

1 **Title:**2 **Arctic greening and bird nest predation risk across tundra ecotones**

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5 **Authors:**

6 Rolf A. Ims^{1,*}, John-Andre Henden¹, Marita A. Strømeng¹, Anders V. Thingnes¹, Mari J.
7 Garmo¹, Jane U. Jepsen²

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9 **Affiliations:**

10 ¹ Department of Arctic and Marine Biology, UiT- Arctic University of Norway, 9037 Tromsø,
11 Norway

12 ² Department of Arctic Ecology, NINA, Fram Centre, 9296 Tromsø, Norway

13

14 *Correspondence to: rolf.ims@uit.no ORCID [0000-0002-3687-9753](https://orcid.org/0000-0002-3687-9753)

15

16 **Summary paragraph**

17 Alarming global-scale declines of birds numbers are occurring under changing climate¹ and
18 species belonging to alpine and arctic tundra are particularly affected^{2,3}. Increased nest predation
19 appears to be involved⁴, but the mechanisms linking predation to climate change remain to be
20 shown. Here we test the prediction from food web theory that increased primary productivity
21 (greening of tundra) in a warming arctic leads to higher nest predation risk in tundra ecosystems.
22 Exploiting landscape-scale, spatial heterogeneity in primary productivity across alpine tundra
23 ecotones supplied with experimental nests in sub-arctic Scandinavia, we found that predation risk
24 indeed increased with primary productivity. The productivity-predation risk relationship was
25 independent of simultaneous effects of rodent population dynamics and vegetation cover at nest
26 sites. Predation risk also increased steeply with altitude, implying that species at the high-altitude
27 end of alpine tundra ecotones are particularly vulnerable. Our study contributes to an improved
28 understanding of how climate change may affect arctic-alpine ecosystems and threaten endemic
29 biodiversity through a trophic cascade.

30

31 **Main Text**

32 Biota belonging to the globe's coldest biomes – alpine and arctic tundra – are expected to be
33 disproportionally exposed to global warming^{3,5}. Indeed, declines in abundance and distribution
34 ranges of arctic-alpine bird species have been reported^{1,2,6-9}. Although, these declines are
35 consistent with recent climate change, the ecological mechanisms involved are mostly unknown.
36 Unravelling such mechanisms will yield improved predictive models of future changes as well as
37 better basis for implementing effective management actions^{10,11}.

38 Birds are often subjected to strong food web interactions, of which predation has pervasive
39 impacts on population dynamics and extinction risk¹². Eggs and nestlings are bird life stages
40 particularly vulnerable to predation¹³. Hence, factors determining nest predation have been the
41 targets of a large number of studies. Yet, how climate change may affect nest predation has been
42 claimed to be a remaining frontier¹⁴.

43 Alpine and arctic birds place their nests on the ground, sometimes in tundra landscapes with
44 sparse vegetation cover. Hence, their nests can be expected to be particularly vulnerable to
45 predation since they are often very exposed (i.e. visible because of little cover) and easily
46 accessible to predator species that are present. Alpine and arctic tundra are also the biomes where
47 climate warming is most profound^{3,5} and a critical question is how this influence nest predation
48 risk. A new study has shown that nest predation in arctic waders has increased steeply concurrent
49 with recent climate warming⁴, but without providing evidence for the ecological mechanisms that
50 may be involved. The most fundamental response of tundra ecosystems to climate warming is
51 increased plant biomass – the tundra is greening^{15,16}. While increased vegetation cover could
52 yield lower exposure of bird nests to predators¹³, food web theory predicts that increased primary
53 productivity in tundra will render species at intermediate trophic levels (such as many ground
54 nesting birds) more suppressed by predation¹⁷. In particular, generalist consumers (omnivores
55 like corvids and foxes) that feed on a variety of food items from several trophic levels, including
56 bird nests, are expected to become more abundant as primary productivity increases. While this
57 expectation is derived from general food web theory, consumers in tundra ecosystem may be
58 particularly sensitive to a warming-induced increase in primary productivity, because primary
59 productivity is initially low and temperature limited in cold regions.

60 Here we test the prediction that higher landscape-scale primary productivity is associated with
61 higher nest predation risk within an 11 000 km² region at 70-71°N in Scandinavia (Fig. 1). The
62 study region is located in the transition between north-boreal forest and sub-arctic tundra. Like
63 large tracts of the circumpolar high north^{3,16,18}, the region has been subjected to a spatially
64 heterogeneous greening⁹ and ground nesting tundra birds such as ptarmigans have been declining
65 over the last decades^{7,8}. The boreal-arctic transition zone is also expected to be particularly prone
66 to invasions by boreal predators in a warming climate, because of its close proximity to forest
67 ecosystems⁸.

68 We selected 9 replicate landscape areas (average area size=13.3km²) with three levels of
69 greenness (i.e. primary productivity) as assessed by the maximum Enhanced Vegetation Index
70 (max EVI). Within each landscape area, we distributed 20 experimental nests along two
71 altitudinal transects (Fig. 1). Each transect spanned an ecotone (i.e. an altitude gradient) starting
72 just above the tree-line in relatively lush low-alpine shrub tundra and ending in more sparsely
73 vegetated middle-alpine tundra. This ecotone design was employed because bird species
74 associated with different alpine vegetation zones in other geographic regions have exhibited
75 contrasting population declines^{2,6} and because this ecotone also constitute a spatial gradient in
76 primary productivity and vegetation cover. We deployed experimental nests according to a much-
77 used standard that provides a measure of *relative predation risk*¹⁹. The experimental nests were
78 exposed for 14 days during the local birds' breeding season of the years 2010-2014. This 5-year
79 period encompassed all phases of the multi-annual rodent population cycle known to strongly
80 influence nest predation risk through the alternative prey mechanism²⁰. We expected the
81 predation risk to peak in the crash phase of the rodent cycle, because predators that have become
82 numerous based on abundant rodent prey in the peak phase (predator numerical response) switch
83 to alternative prey (e.g. bird nests) in the crash phase when rodent prey has become scarce
84 (predator functional response). Overall, predator functional and numerical responses should yield
85 a predation risk cycle that mirrors the rodent cycle with one-year time lag²⁰.

86 Predation risk among the 900 experimental nests exhibited profound temporal and spatial
87 variation (Fig. 2). A GLMM model that included the following four additive fixed effects
88 adequately accounted for this variation: *Primary productivity* (max EVI) at the landscape-level
89 (see Fig. 1), *altitude* (i.e. elevation in meters above the alpine tree-line) and *vegetation cover* at

90 nest sites, and *year* (i.e. the phase of the rodent cycle). In accordance with the prediction, the
91 predation risk increased with landscape-scale primary productivity (max EVI) (Fig. 2a).
92 Landscape areas with the highest productivity level had 72% higher predation risk (odds ratio:
93 2.44, 95% CI [1.25, 4.77]) than landscapes with the lowest productivity level. The largest
94 contrast was between the lowest and intermediate max EVI-levels (Fig. 2a), while the contrast
95 between the highest and the intermediate levels was not significant (Supplementary Table 2).
96 However, as a model with max EVI as a linear, continuous predictor variable appeared to predict
97 predation risk about equally well (Fig. 2a, Supplementary Table 3), the evidence for a non-linear
98 effect is not strong. Within the ecotone transects the predation risk increased linearly with altitude
99 (Fig. 2b); an increase of 100 m yielded 43% higher predation risk (odds ratio: 1.91, 95% CI
100 [1.32, 2.81]). Moreover, nests with very little vegetation cover had 112% higher predation risk
101 (odds ratio: 3.26, 95% CI [1.35, 8.69]) than nests that were almost totally concealed by the
102 ground vegetation. The largest contrast was between the lowest and the intermediate cover levels
103 (Fig. 2c). As expected, altitude and vegetation cover were negatively correlated (Spearman $r = -$
104 0.30), but only moderately, owing to much small-scale patchiness in vegetation cover. A model
105 without cover included yielded an even stronger effect of altitude (odds ratio: 2.48, 95% CI [1.71,
106 3.72]). Finally, predation risk peaked in the crash year 2012 of the 4-year rodent cycle (Fig. 2d)
107 when it was 495% higher (odds ratio: 11.08, 95% CI [5.11, 26.68]) than in the preceding rodent
108 pre-peak year 2010 and 46% higher than the following pre-peak year in 2014 (odds ratio: 1.92,
109 95% CI [1.07, 3.50]).

110 We were able to attribute 54% of predation events to either mammals or birds based on marks left
111 on a plasticine egg in the experimental nest. The majority (80%) of these events with known
112 predator type were due to bird predation (beak marks), but there were no apparent trends in this
113 proportion in space or time.

114 The difference in nest predation risk between landscape areas with contrasting primary
115 productivity, located some tens of kilometers apart in our sub-arctic study region, was of similar
116 magnitude to those previously found across major latitudinal, bio-climatic tundra zones several
117 thousand kilometers apart in the Canadian Arctic¹⁹. The Canadian study also used experimental
118 nests with quail eggs, but did not measure primary productivity or control for the strong impact of
119 the rodent cycle²¹. Thus, our study provides a more direct test of the prediction from food web

120 theory^{17,22}; i.e. that a negative impact of increased primary productivity on intermediate trophic
121 level in the food web (that includes ground nesting birds) is mediated through enhanced
122 predation.

123 While the effect of primary productivity and nest site vegetation cover was according to the
124 prediction, the enhanced predation risk with increasing altitude is intriguing. The altitude effect
125 was strong even when nest site vegetation cover was corrected for in the GLMM model. This
126 indicates that the increased predation pressure with altitude did not result from increased nest
127 visibility. A mechanism that may underlie the altitude effect is a constant proportional spillover
128 of mobile predators (e.g. corvids) from the more productive (low-altitude) onto the less
129 productive (high-altitude) sections of the tundra landscape²², causing an increasing predator-prey
130 ratio with increasing altitude. Such risk gradients resulting from shifting victim-enemy ratios
131 have been demonstrated for other organisms (e.g. insects)²³. In our case an altitudinal risk
132 gradient imply that bird species associated with high-altitude alpine vegetation zones may be
133 particularly vulnerable to climatic warming, a prediction that seems to be consistent with bird
134 population trends from other alpine regions⁶.

135 As expected, the predation risk peaked in the crash year (2012) of the regional-scale, 4-year
136 rodent cycle. However, predation risk estimates did not quite exhibit the expected symmetrical,
137 one-year lagged cycle relative to the rodent dynamics²⁰, since the predation risk in the rodent pre-
138 peak year 2014 did not drop to the low level of the pre-peak year 2012. Accordingly, the link
139 between the population dynamics of ptarmigan and the rodent cycle appear presently weaker than
140 it was four to five decades ago²⁴. Increased availability of food sources such as carrion from
141 ungulate populations²⁵, may have caused a decoupling from the rodent cycle due to omnivore
142 nest predators. Inter-annual variation and long-term changes in population density and breeding
143 phenology within the community of ground nesting birds may also have disturbed the match
144 between the rodent cycle and nest predation risk.

145 Like previous studies, we have resorted to time-for-space substitution¹⁷ and experimental prey
146 items²⁶ for inferring that tundra ecosystems in a warming climate may become subjected to a
147 trophic cascade that yields increased predation pressures on endemic biodiversity. Indeed,
148 although our 5-year study is relatively long-term - especially in context of nest predation studies¹⁴
149 - it is nevertheless too short to simultaneously study temporal trends in climate, vegetation

150 productivity and predation. However, food web theory²² predicts predation to increase with
151 primary productivity regardless of whether the productivity increases across space or time.
152 Moreover, when we infer that nest predation risk is enhanced when primary production increases
153 in tundra ecosystems, we also borrow support from analogous empirical findings from other
154 ecosystems, where primary productivity has been boosted because of human land use. In
155 particular, experimental nests in forest ecosystems have higher predation rates when the forest is
156 encroached by more productive agricultural fields^{27, 28}. Finally, generalist predators originally
157 belonging to boreal ecosystems are presently increasing in the high north^{3, 5, 25}. In our study
158 region, omnivorous corvids (*Corvus* spp.) numerically dominate the predator guild across the
159 focal alpine ecotone²⁹ and are major predators of tundra bird nests³⁰. New studies and
160 technologies are much needed to reveal how different predator species are responding to a
161 greening tundra and how this affects bird species with different nesting habitats and life history
162 strategies.

163 Increased productivity (greening) is a fundamental tundra ecosystem response to global warming
164 likely to have cascading impacts in terms of changed trophic interactions in the food web^{3, 5}. By
165 here substantiating empirically the prediction from food web theory, that arctic greening leads to
166 increased predation pressures on vulnerable prey species, our study contributes to an improved
167 understanding of how climate change may affect arctic ecosystems through a trophic cascade.
168 Unravelling such changed interactions in tundra food webs may also be helpful for biodiversity
169 conservations under climate change¹¹. While the ongoing greening of the Arctic may be
170 impossible to counteract by means of local management, actions made to halt the increase of
171 generalist predators may nevertheless be a management option to preserve alpine-arctic birds in a
172 warming climate. Indeed, such actions are currently implemented in northern Fennoscandia to
173 safeguard the critically endangered population of lesser white-fronted goose (*Anser erythropus*)³¹.

174

175 Correspondence and requests for materials should be addressed to R.A.I.

176

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183

184 **Author contributions**

185 RAI and JAH conceived the study. JAH and JUJ analyzed the data. AVT, MJG and MAS
 186 conducted the experiment. RAI wrote the manuscript with contribution from all authors.

187

188 **Competing interests**

189 There are no competing interests.

190 **References**

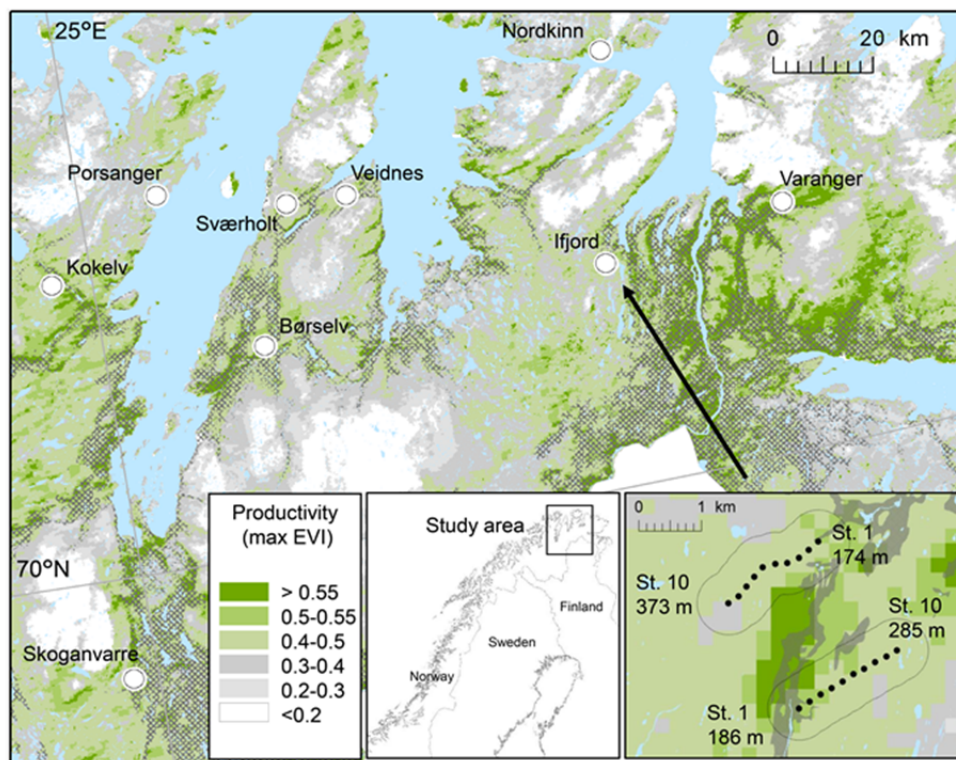
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293

294 **Fig. 1. Study design.** Map of the study region in northern Scandinavia (middle inset map) with
 295 the location of the 9 landscape areas (white dots). The right inset map exemplify how the 2
 296 altitudinal ecotone transects were placed within each landscape area, where black dots are the 10
 297 nest sites per transects. The altitudes (meters above sea level) are given for lowest and highest
 298 sites, while the shapes around each transect denote the buffer zones over which max EVI was
 299 estimated for each landscape area. The degree of greenness is proportional to max EVI according
 300 to the color scale bar inset. Cross-hatched areas denote sub-alpine mountain birch forest.

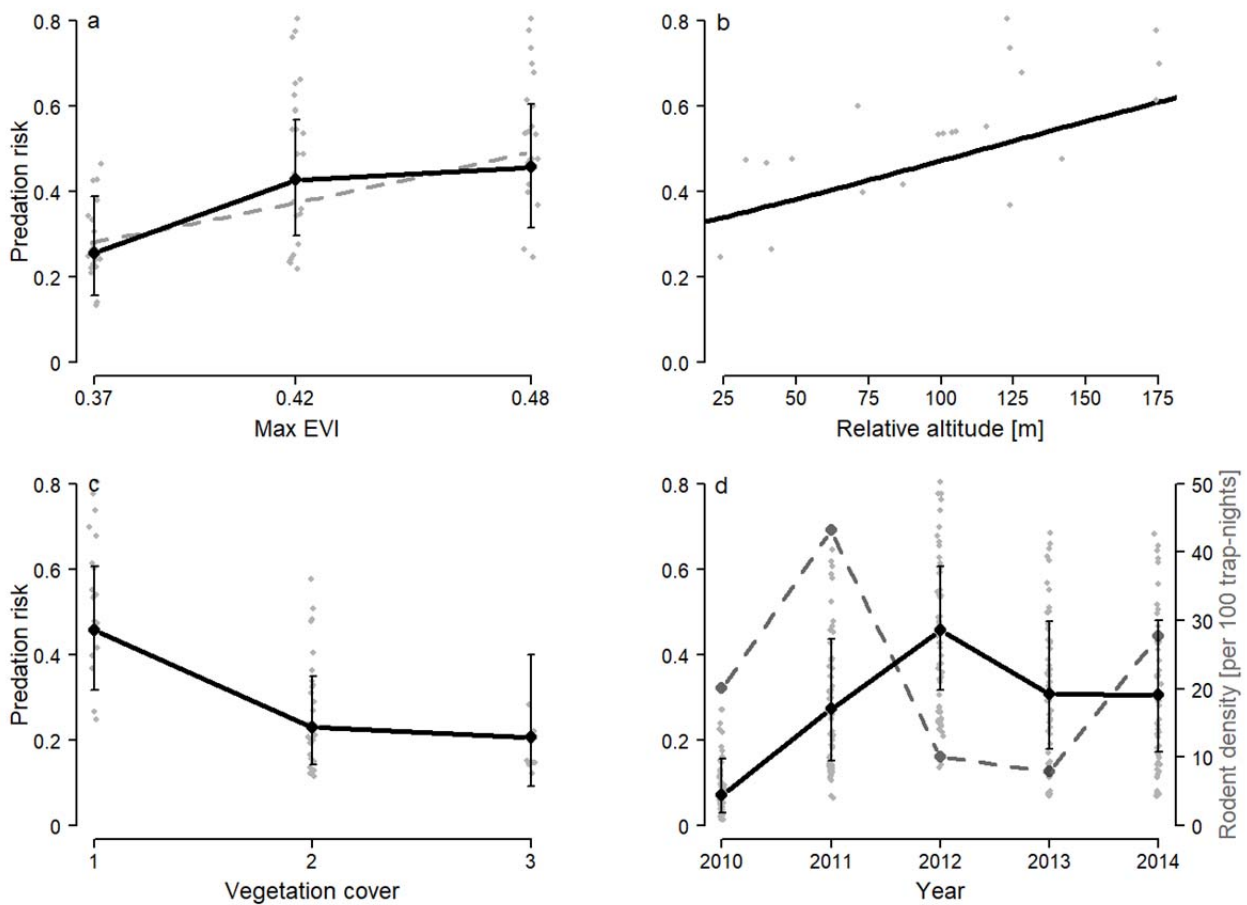


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303 **Fig. 2. Estimated nest predation risk per 14-days exposure periods.** Risk estimates are
 304 functions of (a) max EVI both modelled as a three-level categorical variable (black dots and
 305 lines) and as a continuous predictor (broken gray line), (b) altitude (meters) above the alpine tree-
 306 line, (c) three ordinal levels of vegetation cover and (d) year and the phases of the rodent
 307 population cycle. Error bars denote 95% confidence intervals for the fixed effects, while small
 308 gray dots are random effects from the GLMM. The multi-annual rodent density cycle is shown as
 309 a grey stippled curve in panel d.

310



311

312 **Methods**

313 Field work

314 Two altitudinal ecotone transects within each of 9 landscape areas (Fig. 1) were established with
315 a minimum distance of 2 kilometers between the transects in order to reduce the chance of
316 predation from the same predator individuals. The starting point of each transect was just above
317 the tree-line of the subalpine mountain birch (*Betula pubescens*) forest, which ranged about 50 –
318 350 meter above sea level among the landscape areas. From the starting point 10 experimental
319 nest-sites were placed at fixed 200 meter distance intervals (Fig. 1), generally upslope so as to
320 span the low-alpine to the middle-alpine vegetation zone within each transect. Typically, the low-
321 alpine zone is characterized by continuous vegetation with erect shrubs (e.g. *Betula nana*), while
322 in the middle-alpine zone the vegetation is more discontinuous with prostrate vascular plants and
323 increasing dominance of cryptogams³². At each nest site, we made an experimental nest similar to
324 nests of ptarmigan (*Lagopus* spp.) and waders (Charadriinae) by scraping a small bowl in the
325 ground by hand. Two eggs - one quail (*Coturnix* sp.) egg and one plasticine egg made to mimic a
326 quail egg - were placed in the nest. Quail eggs have similar coloration to the eggs of ground
327 nesting tundra birds (Supplementary Fig. 1). We used mixture of colored plasticine to create
328 similar plasticine eggs. The purpose of the plasticine eggs was to acquire predator identity from
329 bite marks³³. They were attached to the ground by a steel wire to hinder removal by the predators.
330 A small tape mark was placed at a fixed distance (10 meters) and angle from the nest to aid the
331 recovery of the nests. We used rubber gloves to minimize human scent that could attract
332 predators using olfactory cues. Predation on such experimental nests has been found to correlate
333 with real bird nests in tundra habitats³⁴, meaning that they are indicative of spatial and temporal
334 variation in *relative* predation risk. However, care should be taken not to extrapolate predation
335 rates on experimental nests to absolute predation rate on real nests. In particular, it is likely that
336 the eggs of experimental nests without incubating birds are more exposed than natural nests, and
337 thus more subjected to predators using vision (i.e. birds).

338 The amount of ground vegetation that could conceal the eggs was scored on a three-level ordinal
339 scale for each nest; 1: the eggs were fully visible from above, 2: some branches of vascular plants
340 intercepted the view of the eggs and 3: most of the eggs were concealed by vegetation cover (see
341 Supplementary Fig. 1). Also, natural bird nests in tundra habitats may vary much with respect to

342 vegetation cover both between and within species³⁵. We also measured the maximum height of
343 the vascular plants within a triangular sampling frame with sides of 40 cm centered on the nest.
344 These height measurements were strongly correlated with the ordinal vegetation level score (see
345 Supplementary Fig. 2). We used the ordinal scores as three levels of a categorical vegetation
346 cover predictor in the statistical analyses as to facilitate more robust statistical estimation of
347 putative interaction effects (see "Statistical analyses"). Small-scale patchiness of vegetation both
348 in the low- and middle-alpine vegetation zones, owing to mosaics of ridges and snow beds,
349 rendered the correlation between relative altitude and vegetation cover at the nest sites to be only
350 moderately negative ($r=-0.3$). This indicates that we were able to obtain relatively unbiased
351 estimates of the independent effects of primary productivity (at the landscape level), and altitude
352 and vegetation cover (at the nest site level).

353 The experimental nests were deployed during the week 23-30 June each year, which is within the
354 incubation period for ground nesting tundra birds in the study region³⁵. All nests were recovered
355 14 days after deployment. This exposure period is shorter than the typical incubation periods for
356 ptarmigan and waders in tundra (range: 18-24 days³⁵). On the other hand, experimental nests
357 without incubating birds are probably overall more exposed than natural nests and we expected
358 the shorter exposure time to compensate for this. Nests where at least one egg was missing
359 without any remaining signs or evidently eaten at the site (egg shells remaining), were recorded
360 as predation events. The identity of predators was determined as bird and mammal when marks
361 from beaks or teeth, respectively, were left on the plasticine eggs.

362 Small rodents (voles and lemmings) had a distinct 4-year population cycle with strong inter-
363 specific and spatial synchrony across the study region^{31,36,37}. In order to determine the phases of
364 the rodent cycle during the 5-year study period we used data from the trapping program described
365 in ref. 36 conducted near the landscape areas in Varanger, Nordkinn and Ifjord (see Fig. 1). The
366 rodent population trajectory shown in Figure 2d is presented as number of snap-trapped rodents
367 per 100 trap-nights in summer.

368

369 Landscape area primary productivity

370 We used MODIS Enhanced Vegetation Index (EVI) as a measure of vegetation productivity at
371 the spatial scale of the 9 landscape areas included in this study. Both NDVI and EVI are suitable
372 proxies for vegetation productivity, but the advantages of EVI include a lower sensitivity to
373 viewing angle variations and a smoother, more symmetrical seasonal profile with a narrower
374 peak greenness period³⁸. The landscape scale was chosen as previous studies have shown that
375 nest predators typically are wide ranging and that landscape level characteristics are often
376 important predictors of predation rate³⁹⁻⁴¹. The most abundant nest predators in sub-arctic tundra
377 – red fox (*Vulpes vulpes*) and raven (*Corvus corax*) – have home ranges that most often exceed
378 the size of the landscape areas (>20km²) in this study^{42,43}. Moreover, we focused on the inter-
379 annual variation in site productivity (rather than within season variation) and selected temporal
380 and spatial resolution of the MODIS data expected to provide estimates that most robustly
381 reflected the difference in primary productivity among the landscape areas. Therefore, we chose
382 the MOD13Q1 product⁴⁴, which is a temporally coarse 16-day composite product with a pixel
383 size of 250 m. We extracted EVI data for the four 16-day periods covering the peak of the
384 growing season (day 177, 193, 209 and 225, representing late June – mid August) for the years
385 2010 – 2014. MODIS VI products are supplied with two measures of data quality, the Pixel
386 Reliability index (PR), which is a simplified 5-level ranking of overall pixel quality, and the
387 Vegetation Index Quality (VI QA). We used both these indices to judge the quality of the data on
388 a pixel level. We initially kept all pixels with a PR value of either 0 (=‘Good data – use with
389 confidence’) or 1 (=‘Marginal data – useful but look at other QA’). Since it was clear from visual
390 inspection of the data that some pixels with PR=1 contained erroneous values, we further
391 examined the VI QA, and kept only those pixels, which were in the best VI QA category (“VI
392 produced with good quality”). For each remaining pixel we calculated annual growing season
393 maximum EVI as the max EVI over the four 16-day periods. To obtain annual estimates of site
394 productivity for each of the 9 landscape areas, we used all pixels located within a 500 meter
395 buffer around the experimental nest sites within the landscapes (Fig. 1), and calculated the
396 average maximum EVI over all pixels within each landscape. We used estimates based average
397 max EVI over both buffer zones per landscape area (Fig. 1) because this yields estimates less
398 affected by local noise (measurement errors) than estimates based on smaller spatial scales and
399 subsets of pixels (i.e. transects within landscapes).

401 Statistical analyses

402 We analysed the data using Generalized Linear Mixed-effects Models (GLMM) with a logit-link
403 function applied to the binomial response variable that recorded predation events or non-events
404 per experimental nests. The predictions from this model are thus probabilities of predation (i.e.
405 predation risk). Fixed effects included in this model was landscape-scale *primary productivity*
406 (max EVI), relative *altitude* in the ecotone transects, nest *vegetation cover* and *year*. The max
407 EVI values per landscape area and year formed three non-overlapping groups with the following
408 averages and ranges of values: 0.37 [0.33, 0.38], 0.42 [0.40, 0.44], 0.48 [0.46, 0.54]. To better
409 facilitate tests of interaction terms and identification of possible non-linear effects, the
410 productivity predictor was modelled as a categorical variable with three nominal levels based on
411 the clusters of max EVI values. The means for the three max EVI were evenly spaced on a linear
412 scale and this facilitated the identification of possible non-linear effects based on estimates of
413 contrasts (see legend to Supplementary Table 2). Because the alpine tree-line was situated at
414 different altitudes across the study region (Fig. 1), we used *relative altitude* as a continuous
415 variable measured as the altitude difference (meters) between the lowest nest site adjacent to the
416 tree-line and the focal nest site in each transect. Year (2010-2014) and vegetation cover (ordinal
417 levels: 1, 2 and 3) was modelled as categorical variables. GLMMs were fitted using nest site
418 nested within transects nested within landscape as random effects⁴⁵, thus taking into account the
419 repeated censuses within nest sites, transects and landscapes. GLMMs were fitted using the lme4
420 package in the software R (3.4.0)⁴⁶.

421 Model selection started from four pre-defined candidate models⁴⁷. In addition to
422 considering the main baseline model containing only additive effects of the four predictors
423 (which all were statistically significant), we also considered three additional models that included
424 biologically meaningful interaction terms (see footnotes to Supplementary Table 1): One with
425 altitude*max EVI, one with year*max EVI and one with year*altitude. Log-Likelihood ratio tests
426 and AIC-values were used to compare candidate models and to identify the most parsimonious
427 model (see Supplementary Table 1). Logit-scale parameters estimates (slope parameters and
428 contrasts) and associated test statistics from the most parsimonious model are provided in
429 Supplementary Table 2, while odds ratios with 95% confidence intervals are presented in the
430 main text. Predation risk estimates on a probability scale for all levels and full ranges of the

431 predictor variables are presented in Fig. 2. We also compared a model with max EVI taken as
432 continuous, linear predictor against the best model with the same predictor taken as a categorical
433 variable (see above). This comparison was made based a Log-Likelihood test and AIC-values for
434 the two models (Supplementary Table 3). As a second check of non-linear effect of max EVI we
435 tested both the contrast (i.e. difference) between Max EVI levels 2 and 1 and between levels 3
436 and 2 (see caption to Supplementary Table 2).

437 The GLMMs were fitted using the Laplace approximation⁴⁵ and the "bobyqa" optimizer in
438 the package lme4. The models were checked for constant variance of the residuals, presence of
439 outliers and approximate normality of the random effects. We also checked for potential
440 collinearity/confounding between predictors of which only altitude and vegetation cover were
441 moderately confounded (Spearman $r = -0.30$). Finally, we estimated pseudo- R^2 values for the the
442 most parsimonious GLMM model based on the function *r.squaredGLMM* in the *MuMIn* package
443 in the software R⁴⁸. Pseudo- R^2 values both for the fixed effects only (marginal model) and fixed
444 and random effects combined (full model), as well as for the two computation methods
445 ("theoretical" and "delta") provided by the R-package, are given in Supplementary Table 2.

446 About one-half of the predation events (46%) could not be attributed to either mammals
447 or birds because the plasticine eggs was removed or did not have clear marks. This combined
448 with the fact that 80% of the events with known predator type were due to birds, yielded predator
449 identity data that were unsuitable for GLMM analyses. To explore whether there were significant
450 patterns in the proportions of events with known predator type, the data were aggregated into a
451 set of two-dimensional cross-tables; i.e. one for each of the main predictor variable max EVI,
452 altitude, vegetation cover and year. The altitudes were binned on three ordinal classes per transect
453 for this table. The cross-tables were subjected to binomial goodness of fit tests; i.e. assessing
454 whether there were significant deviances from constant proportions across the levels of each
455 predictor variable.

456

457 Data availability

458 The data that support the findings of this study are available from the corresponding author upon
459 request.

460

461 Code availability:

462 The R code used to analyze the data are available from the corresponding author upon request.

463

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