative way to measure the risk of inoculum

293   transference to juniper from herbivores, but stocking density and ground condition only

294   permitted collection of a reliable dataset from Perthshire.

295

296 **Table 1.** List of covariates included in full subset model selection for each population

297 (P = Perthshire, LD = Lake District, C = Cairngorms).

298 Number of sampled quadrats: P = 51, LD = 46, C = 50.

299

Measurement category	Specific measurement	Population		
		P	LD	C
Juniper density 30 x 30 m quadrat	≤ 20 % or > 21 % juniper cover	x	x	x
Juniper metrics 10 x 10 m quadrat	Area of juniper bearing berries (m^2)	x	x	x
	Area of herbivore damage (m^2)	x	x	
Soil moisture	Mean of point samples across quadrat (% VWC)	x	x	x
Vascular plant indicators	Area of individual target taxa (m^2)	x	x	x
Watercourse proximity	Euclidean distance from quadrat centroid to nearest mapped river (m)	x	x	x
Grazing activity	Distance from quadrat centroid to nearest deer or sheep track (m)	x		
Topographic metrics extracted to 10 x 10 m quadrat centroid	Altitude (m)	x	x	x
	Slope (°)	x	x	x
	Aspect (°)			x
Soil type (250 m resolution) extracted to 10 x 10 m quadrat centroid	**Perthshire:** Brown forest Balrownie Brown forest Gourdie Organic soil, peaty gleys Non-calcareous gleys Peaty gleys Balrownie	x		
	Cairngorms: Humus-iron podzols; some brown forest soils, noncalcareous gleys and peaty gleys Humus-iron podzols; some peaty gleys and humic gleys			x
Habitat (NVC community)	**Perthshire:** W19 *Juniperus communis* woodland Acid grasslands (U4, U20, U24) Mires (M10, M23) Mosaic (U5, M15)	x		
	Cairngorms: H12 *Calluna vulgaris – Vaccinium myrtillus* heath W18 Scots pine woodland with heather U4 *Festuca ovina - Agrostis capillaris - Galium saxatile* grassland Coniferous plantation			x

300 .

301

302   The remaining covariates were obtained from existing GIS datasets. Altitude, slope and aspect

303   were extracted to each quadrat centroid from the resampled NeXTPerspectives™ 10 m layers

304   prepared for the plot stratification. Aspect was not included in the Perthshire or Lake District

305   models as more than 60 % of quadrats at each location were clustered in the same octant.

306

307   The soil type underlying each quadrat centroid was extracted from 250 m resolution datasets,

308   obtained from a digitised version of the soil map produced by Forbes (1984), the Soilscapes

309   dataset (Farewell et al., 2011) and the National Soil Map of Scotland (James Hutton Institute,

310   2011) for the Perthshire, Lake District and Cairngorms populations respectively. Soil type was

311   omitted from model selection for the Lake District population as at 250 m resolution all of the

312   quadrats were placed in "freely draining acid loamy soils over rock" (Farewell et al., 2011).

313

314   To test if a broader description of the vegetative community is a better predictor of

315   *P. austrocedri* symptoms, because it captures more information about edaphic conditions than

316   the presence of individual taxa, National Vegetation Classification (NVC) community data,

317   supplied by Scottish Natural Heritage (2017), was included as a covariate for the Perthshire

318   and Cairngorms populations (Table 1). The eight Perthshire communities were simplified to

319   these four broad types (Table 1), amalgamated as follows: acid grasslands (U4 *Festuca ovina*

320   *- Agrostis capillaris - Galium saxatile*; U20 *Pteridium aquilinum - Galium saxatile*; U24

321   *Arrhenatherum elatius - Geranium robertianum*), mires (M10 *Carex dioica – Pinguicula*

322   *vulgaris*; M23 *Juncus effusus/acutiflorus – Galium palustre*) and mosaic communities

323   suggesting transition from drier to wetter soil (U5 *Nardus stricta – Galium saxatile*; M15

324   *Trichophorum germanicum - Erica tetralix* wet heath) (Rodwell, 1991). No NVC data was

325   released for the Lake District population.

326

327

328

329

2.5 Model specification

To investigate the relationships between the area of *P. austrocedri* symptoms and environmental covariates, we used a Bayesian beta-binomial Generalised Linear Mixed Model (GLMM) fitted using the Integrated Nested Laplace Approximation (INLA) method with the R-INLA package (Rue et al., 2009) implemented in R v. 3.4.2 (R Core Team, 2017).

Models were fitted to the number of square metres of symptomatic juniper in each 10 x 10 m quadrat. Using the beta-binomial distribution enabled us to take account of the area of juniper in each cell while allowing the probability of infection to have extra variation associate with spatial clustering of symptoms (overdispersion), thereby accounting for the high frequency of quadrats that contain wholly asymptomatic or symptomatic juniper (Hughes and Madden, 1993).

In particular, our model used the $q = 12$ environmental covariates for the ith location $\{x_{j,i} | 1 \leq j \leq 16\}$ to estimate the mean probability of infection via a logit link function

$$\text{logit}(\mu_i) = \beta_0 + \beta_1 x_{1,i} + \cdots + \beta_q x_{16,i},$$

in which β_0 is an intercept and β_j is the regression coefficient for the jth predictor. This estimate of the mean probability is then used to predict the area of symptomatic juniper in the ith location (η_i) via

$$\eta_i \sim \text{beta-binomial}(\mu_i, \gamma, N_i),$$

in which N_i is the total area of juniper in the ith cell (m²) and γ is the overdispersion parameter of the beta-binomial distribution (that was assumed to be constant across all cells at each site). In our Bayesian estimation procedure all regression parameters, including the intercept, were assumed to have minimally informative priors of the form

$$\beta_q \sim \text{Normal}(0, 1/0.001).$$

2.6 Model selection

All covariates were centred and standardized prior to model fitting and no pairs of covariates used in any models were correlated with a Pearson r^2 value ≥ 0.6 (Appendix D). Models were run in two stages. We first performed a full subset selection using all possible combinations of covariates marked against each population (Table 1) except the vascular plant indicators, producing 1023 models for both Perthshire and the Cairngorms, and 127 models for the Lake District, which had seven as opposed to ten covariates.

Model fit was compared using the Deviance Information Criterion (DIC), a Bayesian generalisation of the Akaike Information Criterion (AIC) derived as the mean deviance adjusted for the estimated number of parameters in the model to provide a measure of out-of-sample predictive error (Gelman and Hill, 2006). The model with the lowest DIC is the model with the most support in the data, but the set of models with DICs within two units of the top model DIC are considered to have equivalent support in the data and formed the "top model set".

The area of each vascular plant indicator, present in ten or more quadrats at each population, were then added to the formulae for the top model set per population to assess (using DIC) if the addition of any one indicator improved model fit. Nine additional models were run for Perthshire and the Lake District, and ten for the Cairngorms (Table 3).

To assess the importance of covariate effects, we summarised marginal posterior distributions using 95 % (0.025 and 0.975 quantiles of the posterior distribution) Bayesian credible intervals (BCI). The relationship between each covariate and the area of symptoms is considered strongest where BCI do not bridge zero, very strong when ≥ 0.95, strong when ≥ 0.90 – 0.94, and weak when ≥ 0.80 – 0.89 of the BCI are above or below zero. Where a strong or very strong relationship was found between the area of symptoms and a covariate, we report the

385   percentage of the posterior predicted data that overlaps zero as calculated in R v. 3.5.2 (R

386   Core Team, 2018) using the *rollmean* function in the zoo package (Zeileis and Grothendieck,

387   2005).

388

389   Model validation was performed using root mean-square error (RMSE) calculated between

390   the predicted posterior mean values and the corresponding mean sampled area of

391   symptomatic juniper. The residuals of the top models were checked for spatial autocorrelation

392   using Moran's I statistic implemented using the *correlog* function in R package ncf v 1.2.8

393   (Bjornstad, 2019). Pairs of plots were divided into different distance bins at 100 m intervals

394   between 0 and the maximum distance between plot pairs for each site and the Moran's I value

395   was then calculated for each distance bin. One hundred paired distances were randomly

396   resampled per distance bin to assess Moran's I correlation significance (Appendix D).

397

398

3.0 Results

3.1 Prevalence of symptoms of *P. austrocedri* infection

Fifty-five percent of juniper surveyed in the Perthshire population showed symptoms compared to 28 % in the Lake District and 23 % in the Cairngorms populations, consistent with a possible earlier pathogen introduction in Perthshire (Fig. 3). Though quadrats containing no symptomatic juniper were found in all three populations, the mean area of symptomatic juniper found in Perthshire quadrats was 19 ± 20 m^2 out of a mean 34 ± 28 m^2 area of juniper, compared to a mean of 7 ± 11 m^2 of symptomatic juniper in quadrats from the Cairngorms population where the mean juniper cover found per quadrat was similar (33 ± 22 m^2). The mean area of juniper in the Lake District quadrats was higher (44 ± 27 m^2) with an intermediate mean area of symptomatic juniper (13 ± 18 m^2).

Because detection of symptomatic lesions is limited to above-ground live tissue, qPCR results are less reliable indicators of infection than symptoms. However, positive qPCR results were obtained across the full extent of each population giving confidence that site-wide observations of symptoms result from *P. austrocedri* infection (Appendix C).

The mean, standard deviation and range of covariates measured and tested in models across all three populations is shown in Table 2. The Perthshire population is characterised by fragmented juniper stands, only 35 % of quadrats contained more than 21 % juniper cover across 30 x 30 m compared to c. 70 % in the Lake District and Cairngorm populations where juniper grows in denser stands (Fig. 3, Table 2). Perthshire population quadrats were never further than 174 m from a river or drain, compared to 840 and 820 m in the Lake District and Cairngorms populations respectively (Fig. 3, Table 2). The Lake District population occupied the largest range of altitude (234 m compared to 132 m in Perthshire and 78 m in the Cairngorms) with up to 45° slopes compared to just 20° in both Scottish populations (Fig. 3;

427   Table 2). The Cairngorms population had the driest soil conditions across the quadrats (Table

428   2) with mean soil moisture of 33 % VWC, which is 27 % and 48 % drier than the mean soil

429   moisture found across Lake District and Perthshire quadrats respectively.

430
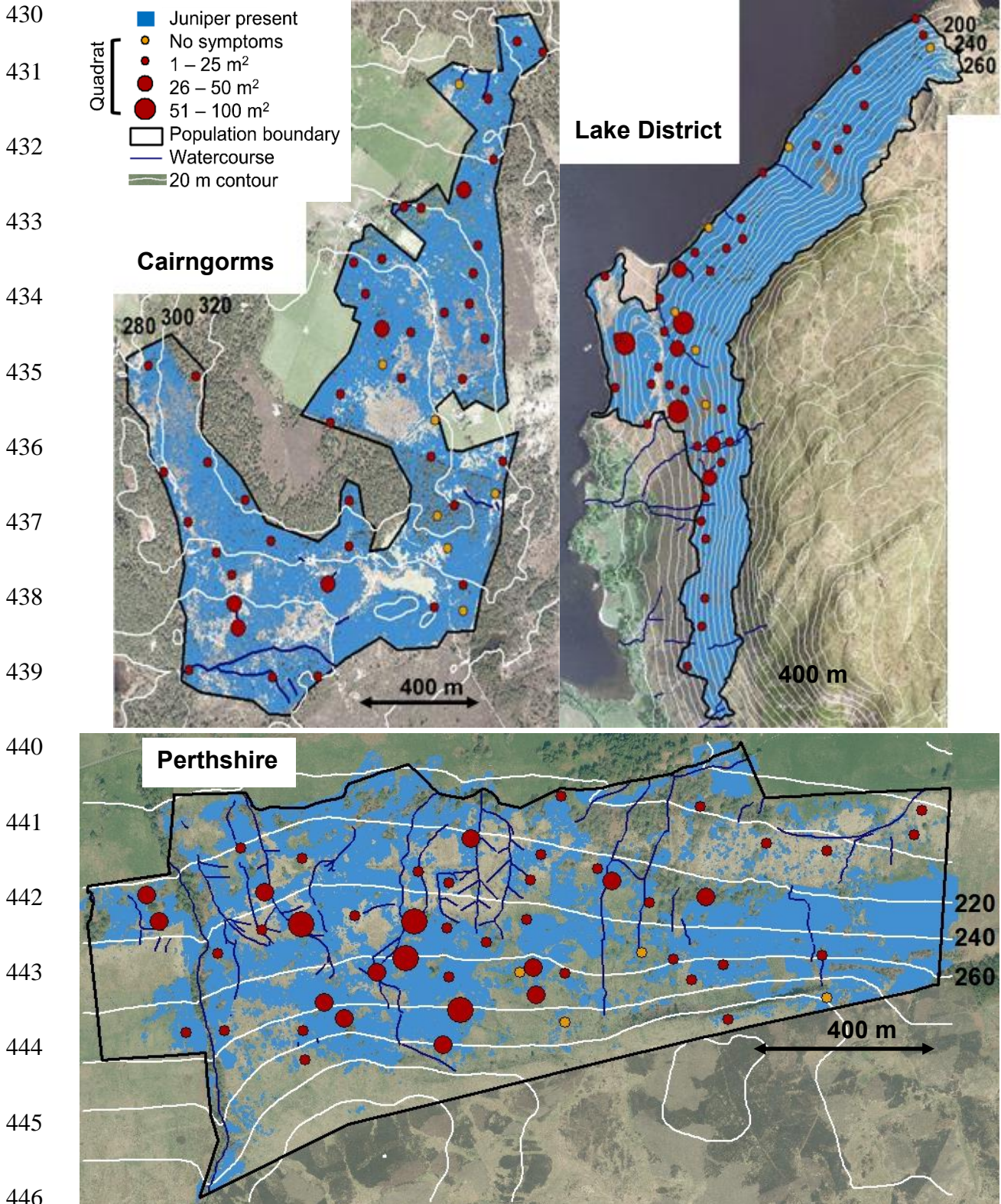
447   **Figure 3.** Map of surveyed juniper populations showing the distribution of juniper in relation

448   to the watercourse, altitude and slope covariates used to stratify sampling. The distribution

449   of samples, collected in 10 x 10 m quadrats, is shown with circles coloured orange where no

450   *P. austrocedri* symptoms were found and red where symptoms were present. Circle size

451   corresponds to categories representing the area of symptoms estimated in each quadrat.

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453   Perspectives™

454

Table 2. Comparison of surveyed juniper population covariate means ± 1 s.d., and ranges, measured from 10 x 10 m quadrats. P = Perthshire, LD = Lake District and C = Cairngorms study populations. Only numerical / binary coded variables included in the first stage of GLMM modelling (i.e. excluding species indicators) are displayed. Covariates not included in models for specific populations are greyed out.

Covariate	Mean ± s.d.per quadrat			Range per quadrat		
	P	LD	C	P	LD	C
Area of symptomatic juniper (m^2)	19 ± 20	13 ± 18	7 ± 11	0 - 79	0 - 70	0 - 45
Area of juniper (m^2)	34 ± 28	44 ± 27	33 ± 22	2 - 99	1 - 90	1 - 80
Juniper density (% quadrats nested in 30 x 30 m with > 21 % juniper cover)	35	72	70	NA	NA	NA
Area of juniper bearing berries (m^2)	10 ± 12	9 ± 15	4 ± 9	0 - 49	0 - 66	0 - 49
Area of herbivore damage (m^2)	2 ± 8	0 ± 1	0 ± 1	0 - 50	0 - 3	0 - 7
Mean soil moisture (% VWC)	45 ± 12	63 ± 17	33 ± 9	28 - 84	33 - 108	15 - 52
Watercourse proximity (m)	42 ± 37	144 ± 209	240 ± 193	1 - 174	0 - 840	2 – 820
Grazing activity (m)	16 ± 16	72 ± 68	31 ± 49	0 - 70	1 - 212	1 - 213
Altitude (m)	250 ± 30	248 ± 63	303 ± 21	182 - 314	150 - 384	256 - 334
Slope (°)	11 ± 4	32 ± 7	6 ± 4	5 - 23	15 - 45	1 – 20
Aspect (°)	158 ± 145	276 ± 53	174 ± 99	2 - 357	88 - 342	10 - 348

Nine vascular plant indicators were present in ≥ 10 quadrats in the Perthshire population, nine in the Lake District and ten in the Cairngorms (Table 3). The mix of indicators recorded highlights the difference in microsites occupied by the juniper study populations (Table 3). Of 42 target indicators, only one, V*accinium myrtillus*, was present at all three study populations

466   while quadrat frequency for the remaining indicators varied from 19 – 42 quadrats. Indicators

467   of drier, moderately fertile soils were only present in the Lake District quadrats, where no

468   indicators of high soil moisture and three indicators of highly acidic, infertile microsites were

469   also found. In contrast, there were two indicators of high soil moisture in the Cairngorms, six

470   for highly acidic, infertile soils (four present in > 40 of 50 quadrats) and no indicators of drier,

471   moderately fertile microsites (Table 3). Quadrats from Perthshire were dominated (both in

472   terms of species composition and prevalence across quadrats) by seven taxa indicating

473   moderate soil moisture (Table 3). However, although only one taxon (*Molinia caerulea*)

474   indicating high soil moisture was recorded, it was found in 21 of the 51 quadrats, suggesting

475   widespread, continuous waterlogging across the site.

476

477 **Table 3.** Number of 10 x 10 m quadrats containing vascular plant indicators (where present

478 in ≥ 10 quadrats). P = Perthshire, LD = Lake District, C = Cairngorms juniper populations.

479 Taxa are colour coded according to soil condition categories devised from Ellenberg reaction

480 (R), nitrogen (N) and moisture (F) values given in Hill, Preston, & Roy (2004).

Taxon	Soil condition		Population		
	R / N	F	P	LD	C
Vaccinium myrtillus	Highly acidic	Lower moisture	19	27	42
Dryopteris affinis		Lower moisture	30	22	
Oreopteris limbosperma		Lower moisture	22	10	
Rubus fruticosus agg.		Lower moisture	12	12	
Molinia caerulea		High moisture	21		15
Juncus conglomeratus		Lower moisture	19		10
Juncus effusus		Lower moisture	14		12
Calluna vulgaris	Highly acidic	Lower moisture		19	46
Betula pendula		Moderate moisture		15	15
Erica cinerea	Highly acidic	Moderate moisture		13	12
Dryopteris dilatata		Lower moisture	31		
Deschampsia cespitosa		Lower moisture	24		
Pteridium aquilinum		Moderate moisture		45	
Ilex aquifolium		Moderate moisture		10	
Vaccinium vitis-idaea	Highly acidic	Moderate moisture			42
Pinus sylvestris	Highly acidic	Lower moisture			31
Erica tetralix	Highly acidic	High moisture			13

Legend:
- Highly acidic (R = 2), low nitrogen (N = 1-2)
- Slightly acidic, moderately fertile (R = 3-5, N = 3-5)
- High moisture (F = 8-9)
- Moderate moisture (F = 6-7)
- Lower moisture (F = 5)

481

482

483 **3.2 Abiotic and biotic drivers of spatial variability in disease symptoms of**

484 ***P. austrocedri***

485

486 The full subset selection modelling resulted in one top model each containing abiotic and biotic

487 covariates for the Perthshire and Lake District populations, and two models for the Cairngorms

488 population (Table 4). All models included a strong relationship between increasing area of

489 *P. austrocedri* symptoms and a measure of increasing soil moisture (Table 5). When the area

490 of different vascular plant indicators was added to these models, this resulted in one top model

491 with improved fit for each population, with strong, positive relationships between increasing

492 symptoms and increasing soil moisture still included but additionally identifying taxa that aid

493   identification of microsites vulnerable to *P. austrocedri* infection in different habitats (Table 4).

494   Across all sites, models with abiotic and biotic covariates vastly outperformed the null model

495   with no covariates.

496

497   **Table 4.** Model results (DIC, RMSE, dispersion and list of covariates present) for each

498   surveyed population, comparing the null model with the top set of models produced before

499   and after addition of vascular plant indicators.

Juniper population	Model	DIC	RMSE	Dispersion	Covariates
Perthshire	Without indicators	167.45	43.89	0.48	Juniper density, berry bearing, herbivore damage, soil moisture, watercourse proximity, grazing activity, altitude, slope, soil type, habitat
	With indicators	134.96	42.59	0.45	As above with area of *Dryopteris dilatata*
	Null	301.98	37.04	0.55	N/A
Lake District	Without indicators	264.64	32.64	0.44	Juniper density, berry bearing, soil moisture, watercourse proximity, altitude, slope
	With indicators	208.84	22.99	0.42	As above with area of *Rubus fruticosus* agg.
	Null	301.77	41.54	0.57	N/A
Cairngorms	Without indicators	226.71	21.22	0.33	Juniper density, berry bearing, soil moisture, aspect, soil type, habitat
		225.40	21.38	0.33	Juniper density, berry bearing, soil moisture, slope, aspect, soil type, habitat
	With indicators	191.92	21.09	0.30	As above with area of *Erica tetralix*
	Null	293.63	43.92	0.58	N/A

500

501   The Cairngorms population models all predicted the distribution of symptoms with reasonable

502   accuracy, as the predicted area of symptoms was within 20 % of observed values (Table 4).

503   Addition of a plant indicator improved symptom prediction by 10 % in the Lake District to within

504   20 % of the observed values. However, predictive model performance was poorer for the

505   Perthshire population where the predicted area of symptomatic juniper was only within 40 %

506   of observed values from both the full subsets and plant indicator models (Table 4). No

507   evidence of overdispersion was found in the residuals of any of the top models (Table 4), nor

508   any consistent, positive, spatial autocorrelation (Appendix D).

509

510   The top model produced for the Perthshire population from the full subset selection included

511   all ten possible covariates (DIC 167.45) with only one strong relationship identified between

512   increasing area of symptomatic juniper and increasing soil moisture (Table 5, BCI = 0.70,

513   4.08). Model fit improved by 32 units (DIC 134.96) when area of *Dryopteris dilatata* was

514   included: a species of large fern that prefers moist, moderately acidic and fertile soils (Table

515   3). In this model, the strongest effect (BCI did not bridge zero) was increasing area of

516   *P. austrocedri* symptoms with increasing area of *D. dilatata* (BCI = 0.70, 4.08). The area of

517   symptoms also increased very strongly with increasing soil moisture (BCI = -0.04, 1.20) and

518   decreasing altitude (BCI = -1.72, 0.05), and strongly with decreasing area of herbivore damage

519   (BCI = -1.41, 0.05).

520

521   Six of the seven potential covariates collected across the Lake District population were

522   included in the top model prior to adding indicators (DIC 264.64) with area of *P. austrocedri*

523   symptoms again showing a strong response to soil moisture related covariates, with

524   symptoms strongly increasing with decreasing distance to watercourses (Table 6, BCI = -0.99,

525   0.08). Including brambles, *Rubus fruticosus* agg., improved the model fit by 56 DIC units

526   (Table 4). The BCI for the relationship between increasing area of symptoms and decreasing

527   distance to watercourses did not bridge zero (BCI = -1.26, -0.14) and the area of symptoms

528   strongly increased with decreasing area of *R. fruticosus* agg. (BCI = -4.19, 0.09), recorded in

529   12 of 46 quadrats.

530

531   Two top models were found for the Cairngorms population including six, and seven, of nine

532   possible covariates; including slope marginally improved model fit (DIC decreased from

533   226.71 to 225.40). In both models the BCI for soil moisture did not bridge zero, showing a very

534   strong relationship between increasing area of *P. austrocedri* symptoms with increasing soil

535   moisture (Table 7). The individual addition of ten indicator taxa to each of these models

536   resulted in one top model, which contained both slope and cross-leaved heath (*Erica tetralix*).

537   Model fit was improved by 35 and 33 DIC units compared to the full subset selection models

538   (Table 4). Increasing area of symptoms with increasing area of *E. tetralix* was the only strong

539   relationship present, for which the BCI did not bridge zero (BCI = 0.26, 1.28). The only indicator

540   for highly acidic, infertile microsites with high soil moisture is *E. tetralix* recorded in 13 of 50

541   quadrats (Table 3).

542

543   In addition to soil moisture directly measured within quadrats, top models for all populations

544   contained positive effects of juniper density and area of juniper bearing berries and negative

545   effects of slope on symptoms, despite differences in the range of variation sampled across

546   each population (Table 2). Soil and habitat (NVC community) types only included in the

547   Perthshire and Cairngorms models were also always present. None of these covariates

548   showed strong relationships with increasing area of symptoms but removing them resulted in

549   poorer model fit (i.e. the DIC increased by more than two units).

550

551

Table 5. Posterior estimates (mean, standard deviation (SD), 2.5 % and 97.5 % quantiles, and % that does

not bridge zero) for fixed effects included in the top model set for the Perthshire juniper population.

	Covariate	Mean	SD	2.5%	97.5%	% does not bridge zero
	Without indicator species (DIC = 167.45)					
	Soil moisture	0.59	0.31	0.01	1.21	100.00
	Altitude	-0.69	0.43	-1.57	0.13	92.71
	Herbivore damage	-0.39	0.29	-1.01	0.14	90.20
	Juniper density	0.29	0.25	-0.20	0.77	87.70
	Intercept	0.05	21.22	-41.61	41.67	50.17
	Berry bearing	0.21	0.25	-0.27	0.70	80.19
	Grazing activity	-0.17	0.26	-0.67	0.34	75.21
	Watercourse proximity	-0.03	0.31	-0.66	0.55	53.17
	Slope	-0.08	0.39	-0.84	0.68	57.69
Habitat	Mosaic	-0.70	15.82	-31.76	30.32	51.17
	Mires	-0.03	15.82	-31.09	31.01	50.17
	Juniper wood	0.80	15.83	-30.28	31.86	52.17
	Acidic grassland	-0.08	15.82	-31.14	30.96	50.17
Soil	Peaty gleys	0.22	14.15	-27.57	27.99	50.17
	Organic peaty gleys	0.37	14.15	-27.42	28.13	51.17
	Non-calcareous gleys	-2.65	14.19	-30.52	25.19	55.18
	Brown forest Balrownie	0.66	14.15	-27.13	28.43	51.17
	Brown forest Gourdie	1.40	14.16	-26.40	29.18	53.17
	With indicator species (DIC = 134.96)					
	Dryopteris dilatata	2.36	0.86	0.70	4.08	100.00
	Soil moisture	0.57	0.32	-0.04	1.20	95.21
	Altitude	-0.81	0.45	-1.72	0.05	95.19
	Herbivore damage	-0.65	0.37	-1.41	0.05	95.20
	Juniper density	0.25	0.52	-0.78	1.26	67.69
	Intercept	0.18	21.22	-41.48	41.81	50.17
	Berry bearing	0.06	0.26	-0.45	0.57	57.68
	Grazing activity	-0.19	0.26	-0.70	0.33	75.21
	Watercourse proximity	-0.18	0.33	-0.85	0.45	67.70
	Slope	0.07	0.41	-0.73	0.87	55.18
Habitat	Mosaic	-0.97	15.82	-32.03	30.06	52.18
	Mires	-0.18	15.82	-31.24	30.86	50.17
	Juniper wood	1.45	15.84	-29.65	32.52	53.17
	Acidic grassland	-0.30	15.82	-31.37	30.73	50.17
Soil	Peaty gleys	-0.14	14.15	-27.93	27.63	50.17
	Organic peaty gleys	0.50	14.15	-27.29	28.26	51.17
	Non-calcareous gleys	-3.05	14.19	-30.91	24.80	57.68
	Brown forest Balrownie	1.06	14.16	-26.73	28.83	52.67
	Brown forest Gourdie	1.62	14.16	-26.18	29.41	54.17

556 **Table 6.** Posterior estimates (mean, standard deviation (SD), 2.5 % and 97.5 % quantiles, and % that does

557 not bridge zero) for fixed effects included in the top model set for the Lake District juniper population.

Covariate	Mean	SD	2.5%	97.5%	% does not bridge zero
Without indicator species (DIC = 264.64)					
Intercept	-1.28	0.45	-2.19	-0.43	100.00
Watercourse proximity	-0.41	0.27	-0.99	0.09	92.70
Soil moisture	0.09	0.25	-0.41	0.58	62.69
Juniper density	0.17	0.50	-0.78	1.17	62.67
Berry bearing	0.00	0.22	-0.45	0.41	52.18
Altitude	0.22	0.24	-0.24	0.70	80.19
Slope	-0.26	0.28	-0.83	0.29	80.20
With indicator species (DIC = 208.84)					
Intercept	-1.29	0.43	-2.16	-0.47	100.00
Watercourse proximity	-0.66	0.29	-1.26	-0.14	100.00
Rubus fruticosus agg.	-1.81	1.09	-4.19	0.09	95.23
Soil moisture	0.00	0.25	-0.51	0.48	50.17
Juniper density	-0.21	0.55	-1.27	0.88	65.19
Berry bearing	-0.04	0.22	-0.49	0.36	55.18
Altitude	-0.24	0.30	-0.82	0.35	77.68
Slope	0.06	0.29	-0.53	0.62	57.70

558

Table 7. Posterior estimates (mean, standard deviation (SD), 2.5 % and 97.5 % quantiles, and % that does not bridge zero) for fixed effects included in the top model set for the Cairngorms juniper population.

	Covariate	Mean	SD	2.5%	97.5%	% does not bridge zero
	Without indicator species (DIC = 226.71)					
	Soil moisture	0.54	0.22	0.09	0.98	100.00
	Berry bearing	0.18	0.18	-0.18	0.53	82.68
	Intercept	-1.15	27.39	-54.93	52.58	51.17
	Juniper density	-0.18	0.44	-1.01	0.70	65.20
	Aspect	-0.02	0.21	-0.45	0.39	54.17
Habitat	Scots pine woodland	0.64	15.82	-30.43	31.67	51.17
	Heath	0.19	15.82	-30.86	31.22	50.17
	Coniferous plantation	-0.73	15.84	-31.83	30.34	51.17
	Acidic grassland	-0.09	15.82	-31.16	30.95	50.17
Soil	Humus-iron podzols; gleys	0.46	22.36	-43.44	44.33	50.17
	Humus-iron podzols; brown forest	-0.46	22.36	-44.37	43.40	50.17
	Without indicator species (DIC = 225.40)					
	Soil moisture	0.57	0.23	0.12	1.01	100.00
	Berry bearing	0.17	0.18	-0.18	0.52	82.68
	Intercept	-1.08	27.39	-54.85	52.66	51.17
	Juniper density	-0.24	0.44	-1.09	0.65	70.19
	Slope	0.13	0.22	-0.31	0.54	72.69
	Aspect	-0.07	0.23	-0.52	0.37	60.17
Habitat	Scots pine woodland	0.67	15.82	-30.39	31.71	51.17
	Heath	0.17	15.82	-30.88	31.20	50.17
	Coniferous plantation	-0.76	15.84	-31.86	30.31	51.17
	Acidic grassland	-0.07	15.82	-31.14	30.97	50.17
Soil	Humus-iron podzols; gleys	0.52	22.36	-43.39	44.38	50.17
	Humus-iron podzols; brown forest	-0.52	22.36	-44.42	43.35	50.17
	With indicator species (DIC = 191.92)					
	Erica tetralix	0.73	0.26	0.26	1.28	100.00
	Soil moisture	0.19	0.27	-0.36	0.71	75.21
	Berry bearing	0.15	0.18	-0.22	0.50	77.72
	Intercept	-1.72	27.39	-55.50	52.02	52.18
	Juniper density	-0.02	0.46	-0.88	0.91	52.68
	Slope	0.04	0.21	-0.39	0.45	57.70
	Aspect	0.05	0.23	-0.42	0.50	57.69
Habitat	Scots pine woodland	1.12	15.82	-29.95	32.16	52.67
	Heath	0.47	15.82	-30.59	31.50	51.17
	Coniferous plantation	-2.26	15.85	-33.39	28.84	55.18
	Acidic grassland	0.69	15.83	-30.39	31.73	51.17
Soil	Humus-iron podzols; gleys	0.30	22.36	-43.60	44.17	50.17
	Humus-iron podzols; brown forest	-0.30	22.36	-44.21	43.56	50.17

4.0 Discussion

Our study provides the first evidence from the northern hemisphere that, out of the wide range of potential abiotic and biotic drivers considered, and despite differences in the range of conditions, geographic location and infection intensity occupied by study populations, soil moisture is the best predictor of *P. austrocedri* symptom distribution in juniper at population scale. This is likely to result from the pathogen's dependence on soil moisture for zoospore dispersal (Green et al., 2015; Greslebin et al., 2007).

Introductions of non-native *Phytophthora* taxa have been reported from 176 countries across a wide range of climatic zones (Barwell et al., in review). Water availability is commonly identified as an important driver of terrestrial *Phytophthora* distributions at a range of scales. Globally, functional and species diversity increases with precipitation (Redondo et al., 2018). Landscape scale examples include increased incidence of *P. lateralis* in Port Orford cedar with increasing creek drainage area (Jules et al., 2008), and increased *P. ramorum* infection of tanoak with increasing stream proximity (Peterson et al., 2014). In individual trees, the length of *P. cinnamomi* lesions increase in Jarrah with increasing precipitation (Bunny et al., 1995) because water is required to stimulate sporangial formation, trigger zoospore release and enable dispersal (Hardham, 2005).

The importance of soil moisture as a driver of *P. austrocedri* infection in juniper populations is likely to vary between sites with different soil types and hydrology. Area of symptoms increased very strongly with point sampled soil moisture in both the Cairngorms and Perthshire populations, which grow on deep soils formed from glacial till, with pockets of gleying, that retain a high volume of soil moisture throughout the year. This is consistent with population level studies of Chilean cedar where *P. austrocedri* infection increases with soil waterlogging caused by high clay content (La Manna and Rajchenberg, 2004a) or features restricting water permeability (La Manna & Rajchenberg, 2004b).

590

591   Though microsite soil moisture is partly a function of soil type, explicitly including soil type in

592   the Cairngorms and Perthshire models always improved model performance but never

593   strongly predicted the area of symptoms, probably because the available data for soil type

594   were too coarse in spatial resolution (250 m) to capture microsite variation.

595

596   Spatial variation in area of symptoms was also linked to soil moisture in the Lake District

597   populations but here the strongest association was between symptoms and decreasing

598   proximity to watercourses rather than point sampled soil moisture. Given the steep site

599   topography and freely draining, shallow, sandy soil type, it is likely that juniper in this

600   population is only exposed to long term waterlogging where it grows adjacent to watercourses.

601   Stands of Chilean cedar growing in comparable (freely draining, volcanic) soils also

602   demonstrate increased infection with increasing proximity to watercourses (Calı´, 1996; La

603   Manna & Rajchenberg, 2004a).

604

605   A key challenge for investigating field scale drivers of disease is obtaining data at a suitably

606   detailed spatial resolution. Modelling microsite soil moisture patterns was prohibited by the

607   availability of fine scale data on hydrological processes (such as precipitation, potential

608   evaporation and runoff generation). Topographic wetness index (TWI), calculated from site

609   topography and watercourse networks, is commonly used as a proxy for soil moisture. In the

610   absence of variability in slope and altitude gradients, the calculation tends to overpredict

611   differences (Grabs et al., 2009) and did not yield an informative distribution map for the

612   Cairngorms juniper population (results not shown). It also assumes uniform soil properties and

613   does not account for complex bedrock surfaces, invalidating the data derived for the Lake

614   District population (results not shown) (Kopecký and Čížková, 2010). Measuring soil moisture

615   directly from stratified quadrats as % volumetric water content captured variation in water table

616   heights but only represents conditions at a single point in time and differences between

617   microsites may be exaggerated by rainfall events that occurred during the sampling period.

618

619   We introduced the area of vascular plant indicators, selected to represent a range of soil

620   moisture preferences, to test whether such indicators capture longer term water table levels

621   than short term soil moisture field observations, or other fine scale soil attributes affecting

622   transmission and disease such as pH and nitrogen content. This was successful in the

623   Cairngorms, where adding area of cross-leaved heath, *Erica tetralix*, resulted in a very strong,

624   positive, relationship with increasing area of symptoms (Δ DIC = 33), corroborating the

625   response with increasing soil moisture as cross-leaved heath grows in constantly wet but not

626   inundated soils (Hill et al., 2004). These findings suggest microsites most vulnerable to

627   *P. austrocedri* infection could be identified using indicator species with distinctive soil moisture

628   preferences.

629

630   Uncoupling relationships between vegetative cover and soil moisture from other factors such

631   as interspecific competition and land management practices proved difficult for the remaining

632   populations. The best Perthshire model was obtained by adding area of broad-buckler fern,

633   *Dryopteris dilatata,* which increased with increasing area of symptoms (Δ DIC = 32, BCI did

634   not bridge zero). This correlation is more likely to result from the fern preferentially colonising

635   dead juniper following *P. austrocedri* induced mortality than suggest a higher percentage of

636   symptoms occurred in the drier soil conditions favoured by the fern (Table 3) (Hill et al., 2004;

637   Rünk et al., 2012).

638

639   Adding area of brambles (*Rubus fruticosus* agg.) yielded the greatest improvement in Lake

640   District model performance (Δ DIC = 56) and showed a strong (BCI 0.90 – 0.94), negative

641   relationship with area of symptoms. While four other short-listed taxa for the Lake District also

642   indicate moderate soil moisture conditions, only brambles indicate neutral, moderately fertile

643   soils (Hill et al., 2004). When considered alongside the relationship found in the Cairngorms

644   model between increased symptoms and area of cross-leaved heath, itself an indicator of

645   highly acidic soils (pH 1-3) (Hill et al., 2004), and increasing infection of Chilean cedar in soils

646 containing low levels of alkaline sodium fluoride (NaF) (La Manna et al., 2012) this might

647 suggest *P. austrocedri* occurs more frequently in acidic soils.

648

649 However, brambles are also highly unpalatable to herbivores, which preferentially avoid eating

650 them (Bee et al., 2009). Thus increasing symptoms in the absence of brambles might point to

651 herbivore mediated dispersal of inoculum. A cost distance analysis comparing three cattle

652 grazing scenarios (no grazing, roaming with intermittent barriers such as steep slopes and

653 free roaming) found total area and dispersion of *P. austrocedri* was higher in Chilean cedar

654 forests with unrestricted grazing (La Manna et al., 2013). Similarly, infection of Port Orford

655 cedar with *P. lateralis* increases along wildlife (including bear) trails that "fill-in" uninfected sites

656 following disease establishment around creek edges (Jules et al., 2008).

657

658 Although our results cannot distinguish between the effects of pH and passive movement of

659 inoculum on herbivore hooves, they do clearly indicate that direct herbivore damage does not

660 increase infection. Herbivore damage was absent from the Cairngorms and Lake District

661 models and though present in Perthshire, symptoms decreased with increasing herbivory (BCI

662 0.90 – 0.94).

663

664 Slope was present in all top models, describing some of the residual variance as a weak,

665 negative relationship with area of symptoms, even in the limited range occupied by the

666 Cairngorms population (Table 2). Positive relationships with area of berry-bearing juniper were

667 also present in all top models and the weak response could indicate female juniper without

668 berries were missed by the survey. Similarly, juniper density was present in all top models

669 showing a weakly positive relationship with symptoms. The intensity of field scale infections

670 of Chilean cedar with *P. austrocedri,* and white oak (*Quercus alba*) with the similarly soil-borne

671 *P. cinnamomi*, were found to increase with increasing host density, suggesting our

672 characterisation of juniper density as ± 20 % cover in 30 x 30 m was too simplistic. This

673   highlights the need for further exploration of the role of host connectivity in facilitating *P.*

674   *austrocedri* spread in future research across a range of different spatial scales.

675

676   Models produced for Perthshire had the lowest accuracy (RMSE 42.59) despite containing the

677   largest number of covariates (11) meaning those included poorly account for the spatial

678   distribution of symptoms. The watercourses mapped for Perthshire include herringbone

679   drainage channels opened in 2011 (Taylor, H., 2019, pers. comm. 1 Nov) after juniper stands

680   started to decline in the late 1990's (Broome et al., 2008) but before isolation of *P. austrocedri*

681   in 2012 (Green et al., 2015). The drainage work may have inadvertently distributed the

682   pathogen across the site by disturbing watercourses and moving contaminated soil in tyre

683   treads. It is unclear if the very strong increase in area of symptoms with decreasing altitude

684   (BCI > 0.95) reflects the location where the pathogen was first introduced or the drainage

685   activity that was concentrated between 220 – 250 m of the 180 – 310 m altitudinal range (Fig.

686   3, Table 2) causing the pathogen to spread further and faster than dispersal through soil

687   moisture alone. This highlights the importance of capturing and integrating the spatial

688   arrangement and intensity of management actions into investigations of drivers of site level

689   variation in plant disease impacts (Fernández-habas et al., 2019).

690

691   **5.0 Conclusion**

692

693   Our study provides valuable insights about how conditions favouring newly invading plant

694   diseases can be delineated by collecting and modelling spatially explicit data at field scale.

695   Directly measuring covariates in the field in sites of different disease status, across key

696   environmental gradients using a carefully designed sampling strategy, enabled us to explore

697   a wide range of potential drivers, identify those with the most explanatory power and make

698   comparisons between populations occupying different ranges along each gradient. In addition,

699   our findings can be used by practitioners to target management interventions that match the

700   inherent scale of pathogen spread.

701

702 Interventions to manage juniper populations at local level such as drainage, grazing
703 exclosures and seedling propagation require significant resources (Forestry Commission
704 Scotland, 2006). The introduction of *P. austrocedri* to the UK risks this investment and the
705 longevity of these actions if measures to prevent disease introduction and establishment are
706 not undertaken.

707

708 Our results suggest *P. austrocedri* is most likely to infect juniper where it occupies wet
709 microsites - in the UK and across its global range. Surveys by plant health inspectors to detect
710 *P. austrocedri* should be prioritised for populations and stands occupying consistently wet
711 microsites, identification of which could be aided by plant species indicators. While improved
712 biosecurity measures, such as cleaning all machinery, equipment and footwear before and
713 after accessing juniper sites (irrespective of known disease status), will reduce the risk of
714 pathogen introduction and spread (Department for Environment Food & Rural Affairs, 2014b),
715 our results suggest activities that disturb watercourses or wet soils (such as drainage and
716 infrastructure installation) pose the highest risk of collecting and transporting *P. austrocedri*
717 oospores and zoospores.

718

719 Our findings further support recommendations published by the UK Department for
720 Environment, Food and Rural Affairs in the Juniper Management Guidelines to divert footpaths
721 away from waterlogged areas and only plant juniper in drier microsites, giving full
722 consideration to the vulnerability of existing populations, suspected disease status, soil type
723 and the watercourse network (Department for Environment Food & Rural Affairs, 2017).
724 Continued emphasis on improving the quality and extent of populations in drier soil conditions
725 by regulating grazing levels, curtailing stand removal and creating spaces for natural
726 regeneration (Broome et al., 2017; Wilkins and Duckworth, 2011) will help maximise resilience
727 of native juniper populations to this new disease threat.

728

729 Acknowledgements

740

741 Appendix A. Mapping juniper study populations

742 Appendix B. Associate species target list

743 Appendix C. Distribution of *P. austrocedri* qPCR results

744 Appendix D. Additional information for model selection

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