Yearling proportion correlates with habitat structure in a boreal forest landbird community

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Landbird vital rates, such as productivity and adult survivorship, can be estimated by modeling mist-netting capture data. The proportion in which an adult breeding bird is one year of age (a "yearling"), however, has been studied only minimally in a few landbird species. Here we relate yearling proportion to habitat-structure covariates, including reclamation age, in a boreal forest landbird community. Data were collected at 35 constant-effort mist-netting stations over a six-year period, and consisted of 12,714 captures of adults, of 29 landbird species, including 4,943 captures of yearlings. Accuracy of age detemination (yearling or older) was assessed based on recapture data and error rates were estimated at a mean of 8.1% (range 0.0% to 19.4%) among the 29 species, with 20 species showing age-error rates <10%. The estimated mean yearling proportion was 0.407, ranging from 0.178 to 0.613 among species. Remote-sensed Enhanced Vegetation Index (EVI), a measure of habitat greenness, was positively correlated with age since reclamation up to 20 years, at which time it became comparable to that of natural stations. The probability of capturing a yearling for species associated with mature forest was lower at stations with higher EVI and the opposite was the case for species favoring successional habitats. These results suggest that yearling birds are being excluded from preferred breeding habitats by older birds through despotism and/or that yearlings are simply selecting poorer habitat due to lack of breeding experience or other factors. This dynamic appears to be operating in multiple species within this forest landbird community. Captured yearlings may also be "floaters," or non-breeding individuals not holding territories. However, presuming that yearlings show lower reproductive success whether floating or not, our results suggest that stations with high yearling proportions could be located within sink as opposed to source habitats. Overall, we infer that yearling proportion may become an important vital-rate measure of habitat quality and reclamation efforts, when combined with indices of population size, productivity, reproductive condition, and survivorship.

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16 **Abstract**
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18 mist-netting capture data. The proportion in which an adult breeding bird is one year of age (a
19 "yearling"), however, has been studied only minimally in a few landbird species. Here we relate
20 yearling proportion to habitat-structure covariates, including reclamation age, in a boreal forest
21 landbird community. Data were collected at 35 constant-effort mist-netting stations over a six-
22 year period, and consisted of 12,714 captures of adults, of 29 landbird species, including 4,943
23 captures of yearlings. Accuracy of age detemination (yearling or older) was assessed based on
24 recapture data and error rates were estimated at a mean of 8.1% (range 0.0% to 19.4%) among
25 the 29 species, with 20 species showing age-error rates <10%. The estimated mean yearling
26 proportion was 0.407, ranging from 0.178 to 0.613 among species. Remote-sensed Enhanced
27 Vegetation Index (EVI), a measure of habitat greenness, was positively correlated with age
28 since reclamation up to 20 years, at which time it became comparable to that of natural stations.
29 The probability of capturing a yearling for species associated with mature forest was lower at
30 stations with higher EVI and the opposite was the case for species favoring successional
31 habitats. These results suggest that yearling birds are being excluded from preferred breeding
32 habitats by older birds through despotism and/or that yearlings are simply selecting poorer
33 habitat due to lack of breeding experience or other factors. This dynamic appears to be
34 operating in multiple species within this forest landbird community. Captured yearlings may also
35 be "floaters," or non-breeding individuals not holding territories. However, presuming that
36 yearlings show lower reproductive success whether floating or not, our results suggest that
37 stations with high yearling proportions could be located within sink as opposed to source
38 habitats. Overall, we infer that yearling proportion may become an important vital-rate measure
39 of habitat quality and reclamation efforts, when combined with indices of population size,
40 productivity, reproductive condition, and survivorship.

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Introduction

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45 Vital rates such as productivity and survivorship have increasingly been used to assess the
46 status of landbird populations and inform conservation actions (*DeSante, Nott & O'Grady, 2001*;
47 *Anders & Marshall, 2005; Saracco, DeSante & Kaschube, 2008; Robinson, Julliard & Saracco,*
48 *2009; Rushing et al., 2015*). While trends in landbird abundance are useful for highlighting
49 species of conservation concern, the assessment of vital rates may help identify causes of
50 declining trends; e.g., whether they are driven by factors on or away from breeding grounds
51 (*Newton, 2004; Albert, 2016*). Data on vital rates collected at constant-effort landbird capture
52 stations can also be used to predict population viability (*Ryu et al., 2016*) and can be modeled
53 as functions of habitat variables to inform conservation-management strategies (*DeSante,1995*;
54 *Saracco et al., 2016; Saracco et al. 2018*), including reclamation and restoration programs
55 (*Foster et al., 2017*). To date, modeled vital-rate terms have primarily included those of
56 productivity, often indexed as the probability that a captured bird at a station had fledged that
57 year, and survivorship of breeding adults, as estimated from capture-mark-recapture models
58 (*Saracco, DeSante, & Kaschube, 2009*).
59   Population age structure within breeding populations of iteroparous species has received
60 less attention but may reflect population dynamics and aspects of habitat quality (*Rodenhouse,*
61 *Sherry & Holmes, 1997*). In landbirds, advances in distinguishing yearlings from older adults for
62 many species (*Jenni & Winkler, 1994; Pyle 1997*) provide new opportunities to estimate
63 proportions of first-year breeding adult landbirds in populations. Yearling proportions have been
64 found to correlate negatively with landbird population densities (*Graves, 1997; Sillett & Holmes,*
65 *2005*) and positively with marginal, lower-quality, or disturbed habitats, likely the result of
66 competitive exclusion of yearlings by older birds from higher-quality breeding habitats (*Graves,*
67 *1997; Holmes, Marra & Sherry, 1996; Hunt, 1996; Bayne & Hobson 2001; Háche & Villard*
68 *2010*). Yearling proportion has also correlated positively with reproductive success within a
69 population the previous year (*Sillet, Holmes & Sherry, 2000*), reflecting a direct demographic
70 effect. Yearling proportions from capture stations have the potential to increase our
71 understanding of landbird demography, habitat selection, and annual recruitment rates;
72 however, assessments of yearling proportion thus far have been limited to a few directed
73 studies on individual species in which one-year-old landbirds, in most cases males only, are
74 readily distinguished from older birds in the field.
75   Here we examine yearling proportions using data from 18,799 captures of 12,714
76 individual landbirds, of 29 species (Table 1), captured at 35 Monitoring Avian Productivity and
77 Survivorship (MAPS) constant-effort bird-capture stations over a six-year period in the oil sands
78 region of northeastern Alberta (Fig. 1). The goals of this study were to (1) examine the
79 accuracy and utility of yearling proportion as a measure of habitat structure in a boreal-forest
80 landbird community, (2) assess the relationship between the probabilities of capturing a yearling
81 and habitat based on multi-species hierarchical models, and (3) assess locally measured and
82 remote-sensed structural vegetation changes in relation to habitat reclamation maturity (e.g.,
83 number of years since reclamation commenced) as it may affect species-specific and habitat-
84 specific variation in yearling proportions.
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Materials & Methods

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MAPS Stations
We established 35 landbird-capture MAPS stations in the oilsands region of northeastern Alberta, Canada (Fig. 1), to monitor landbird demographics. Stations were located in landscapes that included both riparian and upland habitats (*Foster et al., 2017*). Six MAPS stations were operated in 2011, 24 stations were operated in 2012, and 30-35 stations were operated each year in 2013-2016; once a station was established it was operated in all following years, excepting a single station which did not operate in 2013 due to flooding, and five stations that were inaccessible in 2016 due to a regional wildfire. Stations were operated once every 10-day period between 5 June and 7 August, for a total of six days of operation per station per year. On each day of operation, between eight and 14, fixed-location, 12-m mist-nets were operated for six hours, beginning at local sunrise. Captured landbirds were fitted with uniquely numbered leg bands. Birds were aged following *Pyle (1997)* as hatching year (HY) or older (after-hatching-year; AHY), and most AHYs were further determined to be either one-year-old yearlings (second-calendar-year; SY) or older (ASY) adults. Adults undetermined to SY or ASY were aged AHY. Prior to each season, biologists were extensively trained on criteria to distinguish SY and ASY individuals of captured species. Time permitting, digital images were obtained of the body plumage, wings, and tails of birds initially aged AHY that, following detailed examination of the images, resulted in age revisions to SY or ASY.

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Accuracy of age determinations
Our analyses were based on 13,790 year-unique adult captures (different individuals captured in a given year), including 12,714 individuals of 29 species (Table 1). Of the total number of captures, 4,943 were aged as yearling adults (SY), 7,224 were aged as adults older than yearlings (ASY), and 1,623 were of adults that could not be precisely aged (AHY), indicating that 88.2% (range 57.9% for black-capped chickadee to 94.5% for magnolia warbler; see Table 1 for scientific names) of AHY birds were aged to SY or ASY. Other than black-capped chickadee (57.9% aged) and ruby-crowned kinglet (71.0%), we aged >82% of AHYs to SY or ASY among the remaining 27 species (Table 1).

The ability to separate ASY from SY birds is critical to inferring yearling proportion, as errors may be biased toward either of these two age classifications, skewing results. Of 18,799 total adult captures (including within-season captures), 4,754 (25.3%) were initially aged AHY and 3,131 of these (65.9%) were re-determined to be SY or ASY through analysis of digital images from one or more captures. Many of the remaining AHY birds (Table 1) were either processed during times of high capture volume and were released without obtaining photographs, or were of early-molting species (e.g., black-capped chickadee) that had completed or nearly completed the prebasic molt and could not be aged to SY or ASY by the previous year's flight feathers (*Pyle, 1997*). The total number of AHY birds in the data set, 1,623, represents 11.8% of our sample.

Recaptured birds were aged independently of previous age determination; thus, data on birds captured on multiple occasions allowed us to infer error rates. The mean percent of captures in which age was re-assessed (from SY to ASY or vice versa) according to verified

132   recapture data was 8.1%, ranging from 0.0% of 32 recaptured rose-breasted grosbeaks to
133   19.4% of 93 recaptured yellow-rumped warblers (Table 1). Twenty of our 29 species showed
134   age-error rates <10% (Table 1).
135

Vegetation Data

137   We collected *in-situ*, local habitat data on 1-5 broad habitat types at each station within 100m of
138   each station's periphery (*Foster et al., 2017*). Habitat types were delineated based on plant
139   community composition, vegetation structure, and hydrology. For each station and habitat type
140   we estimated cover within three vegetation strata: 1) understory cover (0.5 - 5 m), 2) midstory
141   canopy cover (5 -15 m), and 3) upperstory canopy cover (> 15 m). Previously we have also
142   assessed the proportions of each station that consisted of "natural," "disturbed," and "reclaimed"
143   habitats, with the proportion of natural habitats (excluding open water) ranging from 0% to 98%
144   (*Foster et al., 2017*). For the present analysis, 15 of the 35 stations, those with > 90% of the
145   habitat undisturbed, were considered to be "natural" stations. For the five stations in which >
146   55% of the habitat was reclaimed ("reclaimed" stations), the age since reclamation, calculated
147   as the difference between year of initial vegetation restoration (e.g., tree planting) and year of
148   data collection, ranged from one to 34 years. The remaining 15 stations, which included natural
149   vegetation cover of between 50% and 88%, were classified as "disturbed" stations. To derive
150   station-scale habitat metrics, we calculated weighted averages of each of these variables, with
151   weights equal to the estimated proportion of each habitat type present at the station.
152   For remote-sensed habitat data we used 16-day, 0.25-km resolution, Enhanced
153   Vegetation Index (EVI) data derived from the Moderate Resolution Imaging Spectroradiometer
154   instrument of NASA's Terra satellite (MODIS product MOD13Q1; http://terra.nasa.gov/). We
155   examined relationships between vegetation greenness and: a) *in-situ* habitat parameters, b)
156   % natural cover, and c) probability of capturing a landbird yearling at each station. The EVI is a
157   composite metric which incorporates structural and seasonal components of habitat quality
158   including primary productivity (leaf chlorophyll content), leaf area, canopy cover, and vegetation
159   complexity (*Glenn et al., 2008*), and which has previously been correlated with landbird
160   occurrence and vital rates (*Saracco et al., 2016*). We extracted EVI cell values using the
161   MODISSubsets function of the MODISTools package 30 (*Tuck et al., 2014*) in the statistical
162   software package R (*R Core Team, 2015*) at the 0.25 x 0.25-km scale for 81 cells surrounding
163   each MAPS station, a grid extending 1.13 km in cardinal directions from station centers and a
164   projected area (5.11 km^2) estimated as being sampled by a MAPS station (*DeSante &*
165   *Kashcube, 2009*). For each station, we averaged values for the 81 cells across two June dates
166   to obtain a single EVI value at each station for each year from 2000-2016 (2000 is the first year
167   for which MODIS data are available).
168

Data analysis

170   To investigate habitat changes at reclaimed stations we created plots of cover percentages (for
171   the three vegetation layers collected *in situ*) against years since reclamation at the five
172   reclaimed stations and, for reference, the 15 natural stations. To provide insights into which
173   vegetation layers contributed most strongly to variation in EVI, we plotted EVI values for the five
174   reclaimed stations against years since reclamation for each year between 2000 and 2016 (a
175   total of 85 data points). We also used a two-variable linear regression with year- and site-

176 specific June EVI as the response variable and percent natural cover and years since
177 reclamation as explanatory variables. We included both the five reclaimed stations and 15
178 disturbed stations in this analysis, considering un-reclaimed stations as being zero years since
179 reclamation. The model was fit in R (*R Core Team, 2015*) and bivariate relationship plotted
180 using the 'scatterplot3D' function in the R package scatterplot3D (*Ligges & Mächler, 2003*). A
181 quantile plot of standardized residuals and residuals v. fitted values plot suggested adequate
182 model fit.
183   Our analyses of yearling proportion included 29 landbird species with a mean of ≥ 20
184 individual adult (SY, ASY, and AHY) birds captured per year over the six-year period (Table 1).
185 To investigate the relationship between yearling proportion and EVI we implemented a
186 multispecies hierarchical model using data from all 29 target species. We assumed the age of
187 year-unique individuals to be Bernoulli random variables with success probability $p_{i,j,k,t}$, whereby
188 the *i, j, k,* and *t* represent indices for individual, species, station, and year, respectively. Thus,
189 $p_{i,j,k,t}$ indicated the probability that a year-unique capture of an adult individual represented an SY
190 bird. We modeled $p_{i,j,k,t}$ with a logit-linear model:

191

192 $$\text{logit}(p_{i,j,k,t}) = \alpha_{j[i]} + \beta_{j[i]} \times evi_{k,t} \,,$$

193

194 whereby $\alpha_{j[i]}$ represented random species intercepts and $\beta_{j[i]}$ the species-specific regression
195 coefficients for the relationship with the June EVI value at station k in year t, $evi_{k,t}$. We modeled
196 $\alpha_{j[i]}$ and $\beta_{j[i]}$ as normally distributed with mean μ_a and μ_β, and variances σ_a, and σ_β. We centered
197 the continuous covariate, $evi_{k,t}$ around zero prior to analysis to facilitate estimation. We
198 implemented the model using Bayesian methods in JAGS (*Plummer, 2003*) from R (*R Core*
199 *Team, 2015*) using the R package 'jagsUI' (*Kellner, 2015*). See Supplementary Information for
200 details and model code. For this analysis, AHY individuals were included as unknown-age
201 adults, and thus were estimated based on the model constraints and priors.
202

203 **Data availability and ethics statement**
204 Our study was conducted in accordance with North American Banding Council
205 (https://www.nabanding.net/) and MAPS
206 (http://www.birdpop.org/docs/misc/MAPSManual18.pdf) protocols which minimize the impact of
207 netting and processing on the health and safety of captured landbirds. All birds were captured
208 and banded following protocols and permits issued by the Canadian Wildlife Service Bird
209 Banding Office (Master Permit 10858) and the Alberta Government. The datasets generated
210 and/or analyzed during the current study are available from the Harvard dataverse:
211 https://doi.org/10.7910/DVN/NP2P2V.
212

213

214 ## Results
215   Extent of understory cover as measured *in situ* showed little relationship with station age
216 since reclamation (Fig. 2a) whereas extent of midstory canopy cover increased with age since
217 reclamation and was similar to midstory cover of natural stations by 30 years post reclamation
218 (Fig. 2b). Extent of upperstory canopy cover among reclaimed stations also showed little
219 relationship with station age up to 30 years, as compared to values derived from matured

220 natural stations (Fig. 2c). Remote-sensed, Enhanced Vegetation Index (EVI) values increased
221 with years since reclamation, with the index equating to those of natural stations up to about 20
222 years since reclamation (Fig. 2d). When we compared values among the five reclaimed stations
223 and the remaining 30 stations, the EVI index also correlated with both year since reclamation
224 and proportion of a station's habitat considered natural (Fig. 3).
225   The mean yearling proportion of the 29 species over all six years and 35 stations
226 combined was 0.407, ranging from 0.178 in red-eyed vireo and northern waterthrush to 0.613 in
227 swamp sparrow (Table 1). The probability of a captured adult being a yearling was negatively
228 related to EVI (Fig. 4a), indicating that yearlings overall were found in less-forested habitats.
229 This relationship was strongest for birds typical of forested habitats, as reflected by our capture
230 data of adults, and weakest for species inhabiting earlier successional habitats (Fig. 4b-c). The
231 probabilities of capturing yearlings for species preferring mature forests, such as magnolia
232 warbler, cedar waxwing, northern waterthrush, and mourning warbler, were lower in those
233 forested habitats and higher in successional habitats, whereas species preferring successional
234 habitats, such as song sparrow, clay-colored sparrow, alder flycatcher, savannah sparrow, and
235 chipping sparrow, had lower yearling probabilities in those habitats and higher probabilities in
236 forested habitats (Figs. 4b and 5). We also found significant relationships between EVI
237 coefficients, EVI mean, and EVI range among our 29 species, including a slightly positive
238 correlation between EVI coefficient and range (Fig. 5), suggesting that more specialist species,
239 those found in a narrower range of habitats, tended to have more negative correlations between
240 EVI and yearling probabilities than species found in a wider range of habitats.
241
242

Discussion

244   Among our 35 stations, habitat-development patterns indicate that ground and
245 understory cover do not change markedly after initial planting, that midstory cover develops
246 within the first 30 years after initiation of reclamation, and that upperstory canopy does not
247 noticeably develop until > 30 years after initiation of reclamation activities. This is consistent
248 with other studies on boreal-forest habitat succession, in which trees reach about 40% of their
249 maximum height within 50 years and attain maximum height and canopy development (closure)
250 at about 75 years of age (*Bartels et al., 2016*). EVI values will increase as midstory canopy
251 develops within the first 20 years, but then may not change substantially as upperstory canopies
252 mature and obscure the lower strata. It thus appears that EVI can track habitat characteristics,
253 structure, and development for 20 - 30 years following vegetation planting, but that *in-situ*
254 habitat data or data based on remote imagery that can distinguish canopy layers will be needed
255 once upperstory canopy closure commences.
256   Mean yearling proportions among the 29 species examined show wide variation, from
257 0.178 in red-eyed vireo and northern waterthrush to 0.613 in swamp sparrow. We believe this
258 variation reflects biological factors as opposed to age-determination or capture bias; following
259 increased precision of age determinations though examination of digital images, mean error rate
260 in age-determination was estimated at only 8.1%, with 20 of our 29 species showing age-error
261 rates <10%. The variation in mean yearling proportions may reflect factors related to species-
262 specific variation in 1) the ability or proclivity to exclude yearling birds from higher quality

263   habitats by adults, 2) age-specific variation in capture probabilities, and/or 3) habitat variables
264   among our 35 MAPS stations.
265   Despite this variation in yearling proportions, forest-dwelling landbird species (cf.
266   Rodewald 2015), those captured at higher rates in forested stations of our study, showed lower
267   probabilities of yearling capture in stations with higher EVI, whereas species captured more
268   frequently in successional breeding habitats showed higher capture probabilities of yearlings in
269   forested habitats. Both of these results are consistent with hypotheses suggesting that yearling
270   birds are excluded through despotism to suboptimal breeding habitats (*Holmes, Marra & Sherry,*
271   *1996*; *Bayne & Hobson, 2001*; *Rohwer, 2004*; *Háche & Villard, 2010*). Alternatively, yearlings
272   may also be selecting poorer habitats due to lack of breeding experience or other factors. In
273   either case, it is possible that stations with high yearling proportions may occur in sink as
274   opposed to source habitats (*Pulliam, 1988*; *Donovan et al., 1995*; *Faaborg et al., 2010*),
275   presuming that yearling landbirds also average poorer reproductive success than older birds
276   *(Holmes, Marra & Sherry, 1996)*. Our study also indicates that despotic exclusion or other
277   factors affecting yearling dynamics may operate selectively and specifically among different
278   species within a forest landbird community. Maintenance of high yearling proportions in
279   suboptimal habitats for the species may promote emigration of yearlings to more suitable
280   habitats for their second year of breeding (*Greenwood & Harvey, 1982*; *Rohwer, 2004*),
281   underscoring the need to model population age structure and habitat dynamics at the meta-
282   population level over multiple years (*Faaborg et al. 2010*).
283   Using capture data from the same study areas reported on here, *Foster et al. (2017)*
284   found significant correlations between habitat covariates and captures of adult birds, young (HY)
285   birds, and/or the probability of capturing a young bird (productivity). They also found that
286   positive responses to reclamation age from obligate forest-dwelling species took more years to
287   become evident than those for species preferring early successional-stage habitats. Our
288   analyses further support relationships between demographic variables and habitat structure,
289   including those related to habitat succession, suggesting that recruitment into the breeding
290   population by yearling landbirds could be an initial indication of successful boreal-forest
291   reclamation. We infer that yearling proportion can become an important vital-rate measure of
292   both species-specific habitat suitability and the progress of reclamation efforts.
293   Captured yearlings may be "floaters," or non-breeding individuals not holding territories
294   that are simply passing through the territories of breeding individuals (*Sherry & Holmes, 1989*;
295   *Barber & Robertson, 1999*; *Bayne & Hobson, 2001*). Demographic analyses using capture data,
296   for example those examining correlations of yearling proportion with population density or
297   productivity (*Graves, 1997*; *Sillett, Holmes & Sherry, 2000*; *Bayne & Hobson, 2001*; *Rohwer,*
298   *2004*; *Háche & Villard, 2010*), should account for the possible presence of floaters. We suggest
299   that breeding condition data, e.g., the extent of brood-patch or cloacal-protuberance
300   development (*Pyle, 1997*) or recapture data confirming length of stay, may be useful in
301   assessing the occurrence of yearling and older floaters in capture data sets (*Barber &*
302   *Robertson, 1999*). Habitat selection processes by age may also be subject to interannual or
303   density-dependent effects (*Rodenhouse, Sherry & Holmes, 1997*). By incorporating all
304   demographic and breeding-condition variables in population models, that in turn include multiple
305   species and multiple years of data, we suggest that yearling proportion may eventually be useful
306   in estimating first-year recruitment and survivorship, the latter widely considered to be much

307 lower than survivorship of older adults but is difficult to estimate due to low natal fidelity in most
308 landbird species (*Hobson, Wasenaar & Bayne, 2004*; *Anders & Marshall, 2005*; *Cooper, Daniels*
309 *& Walters, 2008*; *Faaborg et al., 2010*). In any case, presuming that yearlings show lower
310 reproductive success than older birds, our results indicate that habitats with high yearling
311 proportions could be located within sink as opposed to source habitats.
312

Conclusions

314 To our knowledge, this study represents the first attempt to model the probability of capturing
315 yearling landbirds against habitat factors using a multi-species approach. For many landbird
316 species, age can only be accurately determined in the hand, so our dataset provides the only
317 large-scale, long-term data set that we are aware of that permits estimation of yearling age-
318 structure of both sexes combined. Key to deriving accurate yearling proportions is observer
319 training in age-determination criteria and validation through a procedure like the photographic
320 review and aging confirmation processes used here.
321   Our results suggest that yearling landbirds are excluded from optimal breeding habitats
322 by older adults, although they might disperse into more optimal habitats the year following
323 breeding as yearlings. The probability of capturing a yearling of forest-dwelling species was
324 higher in successional-stage habitats, and vice versa. In conjunction with other vital rates
325 estimated using MAPS data (i.e., productivity, survivorship), yearling proportion may help
326 identify sink habitats and estimate juvenile survival, on a species-by-species basis.
327

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Table 1 for *Yearling proportion correlates with habitat structure in a Boreal forest landbird community.*

Table 1. Sample summaries, age error rates, and yearling proportions for landbird species captured in the boreal forest of northeastern Alberta. Four-letter alpha codes presented here are used in Figures 4 and 5. Number of stations in which the species was captured is indicated (Stas.) Year-unique individuals (Year-Inds.) indicate the summed number of individuals captured per year (including between-year recaptures). Numbers of yearling adults (SY), older adults (ASY), and adults undetermined to age (AHY) are given for each species. Age error rates were calculated as the proportion of instances an age determination of SY or ASY was changed for recapture records, as verified by recapture data, among the given sample. Yearling proportion calculated as SY/(SY+ASY).

1 **Yearling proportion correlates with habitat structure in a Boreal forest landbird community**

3 **Table 1.**

Common name	Scientific name	Code	Stas.	Year-Inds.	SY	ASY	AHY	Age error rate (n)	Yearling prop.
Yellow-bellied sapsucker	*Sphyrapicus varius*	YBSA	33	267	132	120	15	0.056 (178)	0.524
Alder flycatcher	*Empidonax alnorum*	ALFL	36	845	166	573	106	0.119 (345)	0.225
Least flycatcher	*Empidonax minimus*	LEFL	35	517	209	252	56	0.086 (163)	0.453
Red-eyed vireo	*Vireo olivaceus*	REVI	31	507	78	360	69	0.042 (143)	0.178
Black-capped chickadee	*Poecile atricapillus*	BCCH	29	190	48	62	80	0.071 (99)	0.436
Ruby-crowned kinglet	*Regulus calendula*	RCKI	18	155	48	62	45	0.021 (47)	0.436
Swainson's thrush	*Catharus ustulatus*	SWTH	36	747	276	356	115	0.046 (263)	0.437
American robin	*Turdus migratorius*	AMRO	35	471	204	210	57	0.132 (151)	0.493
Cedar waxwing	*Bombycilla cedrorum*	CEDW	27	358	142	191	25	0.017 (60)	0.426
Chipping sparrow	*Spizella passerina*	CHSP	38	801	302	427	72	0.080 (224)	0.414
Clay-colored sparrow	*Spizella pallida*	CCSP	23	755	299	399	57	0.128 (344)	0.428
Savannah sparrow	*Passerculus sandwichensis*	SAVS	5	266	71	179	16	0.140 (136)	0.284
Song sparrow	*Melospiza melodia*	SOSP	15	141	39	88	14	0.134 (97)	0.307
Lincoln's sparrow	*Melospiza lincolnii*	LISP	35	546	203	277	66	0.180 (417)	0.423
Swamp sparrow	*Melospiza georgiana*	SWSP	23	216	119	75	22	0.088 (159)	0.613
White-throated sparrow	*Zonotrichia albicollis*	WTSP	37	1474	450	853	171	0.089 (1093)	0.345
Ovenbird	*Seiurus aurocapilla*	OVEN	37	567	212	278	77	0.084 (178)	0.433

Northern waterthrush	*Parkesia noveboracensis*	NOWA	19	127	19	88	20	0.061 (66)	0.178
Black-and-white warbler	*Mniotilta varia*	BAWW	30	261	117	113	31	0.026 (77)	0.509
Tennessee warbler	*Oreothlypis peregrina*	TEWA	37	2399	968	1148	283	0.055 (660)	0.457
Mourning warbler	*Geothlypis philadelphia*	MOWA	20	220	73	130	17	0.077 (195)	0.360
Common yellowthroat	*Geothlypis trichas*	COYE	28	236	67	145	24	0.081 (111)	0.316
American redstart	*Setophaga ruticilla*	AMRE	22	214	85	106	23	0.049 (81)	0.445
Magnolia warbler	*Setophaga magnolia*	MAWA	27	292	143	133	16	0.073 (219)	0.518
Yellow warbler	*Setophaga petechia*	YEWA	21	309	106	167	36	0.041 (197)	0.388
Yellow-rumped warbler	*Setophaga coronata*	YRWA	29	278	124	137	17	0.194 (93)	0.475
Canada warbler	*Cardellina canadensis*	CAWA	22	304	129	121	54	0.133 (165)	0.516
Wilson's warbler	*Cardellina pusilla*	WIWA	28	193	70	93	30	0.132 (91)	0.429
Rose-breasted grosbeak	*Pheucticus ludovicianus*	RBGR	22	134	44	81	9	0.000 (33)	0.352

5 **Table 1.** Sample summaries, age error rates, and yearling proportions for landbird species captured in the boreal forest of northeastern
6 Alberta. Four-letter alpha codes presented here are used in Figures 4 and 5. Number of stations in which the species was captured is
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Figure 1

Study region.

(A) Study region within Alberta, Canada. (B) MAPS station locations; stations comprised largely (> 90%) of natural boreal habitats (n = 15) are indicated with green triangles, those affected by disturbance from resource development activities (n=15; 0-89% natural habitats) with open orange squares, and stations in reclaimed sites (n = 5) are indicated with open yellow circles. (C) Surrounding habitats for five reclaimed stations, with color coding corresponding to that in Fig. 2; see *Foster et al. (2017)* for station codes. Map data for B: Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL; Map data for C: Google, TerraMetrics).
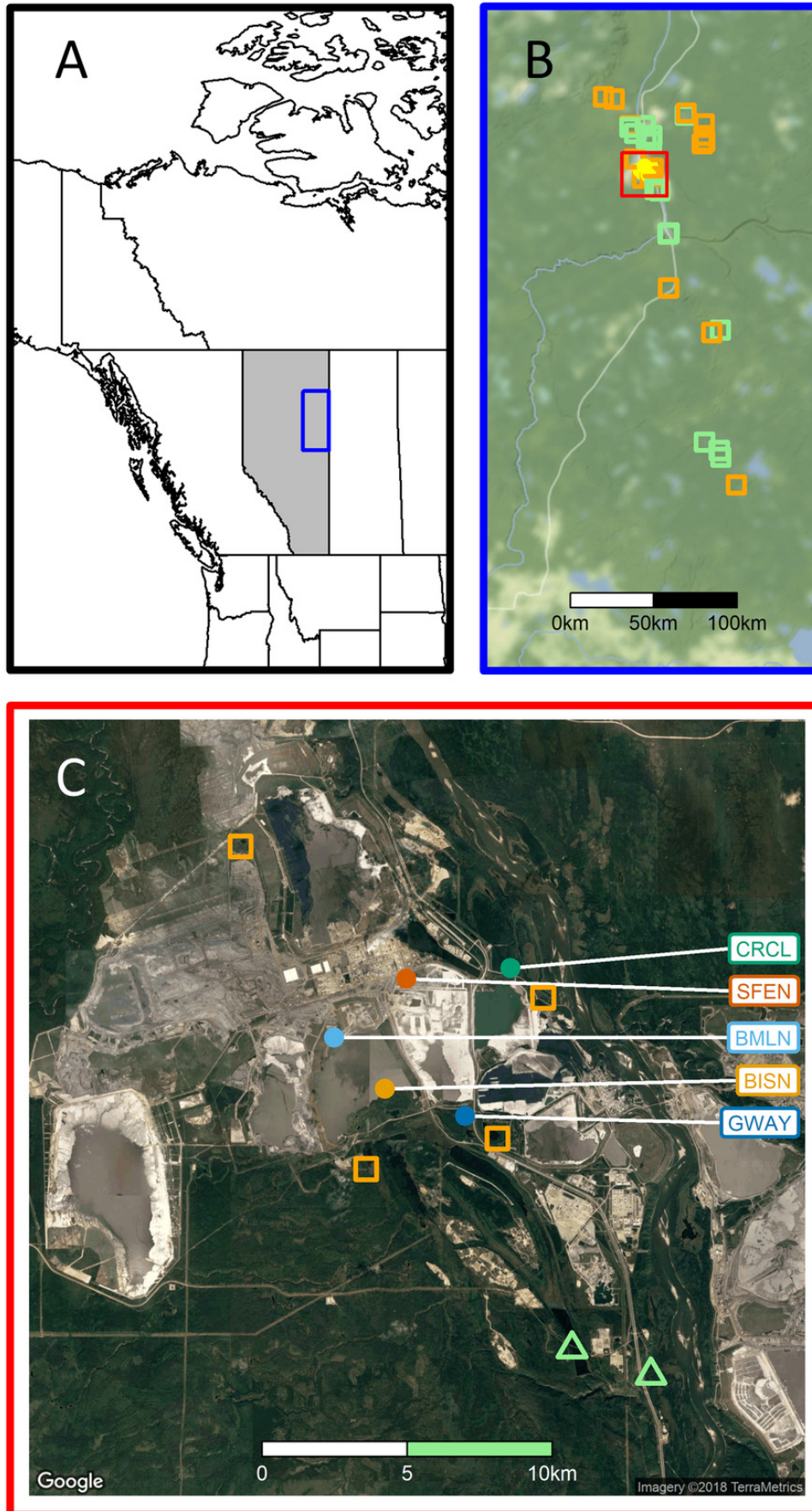
Figure 2

Relationships between habitat variables and years since initiation of reclamation at 15 MAPS stations dominated by natural vegetation and five stations with predominantly reclaimed habitat.

Colors denote individual reclaimed stations (see Fig. 1). Natural sites (those with >90% natural boreal habitats; n = 15) are aggregated into boxplot to right. (A-C) Points represent values from in-situ habitat assessments in 2013. (D) Points represent June Enhanced Vegetation Index (EVI) values from up to 16 years per station (among years 2000-2015). Note that both understory and upperstory cover showed little correlation with years since reclamation whereas mid-story cover showed substantial increases, approaching those of natural sites by 30 years post reclamation. EVI values appear to reflect mid-story development, equating with natural stations at 15-20 years post reclamation.
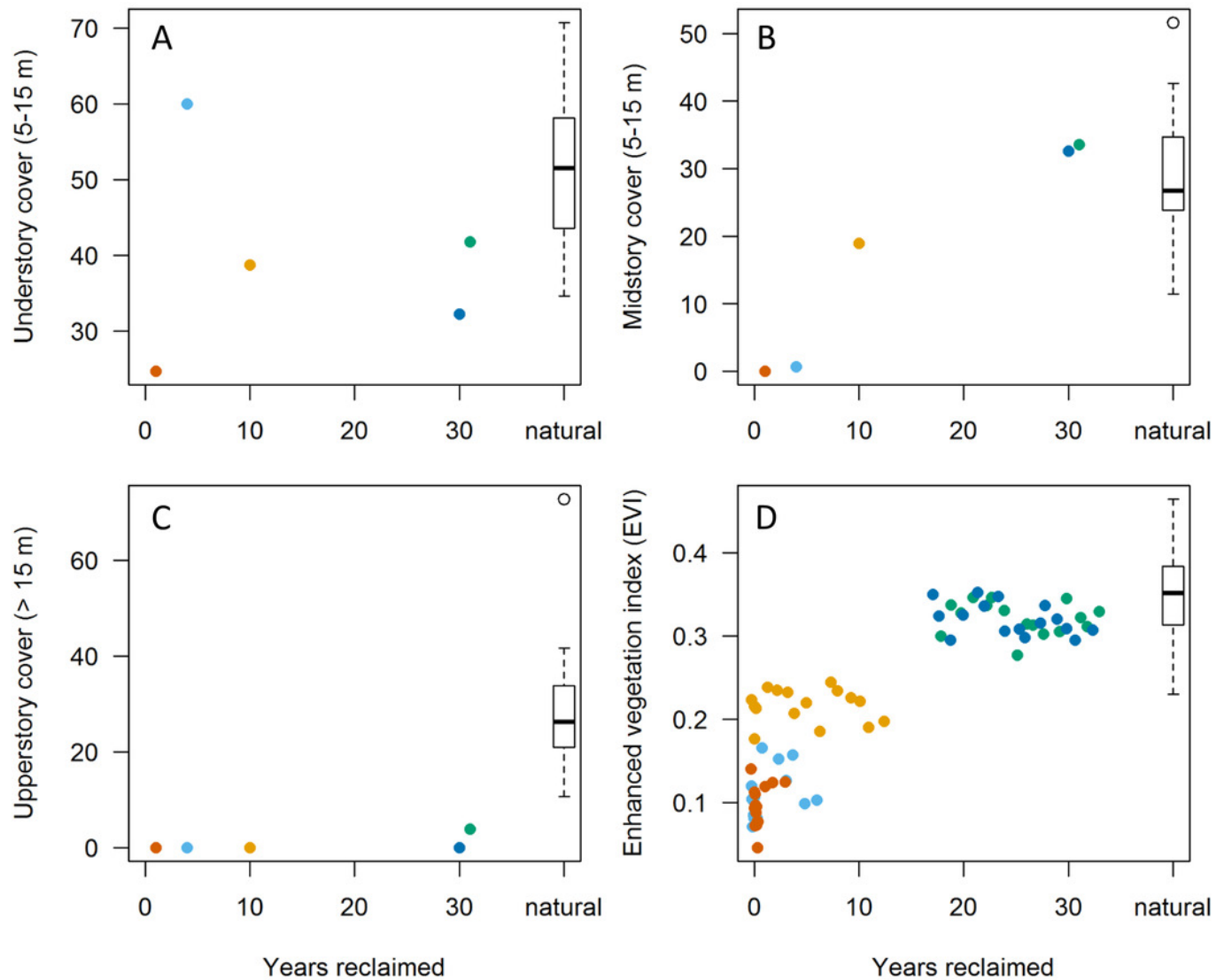
Figure 3

Three-dimensional scatterplot indicating that Enhanced Vegetation Index (EVI) increases with % natural vegetation and years since habitat reclamation commenced.

The dashed plane shows the bivariate linear regression fit (R^2 = 0.35). Standardized regression coefficient for % natural was 0.064 (95% CI: 055, 0.074) and for years reclaimed was 0.030 (0.021, 0.040). Colors distinguish individual stations (see Figs. 1 and 2); other colors represent the 15 stations affected by disturbance from resource development activities, ranging from 0% to 89% of the station estimated to be in natural habitats (*Foster et al., 2017*).
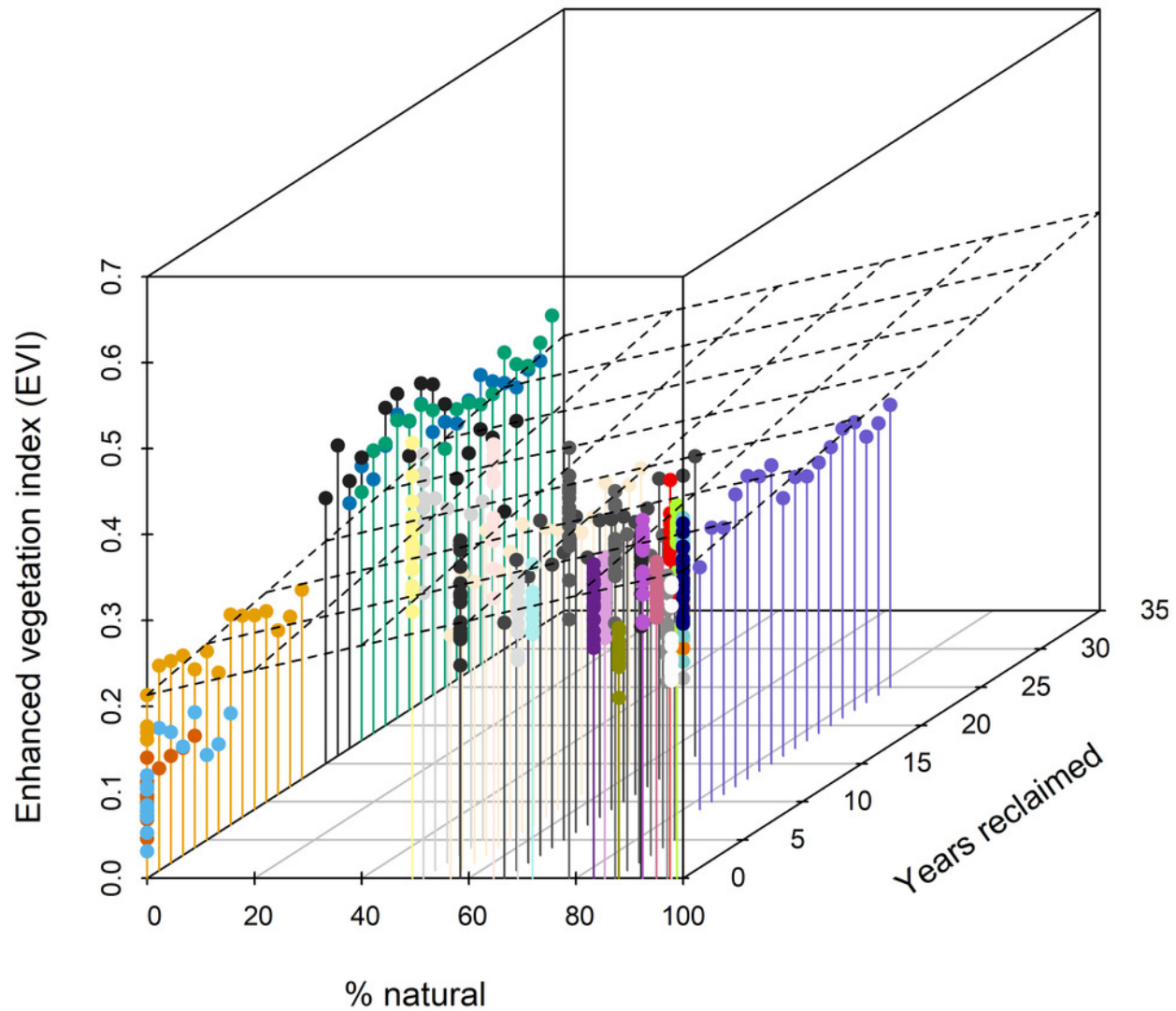
Figure 4

Results of multispecies hierarchical model to investigate the relationship between the age structure of adult birds and Enhanced Vegetation Index (EVI).

Mean estimates for species in which adults were captured at highest rates in successional (tan; lowest EVI quartile), intermediate (light green; middle two EVI quartiles), and mature forest (dark green; upper EVI quartile) habitats, as measured by our *in-situ* habitat structure data, are shown to highlight potential habitat-related differences in yearling responses. (A) Estimated mean yearling probability (black line) ± 95% cred. int. (gray polygon) across observed range of EVI values (μ_{β} = - 1.29; 95% cred. int.: - 2.49, -0.18). (B) EVI coefficient estimates (± 95% cred. int.) for each of the 29 target species, sorted from most negative (top) to most positive (bottom) EVI coefficient; species codes are defined in Table 1. The estimated mean species-EVI effect is indicated by a dashed line and gray region delineates the 95% credible region. (C) Box plots show distribution of mean coefficients for the 3 species groupings. The mean EVI coefficient for species with EVI values in the lowest quartile across species was -0.55 (95% conf. int: -3.64, 3.67), that for species in the middle half was -1.38 (95% conf. int: -5.60, 2.88), and that for species in the highest quartile -1.95 (95% conf. int: -6.72, 1.83). This indicates that yearling proportions for forest-dwelling species are lower in more-forested (greener) habitats whereas those of successional-habitat species is higher in forested habitats.
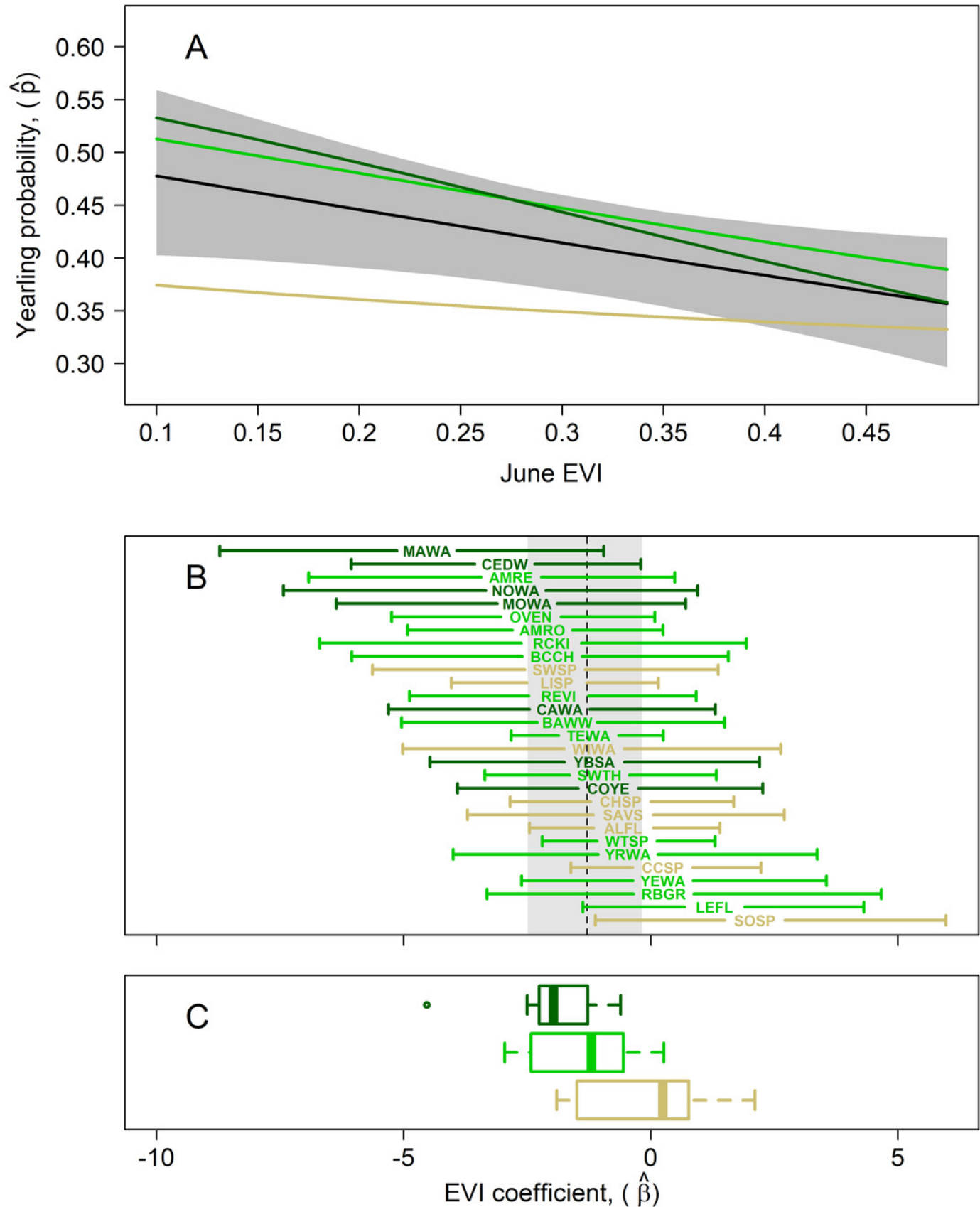
Figure 5

Relationship between species coefficients as a function of the EVI mean and EVI range observed for that species.

The plane shows the bivariate regression fit (R-squared = 0.28). This relationship is highly significant (standardized regression coefficient = -0.717, 95% CI: -1.206, -0.278) and there was a slightly positive relationship between the EVI coefficient and the EVI range. Four-letter codes (see Table 1) for outlying species are shown; see Fig, 4 for species-habitat color representation.