Habitat mediates coevolved but not novel species interactions

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Abstract

On-going recovery of native predators has the potential to alter species interactions, with community and ecosystem wide implications. We estimated co-occurrence of three species of conservation and management interest from a multi-species citizen science camera trap survey. We demonstrate fundamental differences in novel and co-evolved predator-prey interactions that are mediated by habitat. Specifically, we demonstrate that anthropogenic habitat modification had no influence on the expansion of the recovering native pine marten in Ireland, nor does it affect the predator's suppressive influence on an invasive prey species, the grey squirrel. In contrast, the direction of the interaction between the pine marten and a native prey species, the red squirrel, is dependent on habitat. Pine martens had a positive influence on red squirrel occurrence at a landscape scale, especially in native broadleaved woodlands. However, in areas dominated by non-native conifer plantations, the pine marten reduced red squirrel occurrence. These findings suggest that following the recovery of a native predator, the benefits of competitive release are spatially structured and habitat specific. The potential for past and future landscape modification to alter established interactions between predators and prey has global implications in the context of the on-going recovery of predator populations in human-modified landscapes.

Key words: habitat complexity; interspecific interactions, predator-prey interactions, occupancy, native predator, invasive species, native prey, predator-prey, multi-species models

Introduction

Determining the mechanisms underpinning species occurrence and how perturbations can alter species co-existence and biodiversity patterns is a fundamental goal in ecology. Although typically viewed as pairwise, species interactions are embedded within complex multi-trophic networks. Outcomes of interactions cannot be understood without considering the indirect interactions resultant from the presence of extra-pair predators, pathogens, or prey (Holt & Bonsall, 2017), and simplifying systems to pairwise interactions necessarily omits important complexities posed by real

48   world systems (Geary *et al.* 2020). The planetary-scale influence of human activity has brought into

49   sharp focus the need to predict how whole communities respond to multiple anthropogenically-driven

50   stressors. This requires an explicit focus not only on how specific species respond to change, but also

51   how interactions and interdependencies among species are affected by changing environments.

52   Invasive species have been associated with increased vertebrate extinctions more than any

53   other factor (Bellard *et al.* 2016; Seebens *et al.* 2017) and provide compelling examples of how novel

54   indirect interactions can alter established species interactions, with potential outcomes ranging from

55   complete exclusion and species extirpation to fugitive co-existence (Bonsall & Hassel, 1997). For

56   example, in Great Britain and Ireland, landscape scale declines and extirpation of native red squirrels

57   (*Sciurus vulgaris)* results from disease-mediated competition with invasive North American grey

58   squirrels (*Sciurus carolinensis,* Tompkins *et al.* 2003), the reservoir host of the squirrelpox virus, a fatal

59   pathogen to the native red squirrel.

60   Despite populations being globally depleted, far below natural levels due to human

61   persecution, certain native predator populations, both large and small bodied, are recovering in

62   response to protective legislation and conservation efforts (Chapron *et al.* 2014; Sainsbury *et al.* 2019).

63   Native predators are returning to landscapes that have been greatly altered since their extirpation,

64   both through human modification of habitats as well as through the introduction of non-native

65   species. Emerging research suggests that native predator recovery has the potential to benefit native

66   prey populations indirectly through biological control of naive invasive prey / competitor species over

67   spatial scales meaningful to the conservation and management of wildlife populations (Louette, 2012;

68   Sheehy & Lawton, 2018; Twining *et al.* 2021). However, the generality of such predictions remains

69   equivocal due to the presence of indirect interactions between species, and the heterogeneity

70   exhibited by most landscapes that novel interactions occur in.

71   Heterogeneity in the structure and configuration of habitat can mediate predator-prey

72   interactions through its influence on the density and type of functional response exhibited by

73   predators (Dunn & Hovel, 2020; Twining *et al.* 2020a). Habitat is a determining factor in the hunting

74   capacity of predators, and the ability of prey to detect, avoid, or escape predators (Schmitz *et al.* 2004;

75   2017). Changes to habitat complexity through human modification could hypothetically alter the

76   outcome of species interactions through altering the functional response, attack rate, and handling

77   time of predators (Mocq *et al.* 2021). Thus, extrapolating inference on species interactions from one

78   position on a spatial or environmental gradient to another, where the densities or functional

79   responses of species are different, could lead to unexpected outcomes.

80   Despite the relevance of habitat in mediating indirect species interactions in the face of ever-

81   increasing global change, empirically demonstrating the influence of habitat on predator-prey

82   interactions is quantitatively challenging, particularly when focusing on wide ranging, low density, and

83   elusive vertebrate predators. Manipulative experiments at characteristic spatial scales are typically

84   implausible within the strictures of research funding and longevity, and thus, evidence is often

85   observational, based on natural landscape scale investigations such as those presented by

86   asynchronous predator recovery dynamics (e.g. Estes & Palmisano, 1974; Sheehy *et al.* 2018). The

87   standard of evidence required to inform policy is necessarily high and, thus, appropriate data

88   collection and associated modelling techniques that, for example, explicitly account for species

89   interactions and imperfect detection are essential.

90   The difficulties of making robust predictions about novel species interactions in an applied

91   context are compounded in landscapes which are modified by human activity and display pronounced

92   spatial heterogeneity, as is typical of contemporary landscapes across the globe. Without sufficient

93   understanding of the role of habitat in mediating predator-prey interactions, conservation policies

94   focused on ecological recovery and restoration, including the reintroduction of predator populations,

95   could result in unintended, adverse consequences for native prey. The consequences of failing to

96   predict novel species interactions are exemplified by numerous ill-fated attempts to introduce non-

97   native generalist predators as biological control agents to island ecosystems, leading to disastrous

98   impacts on naïve native prey species, often resulting in severe decline, extirpation, or extinction (King,

99   2019).

100   Here, we investigate the role of habitat in mediating the impacts of the recovery of a native

101   predator, the pine marten, on native red and invasive grey squirrels in Ireland; two species that are

102   linked through competition and pathogen-mediated apparent competition. We use multi-species

103   occupancy models applied to a dataset collected on three occasions over five years from 2015 to 2020

104   to examine whether species co-occurrences and interactions differ along environmental and spatial

105   gradients. We expect 1) the impact of the pine marten on grey squirrels to be consistent regardless

106   of local habitat due to the naivety of the invasive species to the native predator (Twining *et al.* 2020b);

107   2) the interactions between the pine marten and the red squirrel to be dynamic and dependant on

108   habitat, with more structurally complex and diverse habitats resulting in lower impacts on the native

109   prey species; and 3) the competitively linked native-invasive prey species interactions to be mediated

110   by habitat (Slade *et al.* 2021).

Methods

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Multi-species surveys

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113   A survey spanning a five-year period documenting the occurrence of pine marten and grey and red

114   squirrel was conducted throughout Northern Ireland between 2015 and 2020. The survey was

115   repeated three times, initially in 2015 with 332 sites surveyed by citizen scientists provided with

116   camera traps and trained for their consistent use (for full Methodology see Twining *et al.* 2021). This

117   survey was repeated in 2018 with 172 sites, and in 2020 with 207 sites using the same methods. At

118   each site, a single camera trap was deployed at a point randomly selected by the surveyor within an

119   independent 1km grid. Cameras were installed at head height on a tree overlooking a wooden squirrel

120   feeder erected on an adjacent tree. Feeders were baited with peanuts and sunflower seeds in 2015

121   and 2020, but just sunflower seeds in 2018. Cameras were set to take three images per trigger with a

122   1s reset time. Camera traps were deployed for 7 - 14 days at each location (mean = 10.3 days) after

123 which cameras were retrieved for data extraction and species identification. Detection records were

124 created for each species over the recording period. Only one detection was allowed per species for

125 each 24-hr period of sampling to ensure independence. Any variation in survey effort (duration of

126 camera deployment) was recorded and accounted for during analysis. A map of the sampling sites,

127 and the makes and models of the cameras and the settings used in this study are reported in Appendix

128 3.

Occupancy modelling

130 Our focus is on estimating the co-occurrence of pine marten, red squirrel, and grey squirrel, which we

131 do using a hierarchical modelling framework, specifically, the recently developed multi-species

132 occupancy model for interacting species (Rota *et al.* 2016). This approach extends the standard

133 occupancy model (Mackenzie *et al.* 2002), that accounts for imperfect detection using a repeat visit

134 sampling design, to include an explicit component for how species interact, including modelling these

135 interactions as a function of covariates.

136 To explain variation in marginal occupancy rates (the occupancy of a species in the absence of

137 the effects of other species) and conditional occupancy rates (the occupancy of a species conditional

138 on the presence of another species), we considered six landscape variables that had previously been

139 observed to influence the three species (Flaherty & Lawton, 2019; Twining *et al.* 2021). These variables

140 were related to forest composition (% broadleaf woodland; % coniferous plantation), human

141 disturbance (number of people per km^2; % urban and suburban land cover) and non-forested and

142 aquatic habitat conditions (% heath; river and stream density). For details on the mean and variation

143 of covariates see Table S3.1. We controlled for potential geographic variation in occupancy by

144 including latitude and longitude (and their interaction) of camera trap sites as covariates. We divided

145 Northern Ireland into 14,402 1km^2 grid squares and each covariate was summarised at the 1km^2 scale.

146 A 1km^2 resolution was selected for two reasons: i) it approximates the home range size of a female

147 pine marten, being the largest of the three species (Twining *et al.* 2020a); and ii) it is a typical intuitive

148   map scale frequently used at regional and national scales. It is true that squirrels have smaller home

149   ranges (e.g. Andrén & Delin, 1994), but this was deemed less important as one of the fundamental

150   assumptions of the models used is that of independence. Therefore, by ensuring independence of the

151   species with the largest range, then independence is met for the other two species with smaller home

152   ranges. The values for each camera site were the values for the grid within which they occurred. To

153   explain variation in detectability, we considered three observation covariates. These were bait type

154   (sunflower seeds and peanuts in 2015 and 2020 vs. sunflower seeds only in 2018), a behavioural

155   response (1 if the focal species had been observed previously, 0 if not), and the number of sampling

156   occasions (ranging from 7-14, where a sampling occasion is one day). All continuous covariates were

157   scaled and standardised to have unit variance and a mean of zero, and, based on variance inflation

158   factors, there was no evidence of collinearity between any covariates (e.g. Zuur et al. 2009).

159   The core of the co-occurrence model is a state model for estimating latent state of a site (ψ),

160   where, if s is the number of species, the possible states are the (2^s-1) possible combinations of species.

161   For example, if there are two species, the possible states are $Z = ([00], [01], [10,], [11])$, and ψ_i is

162   the probability of being in the $i = 1, 2, 3, 4th$ state. Here, the ψ's are assumed to be multivariate

163   Bernoulli random variables and can also be modelled as a function of covariates. Importantly, each

164   state is first order if occupied by single species, second order if occupied by two species, and so on up

165   to order S, and each combination can be modelled using standard linear modelling. This means that

166   covariate models can be constructed for species-specific occupancy (first order) and for pairwise

167   interactions (second order) to investigate how species occupancy responds to interspecific (other

168   species) and environmental factors. For example, using this approach, Rota *et al*. (2016) found that

169   coyote (*Canis latrans)* occupancy increased with disturbance in the absence of bobcats (*Lynx rufus)*,

170   but decreased when bobcat was present, highlighting how species interactions can vary in response

171   to environmental gradients.

172   Here we specify first order models for each species based on results from single species

173   occupancy models. For each species, we considered all additive combinations of the eight occupancy

174   covariates to describe variation in occupancy (see above), and all additive combinations of the three

175   observation covariates and six landscape covariates to explain variation in detection probability (see

176   above). We note also that these data were collected across three primary survey periods (2015, 2018,

177   2020), and because the focus was not in estimating colonisation-extinction dynamics (which would be

178   unadvisable with only three years of data), we used a "stacked" design whereby each site-year

179   combination was treated as a distinct site. As such, we include a year effect in all models to account

180   for any non-independence. Temporal replication between years was limited (see Fig S3.1), thus it was

181   not possible or necessary to fit a site effect on the models. Using the secondary stage approach (Morin

182   et al. 2020), we first used AIC to find the most parsimonious covariate combination for detection

183   probability keeping occupancy constant (i.e., $\psi(.)$), and then, keeping detection constant (i.e., $p(.)$),

184   used AIC to determine the most parsimonious covariate combination for occupancy. Parameter

185   redundancy was evaluated following Arnold (2010) such that the parameters that were included but

186   resulted in less than -2 AIC units from the next best model were considered uninformative and

187   removed. The single species analysis was conducted in R version 3.6 (R Core Team, 2020) using the

188   package "*unmarked*" for model fitting (function *occu()*) and goodness of fit testing (*parboot()*), the

189   latter showing no issues with model fit (Fiske & Chandler, 2011), and AIC-based model ranking was

190   conducted using the package "*MuMin*".

191   The combination of the AIC-best models for each model component was used to specify the

192   species-specific (i.e., first order) models in the multi-species model (see Table 1). Specifically, the top

193   pine marten (PM) model included %coniferous plantation, %broadleaf forest, %urban and latitude,

194   with detection varying by the bait used, the occasion number, a behavioural response, and

195   %coniferous plantation. The top red squirrel (RS) model included %coniferous plantation, %urban and

196   latitude, with detection varying by the human population density, a behavioural response, and

197   %broadleaf forest. The top grey squirrel (GS) model included %coniferous plantation, %broadleaf

198   forest, %urban and both latitude and longitude, with detection varying by the bait used, a behavioural

199   response, the %broadleaf, %urban and the stream and river density.

200   The multi-species model allows formal investigation of how habitat mediates species

201   interactions by specifying models for multiple pairwise interactions for each species pair

202   simultaneously. Specifically, we were interested in examining how the probability of two species

203   cooccurring at the same site was mediated by the two main habitat types for each of these forest

204   dwelling species: broadleaf forest native woodland (BL) and non-native coniferous timber plantations

205   (CP, Twining *et al.* 2021). For each species we considered three possible second order scenarios; 1)

206   the *independence* hypothesis that the species occur independently of one another as a function of

207   habitat covariates only; 2) the *constant* hypothesis that species exhibit constant pairwise dependence

208   that do not vary across space; and 3) the *habitat* hypothesis that co-occurrence between the species

209   varies as a function of habitat. We constructed a candidate model set with second order models that

210   represent the possible combinations of the three hypotheses for each species, resulting in a total of

211   27 models. Following the 'natural parameter' terminology of Rota *et al.* (2016), parameters f_1, f_2, and

212   f_3 are the natural scale first order occupancy probabilities for pine marten, red squirrel, and grey

213   squirrel, and are described in the text above (see also Table 1). The second order models that describe

214   how the interaction between species *i* and *j*, $f_{i,j}$ depend on the hypothesis and are:

217    $$f_{ij} = 0$$

218    $$f_{ij} = \beta_0$$

219    $$f_{ij} = \beta_0 + \beta_1 \text{BL} + \beta_2 \text{CP}$$

215   for the *independence*, *constant*, and *habitat* hypothesis, respectively. Here, β_0 is the intercept and β_1

216   and β_2 are estimated effects of broadleaf and coniferous covariates, respectively.

220   We fit the multi-species occupancy models in R version 3.6 (R Core Team, 2020) using the

221   package "*unmarked*" and the function *occuMulti()* for model fitting (Fiske & Chandler, 2011). Given

222   our multiple competing hypotheses, we used "*AICcmodavg*" for AIC based model ranking (Mazerolle,

223 2020), models with ΔAIC values <5 when compared with the most parsimonious model are presented

224 (Morin *et al.* 2020). Akaike weights were used to determine the relative importance of independent

225 variables across models. Likelihood ratio tests were used to compare models representing the

226 hypothesis tested by comparing the difference in deviance between pairs of models to the critical

227 value of the χ^2 square distribution.

Results

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230 Total effort for the three surveys over the five-year period was 7,286 sampling days (24-hr periods)

231 across 712 sites (2015 = 2,631 at 332 sites; 2018 = 1,845 at 173 sites; 2020 = 2,881 at 207 sites). Over

232 the course of the 5-years there was a total of 2,452 independent detections of the three focal species,

233 composed of 830 pine marten detections (2015, n = 214; 2018, n = 89, 2020 n = 527), 963 red squirrel

234 detections (2015, n = 210; 2018, n = 263, 2020, n = 490), and 659 grey squirrel detections (2015, n =

235 332; 2018, n = 113; 2020, n = 214).

236 Using AIC to compare the multi-species models, we found clear evidence of interspecific dependence

237 among all three species, and habitat mediation of co-evolved but not novel predator-prey interactions

238 (Table 2). Specifically, the top model supported the hypotheses that the probability of co-evolved pine

239 marten and red squirrel co-occurrence depended on habitat, but that novel interactions between the

240 native-invasive pairs (pine marten-grey squirrel, and red squirrel-grey squirrel) were constant, i.e.,

241 were not mediated by habitat. All subsequent results are from the top model, apart from when

242 explicitly stated otherwise. All values reported are mean estimates ± standard error.

243 The probability of occupancy of both the pine marten and the red squirrel considerably increased

244 across the five-year period (Appendix 2. Fig S1; pine marten from 0.27 ± 0.09 to 0.53 ± 0.11 and red

245 squirrel from 0.27 ± 0.07 to 0.38 ± 0.05). The opposite was true for grey squirrels, their occupancy

246 declined substantially from 0.23 ± 0.06 to 0.11 ± 0.04. Marginal probabilities of occupancy show that

247 pine marten occurrence was positively associated with both broadleaf and mixed forests (β = 0.27 ±

248   0.15) and coniferous plantations (β = 0.96 ± 0.27), and negatively associated with urban and suburban

249   areas (β = -0.30 ± 0.17; Fig. 1). Red squirrels showed a similar pattern: occupancy was positively

250   associated with coniferous plantations (β = 0.50 ± 0.22) and negatively associated with urban and

251   suburban areas (β = 0.32 ± 0.15, Fig. 1). Grey squirrel occurrence was positively related to urban and

252   suburban areas (β = 0.44 ± 0.12) and broadleaf woodland (β = 0.43 ± 0.12), but negatively associated

253   with conifer plantations (β = -0.56 ± 0.22, Fig. 1).

254   Spatially explicit predictions of occupancy over the five years show the rapid recovery of the

255   pine marten, with the species now occurring throughout the region, although occupancy remains

256   highest in the south-west and in forested areas (Fig. 2). Red squirrels have undergone a similar

257   recovery in the same locations as the pine marten, with mean occurrence increasing across the

258   landscape but with highest probabilities of occupancy in the south and forested areas (Fig. 2). In

259   contrast, grey squirrels have undergone declines and have gone from the most widespread of the

260   three species to the most range restricted (Fig. 2).

261   Credible intervals of the pairwise intercept parameters for species interactions (β_0 from the

262   second order models) e.g. $f_{12}, f_{13},$ and f_{23} did not overlap 0, demonstrating statistical support for the

263   integral role of the interspecific interactions driving the occurrence patterns of the three species

264   across the landscape. Overall, pine marten and red squirrel were positively associated (β_0 = 0.95 ±

265   0.33), there was a negative association between pine marten and grey squirrels (β_0 = -2.24 ± 0.59),

266   and likewise, grey squirrels and reds squirrels were negatively associated (β_0 = -1.68 ± 0.47).   The co-

267   occurrence of the pine marten and the grey squirrel did not vary across habitats, with strong

268   suppression of the grey squirrel by the native predator across the entire gradient of both forest habitat

269   types (Fig. 3). This was also the case for the competitive interaction between the red squirrel and the

270   grey squirrel, where predicted occurrence of red squirrels remained close to zero in the presence of

271   the invader, regardless of changing proportions of habitat composition (Fig. 3). In contrast to the naïve

272   pairs, the co-occurrence of the evolved predator-prey pairing of pine marten and red squirrel, was

273 mediated by habitat. While red squirrels were observed to be outcompeted and suppressed in

274 broadleaf woodlands in the presence of grey squirrels, they reached high occupancy probabilities in

275 broadleaf woodlands in the presence of their shared predator, the pine marten (Fig. 3; β_1 = 0.16 ±

276 0.14). On the contrary however, this positive effect was reversed in conifer plantations, with pine

277 marten presence having a negative effect on red squirrel occurrence as the proportion of commercial

278 plantation increased (Fig. 3; β_2 = -0.58 ± 0.29).

279   It is worth nothing that the second highest ranked model, which had a weight of 0.24 (Table

280 2), also included habitat effects for the pine marten and grey squirrel, but they were consistently

281 negative across both habitats, with one of the effects overlapping zero and thus not significant (β_1 = -

282 58 ± 0.43, β_2 = -0.49 ± 0.73). As such, the inferences drawn from the top model are qualitatively and

283 quantitively identical with the exception that slightly stronger suppression of grey squirrels is

284 predicted in the second ranked model (See Appendix 2, Fig S2 – S3).

285   Finally, a learned response explained the most variation in detection probability of all three

286 species with detection probability increasing after an initial detection (pine marten β = 0.73 ± 0.08,

287 red squirrel β = 0.74 ± 0.07 and grey squirrel β = 0.46 ± 0.01). Detection probability of pine martens

288 and grey squirrels also varied as a function of the bait used at the feeders (pine marten β = 0.41 ± 0.06,

289 grey squirrel β = 0.21 ± 0.07; detection of both decreased in the absence of peanuts), however, this

290 was not observed in red squirrels (Appendix 2, Fig S3). Detection probability of the three species also

291 varied as a function of a small number of environmental (broadleaf, conifer, river) and human

292 disturbance (people per km^2 and urban/suburban) covariates but only to a small degree relative to the

293 effect of a learnt response and bait (Appendix 1, Table S1).

294 Discussion

295 We provide empirical evidence that habitat modifies the direction and strength of coevolved predator-

296 prey interactions, but not interactions between evolutionarily naïve species pairs. Overall, the

297   occurrence of the native red squirrel was higher in the presence of the native pine marten, an effect

298   that increased in native broadleaf woodlands but was reversed in non-native commercial conifer

299   plantations. In fact, in these simplified conifer landscapes, the presence of the pine marten reduced

300   the likelihood of red squirrel occurrence. In contrast, neither the direction nor strength of interactions

301   between the novel pairings were influenced by habitat. First, pine martens suppressed grey squirrels

302   regardless of habitat, directly supporting the hypothesis that the restoration and recovery of native

303   predator populations can provide highly valuable biological control of established invasive species,

304   even in highly human-modified landscapes. Second, grey squirrels suppressed red squirrels, directly

305   supporting the competition hypothesis. Combined, these results demonstrate that, while habitat

306   modification has the potential to disrupt established predator-prey interactions between co-evolved

307   species, these negative effects are far outweighed by the benefits of competitive release where a

308   dominant invasive competitor is controlled by the recovering predator.

309   While habitat complexity has been shown to reduce attack rates and foraging efficiencies of

310   predators (Crowder & Cooper, 1982; Gotceitas & Colgan, 1989), we demonstrate clear differences in

311   the effects of habitat on predator-prey interactions between native and invasive species. Habitat

312   specific differences in the interactions between a shared native predator and native and invasive prey

313   could stem from the degree of naivety to the predation threat (Twining *et al.* 2020b). With coevolved

314   prey having developed appropriate and effective predator recognition and anti-predator behaviours,

315   which remain absent in the invasive species. This disparity in anti-predator behaviours may result in

316   the native prey only being targeted in simplified habitats where alternate prey is limited. Whereas,

317   the naive invasive analogue, being more susceptible to predation, remains a highly profitable prey

318   item regardless of local habitat complexity. The native prey is, however, suppressed in the presence

319   of the native predator in the habitat where the invasive competitor does not occur, suggesting an

320   alternate mechanism. In the absence of pine martens, red squirrels are able to persist in conifer

321   plantations due to a competitive advantage over grey squirrels (Slade *et al.* 2021). Thus, in conifer

322   plantations, the red squirrel does not benefit from competitive release from grey squirrels following

323   pine marten recovery but is subject to predation by the shared predator (Twining *et al.* 2020c). How

324   habitat mediates the impacts of a recovering predator on a native prey population appears to be

325   underpinned by additional indirect interactions from an invasive competitor.

326   These results are of global significance when considering the benefits of predator recovery

327   (Ripple & Beschta, 2015; Sheehy *et al.* 2018), and mounting calls for reintroductions of carnivores to

328   their previous ranges to restore ecosystem function (Ritchie *et al.* 2012; Wolf & Ripple, 2018). We

329   highlight the need to further understand how human-modified landscapes may affect interactions

330   between recovering carnivore populations and native species in the absence of invasive species, to

331   better predict the impacts of such recoveries. Our research demonstrates that the indirect benefit of

332   controlling an invasive competitor is far stronger than the negative effect of direct predation. The

333   occurrence of a native prey species increases on average across the landscape following the return of

334   one its key predators (Storch *et al.* 1990; Pulliainen & Ollinmaki, 1996; Twining *et al.* 2020c). Thus,

335   native predator recovery benefits native prey populations when it results in a release from

336   competition with invasive counterparts. This process shares the same mechanistic underpinning and

337   consequences recently observed in the recovery of native northern spotted owls (*Strix occidentalis*

338   *caurina)* following large scale human control efforts of the invasive barred owl (*Strix varia,* Wiens *et*

339   *al.* 2021)

340   Pine marten occupancy more than doubled over a five-year period from 2015 to 2020, while

341   red squirrel occurrence increased by approximately a third in the same period. Moreover, the

342   recoveries of both species were also geographically coupled, with the majority of (re)colonization

343   occurring in the south of the country (Fig 2). In contrast to the native species, the occupancy of the

344   invasive grey squirrel more than halved from 2015 to 2020 and declined in the same areas where pine

345   martens have recovered. Our results far exceed predictions from a single survey (Twining *et al.* 2021).

346   This has critical implications for the management of invasive species and the monitoring of recovering

347 predator populations in the future. Repeated surveys through time are necessary to ensure that

348 predictions are robust, and not an ephemeral by-product resultaing from the temporality of sampling.

349   While our approach is not strictly experimental, we couple probabilistic methods that

350 explicitly account for imperfect detection with a large and representative sample, thus meeting the

351 statistical rigour required to inform policy on wildlife conservation and management. Our multi-

352 species approach provides key insights into factors driving the occurrence and interactions of a

353 complex and conservationally important interaction network which were not otherwise evident. For

354 example, previous research has suggested that interactions between red and grey squirrels depend

355 on habitat alone, with predictions ranging from complete extirpation of the native inferior competitor

356 in native broadleaf woodlands, to the persistence of the inferior native competitor in large commercial

357 conifer plantations (Slade *et al.* 2021; Twining *et al.* 2021). This has led to recommendations that

358 national conservation strategies for red squirrels should focus on the planting of commercial conifer

359 plantations as opposed to native broadleaf forests, where grey squirrels have a competitive advantage

360 (Slade *et al.* 2021; Twining *et al.* 2021). Our results suggest that such management strategies could

361 undermine ongoing red squirrel recovery efforts, with consequences likely antithetical to their

362 intention. When accounting for additional actors, and the mediating role of habitat, we observed a

363 reduction in the occurrence of red squirrels in large structurally simple conifer plantations where pine

364 martens were present. Such commercial plantations constitute the majority of Ireland and Scotland's

365 forest cover, where they continue to be planted under the guise of saving the red squirrel (Slade *et al.*

366 2021). Our results suggest that that landscape management strategies for red squirrel conservation

367 would be best focused on planting native broadleaf woodlands alongside continued pine marten

368 restoration efforts.

369   Here, we show that in the presence of invasive species, human modification of habitats does

370 not alter the beneficial impacts of native predator recovery on native prey species through

371 competitive release. However, in the absence of invasive competitors, habitat composition has the

372 potential to benefit, or alternatively, to have deleterious impacts on native prey populations following

373 predator recovery. We highlight the necessity of including interspecific interactions in models

374 predicting the occurrence of species for management plans and conservation strategies. Conservation

375 strategies that fail to consider the interactions between environmental conditions and interspecific

376 interactions are likely subject to biases that may, in turn, lead to misguided, and potentially disastrous

377 wildlife management strategies. We conclude that while predator restoration is a vital conservation

378 strategy in the face of increasing invasions and declining global diversity, it should be in conjunction

379 with efforts to restore and maintain a range of natural, structurally complex habitats.

Acknowledgements

Data availability statement

388 All data (detection-non detection data for each species from the three surveys and associated site

389 level covariate data) has been uploaded to a public dryad repository and is available here:

390 doi:10.5061/dryad.r4xgxd2dv.

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476 # Figures captions and tables

477

478 **Table 1.** The top ranked first order occupancy and detection models for the pine marten, the red

479 squirrel, and the grey squirrel. For full model selection tables see Table S1 – S4.

Species	Top occupancy model (ψ)	Top detection model (p)
Pine marten	ψ(Broadleaf, Conifer, Built, Year, Latitude),	p(Bait, Occasion, Previous, Conifer, Year)
Red squirrel	ψ(Built, Conifer, Year, Latitude),	p(Occasion, Previous, Broadleaf, People, Year)
Grey squirrel	ψ(Broadleaf, Conifer, Built, Year, Latitude, Longitude)	p(Bait, Occasion, Previous, Broadleaf, Built, River, Year)

480

481 **Table 2.** AIC model selection between the 27 *a priori* multi-species candidate models representing

482 different hypotheses regarding the impacts of habitat on species interactions and their importance as

483 drivers of occurrence and co-occurrence of the red squirrel, the pine marten, and the grey squirrel.

484 Only models with ΔAIC values <5 are shown. K = number of parameters, AIC is the Akaike information

485 criterion, and ω_i is the model weight. PM is pine marten, RS is red squirrel, and GS is grey squirrel.

| Model	K	-2 Log likelihood	AIC	ΔAIC	ω_i
$f_{PM-RS}(habitat), f_{PM-GS}(constant), f_{GS-RS}(constant)$	41	-4474.39	9030.78	0	0.43
$f_{PM-RS}(habitat), f_{PM-GS}(habitat), f_{GS-RS}(constant)$	43	-4472.98	9031.97	1.19	0.24
$f_{PM-RS}(constant), f_{PM-GS}(constant), f_{GS-RS}(constant)$	39	-4477.82	9033.63	2.86	0.1
$f_{PM-RS}(habitat), f_{PM-GS}(constant), f_{GS-RS}(habitat)$	43	-4473.98	9033.95	3.17	0.09
$f_{PM-RS}(constant), f_{PM-GS}(habitat), f_{GS-RS}(constant)$	41	-4476.32	9034.64	3.87	0.06
$f_{PM-RS}(habitat), f_{PM-GS}(habitat), f_{GS-RS}(habitat)$	45	-4472.78	9035.56	4.79	0.04

486

487
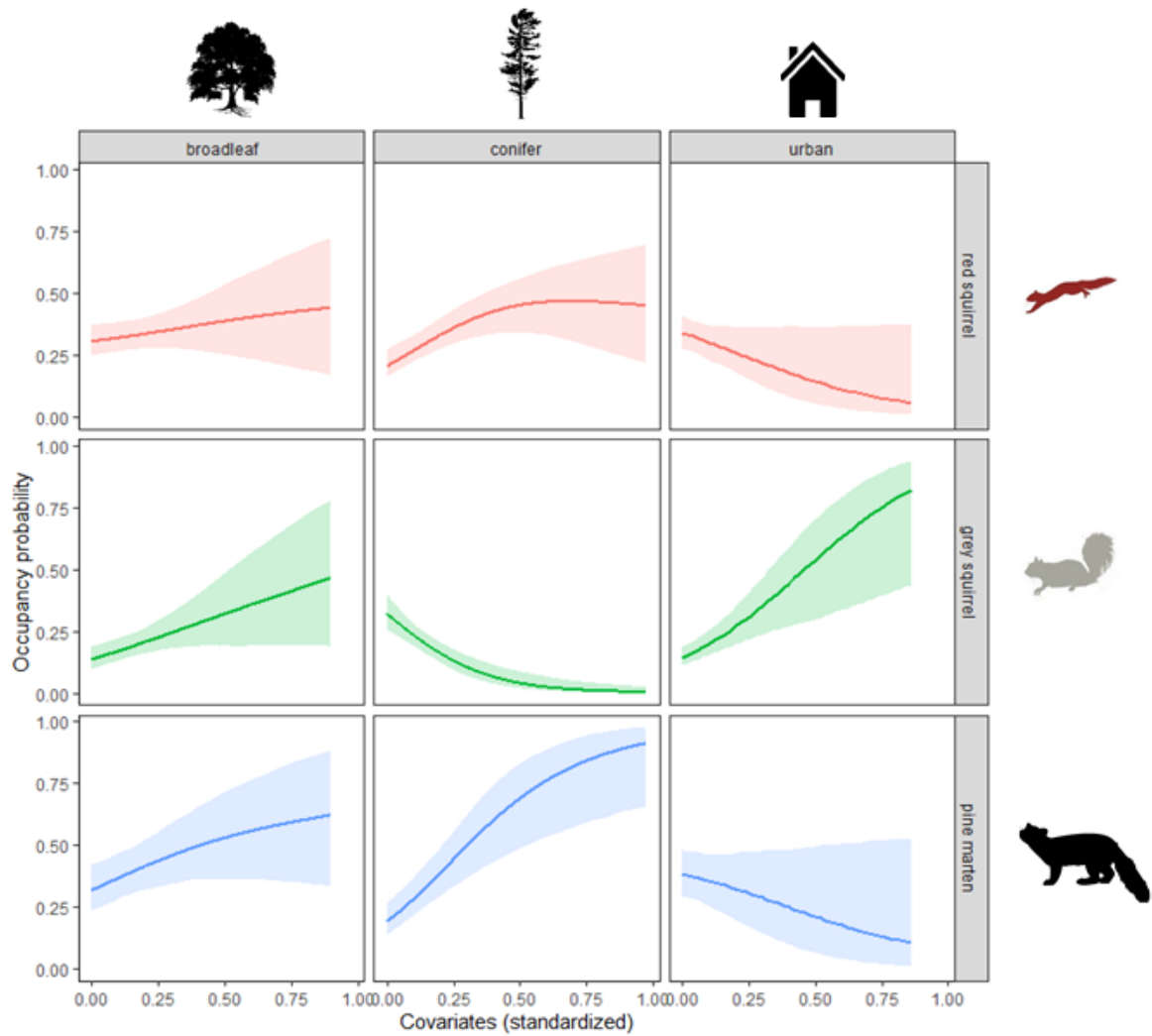
Figure 1. Marginal probability of occupancy for the red squirrel (red), grey squirrel (green) and pine

marten (blue) as a function of proportion of broadleaf woodland, coniferous plantation, and urban

and suburban land use.

491
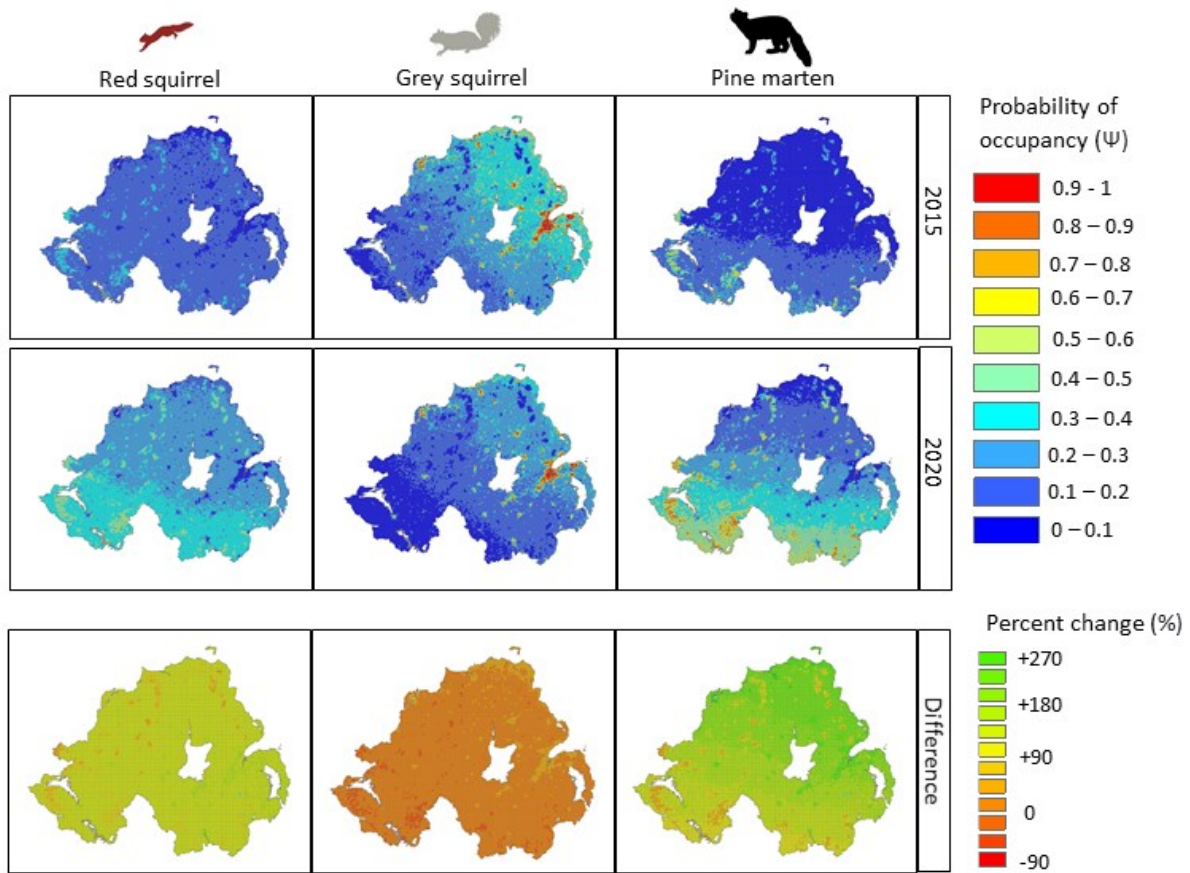
Figure 2. Predicted probability of occurrence across 14,401 km^2 of Northern Ireland from 2015 – 2020
for the pine marten, grey squirrel and red squirrel based on multi-species occupancy models applied
to the entire 2015 – 2020 survey data (n = 706) predicting occupancy for each year of sampling or the
specific land-cover covariates of each 1km^2 of the region and the percent change in occupancy
estimates from 2015 to 2020.

497
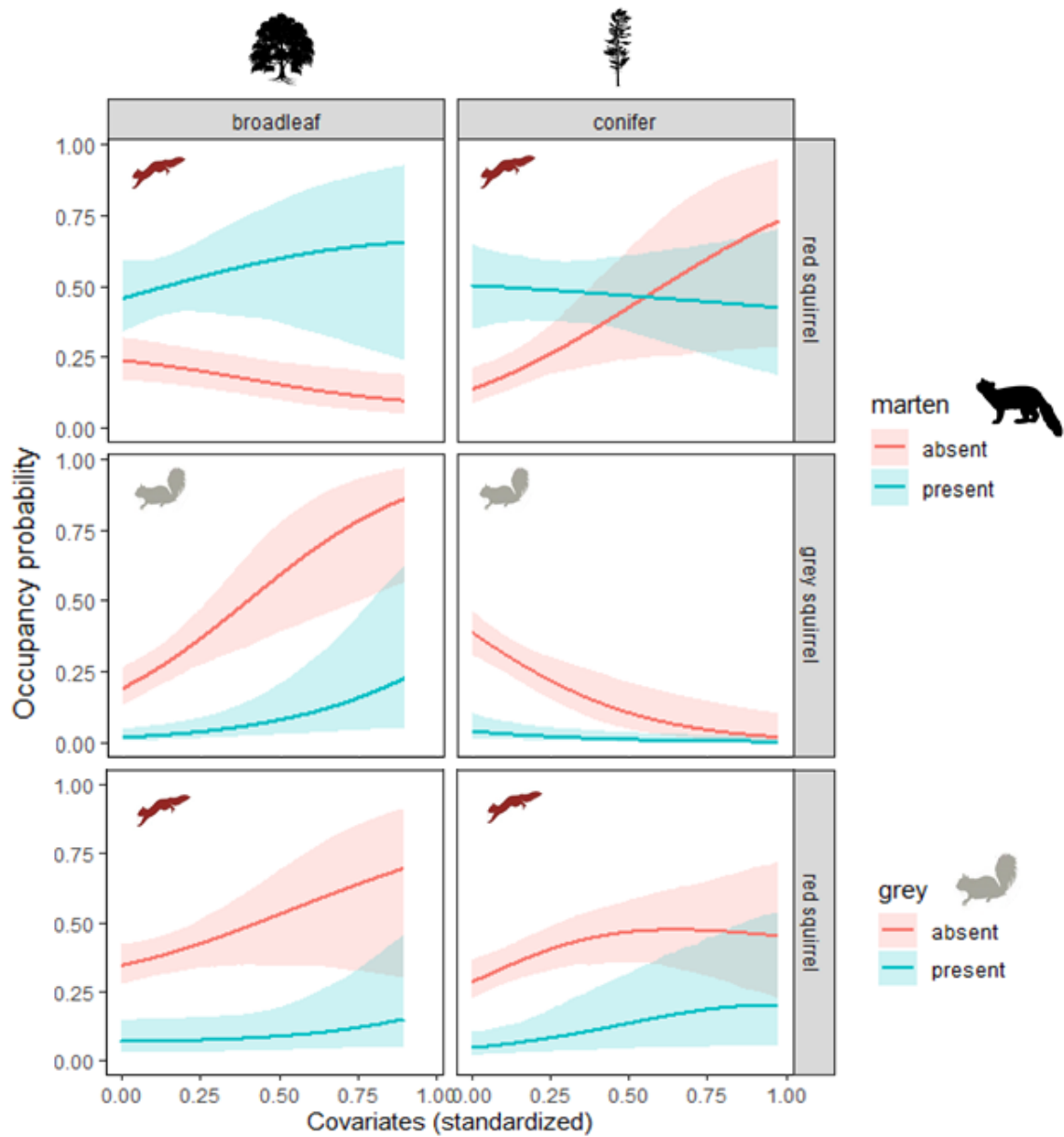
Figure 3. Occupancy probability of the red squirrel and the grey squirrel conditional on the presence

499 (blue) and the absence (red) of their shared predator, the pine marten (top and centre panels). and

500 the grey squirrel (bottom panels) in the two main habitat types available to the species, native

501 broadleaf woodlands (left) and commercial conifer plantations (right). All variables not included in a

502 panel are fixed at their observed means.