Biological Conservation 320 (2026) 111915

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Predicting the occurrence of a protected orchid and other old-growth specialists: A cost-effective approach using open geodata

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ARTICLE INFO

Keywords:
Boreal forest
Conservation planning
Goodyera repens
Orchid
Species distribution model
Species of conservation concern

ABSTRACT

Predicting species occurrence across landscapes is fundamental to conservation planning, yet many approaches rely on costly field data. We developed and validated a model for predicting the occurrence of *Goodyera repens*, a threatened orchid associated with old-growth coniferous forests and legally protected in Sweden. Using 4805 plots from the Swedish National Forest Inventory (2013–2022), we modelled occurrence probability with logistic regression based on three predictors derived from publicly available geodata: basal area, soil moisture, and proportion of old forest in the surrounding landscape. Basal area had the strongest positive effect on occurrence ($\beta = 1.01$, $\Delta AIC = 61.5$), followed by proportion of old forest (≥80 years) within 100 m ($\beta = 0.61$, $\Delta AIC = 30.5$), while soil moisture had a negative effect ($\beta = -0.37$, $\Delta AIC = 5.5$). Model validation in southeastern Sweden using 227 independent records from the Swedish Species Observation System yielded an AUC of 0.88, with predicted probabilities at validation locations nearly 12 times higher than at random background points. The model also performed well for other conifer-associated species of conservation concern (AUC = 0.79), suggesting it captures general characteristics of high-quality conifer forest habitat. Performance was comparable in independent validations in central and northern Sweden (AUC = 0.91 for *G. repens* and 0.77 for indicator species), demonstrating geographic transferability. Our results show that simple geodata-based models can effectively predict the distribution of declining old-forest specialists, offering a cost-effective tool for habitat screening and forest management decisions in production landscapes.

1. Introduction

Global biodiversity loss continues at an unprecedented rate, with current extinction rates estimated to be 100–1000 times higher than natural background rates (IPBES, 2019). Habitat degradation and land-use changes serve as primary drivers of ecosystem disruption and species decline worldwide (Maxwell et al., 2016). Forest ecosystems, which harbour approximately 80% of terrestrial biodiversity, are particularly affected by anthropogenic activities that homogenize once-heterogeneous landscapes into structurally uniform stands (FAO, 2020; Paillet et al., 2010).

The ability to predict species occurrence across landscapes is fundamental to conservation planning and effective responses to biodiversity loss (Margules and Pressey, 2000; Guisan et al., 2013). Species distribution models can guide the identification of suitable habitat, inform land-use decisions, and help prioritize areas for protection or management interventions (Edenius and Mikusiński, 2006; Elith and Leathwick, 2009; Franklin, 2010). However, many predictive approaches rely on detailed field data or complex environmental variables that are costly to obtain and difficult to apply at large scales (Guisan and Thuiller, 2005). In contrast, models based on openly available geodata—such as remotely sensed forest attributes and national land cover databases—offer a practical alternative that can be applied across entire regions at minimal cost (He et al., 2015; Lehtomäki et al., 2015). Such approaches are particularly valuable for threatened species in production landscapes, where rapid assessment tools are needed to inform forestry planning and ensure compliance with conservation legislation (Pecchi et al., 2019; Mikkonen et al., 2023).

The need for efficient prediction tools is pressing in boreal forests, which represent nearly one-third of global forest cover and provide essential ecosystem services including timber production, climate regulation, carbon sequestration, and biodiversity maintenance, though the demand for wood products is itself a primary driver of biodiversity loss in these forests (Gauthier et al., 2015; Bradshaw et al., 2009). Intensive forestry practices have substantially simplified these landscapes, resulting in altered microclimates and diminished refuges for

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https://doi.org/10.1016/j.biocon.2026.111915
Received 23 March 2026; Received in revised form 12 May 2026; Accepted 15 May 2026
Available online 18 May 2026

species sensitive to environmental change (Gustafsson and Perhans, 2010; Halpern, 1989; Heithecker and Halpern, 2007). Species dependent on old-growth forest characteristics—including stable microclimates, structural complexity, and ecological continuity—are particularly vulnerable to habitat loss caused by modern forestry operating on rotations that prevent forests from developing mature characteristics (Nordén et al., 2014; Lindenmayer et al., 2006). In Fennoscandia, intensive forestry has led to significant declines in old-growth forests and associated biodiversity (Kouki et al., 2001; Kuuluvainen et al., 2015). In Sweden, approximately 18% of forest-associated species are classified as threatened or near-threatened on the Swedish Red List (SLU ArtDatabanken, 2026), with many populations declining and becoming increasingly fragmented. Previous studies have demonstrated negative effects of logging across various taxonomic groups, including vascular plants, bryophytes, lichens, and fungi (Bergman et al., 2025, 2026; Hylander and Weibull, 2012; Johansson et al., 2018; Dahlberg et al., 2001; Lõhmus and Kull, 2011).

One species for which simple geodata-based predictive tools would be particularly valuable is *Goodyera repens* (L.) R. Br., a small evergreen orchid associated with old-growth coniferous forests. The species occurs primarily in mature, conifer-dominated stands with high basal area, well-developed moss carpets, and stable microclimate, and exhibits high sensitivity to clear-cutting and other interventions that reduce stand density (Johansson et al., 2025, 2026; Lõhmus and Kull, 2011). In Sweden, *G. repens* is classified as Vulnerable (VU) on the Red List (SLU ArtDatabanken, 2026) and is legally protected since 1992 under successive Swedish species protection legislation (currently SFS 2007:845), which prohibits intentional damage or removal of individuals. This legal status can halt planned logging operations where populations occur, making *G. repens* a contentious topic in forest management debates (Johnson, 2014; Widenfalk and Weslien, 2009). Recent research has documented a 66% decline in *G. repens* occurrence across Swedish forests over the last 30 years (Johansson et al., 2026) and stands containing the species shown to harbour more species of conservation concern than randomly selected stands, likely because *G. repens* shares habitat requirements with many other old-forest specialists (Johansson et al., 2025). Despite the species' ecological and legal significance, efficient landscape-scale methods for predicting its occurrence remain underdeveloped.

The aim of this study was to develop and validate an occurrence model for *G. repens* using explanatory variables derived exclusively from publicly available geodata, enabling model predictions to be generated across the landscape without access to restricted datasets. Specifically, we assessed whether basal area, soil moisture, and the proportion of old forest in the surrounding landscape can predict the species' occurrence probability. We evaluated model performance using independent occurrence records and tested whether the model can also predict the occurrence of other species of conservation concern, to assess its broader utility for conservation planning in managed boreal forests.

2. Methods

2.1. Study species

Goodyera repens (L.) R. Br. is a small, evergreen orchid (Fig. 1f) with a circumpolar distribution across the boreal and hemiboreal regions of Europe, Asia, and North America. The species reproduces both vegetatively through rhizomes and sexually via wind-dispersed seeds. Like many orchids, *G. repens* depends on mycorrhizal fungi not only for germination but throughout its life cycle, receiving both carbon and

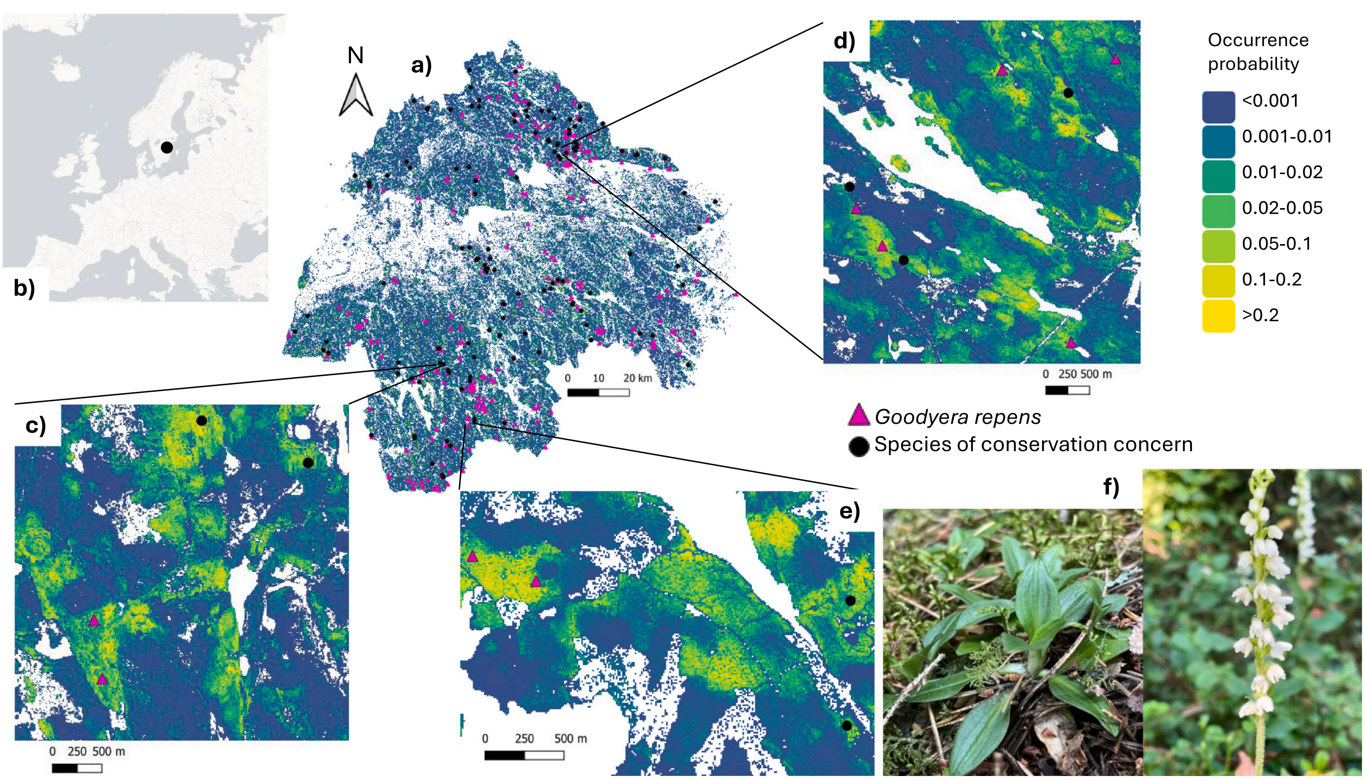

Fig. 1. Predicted occurrence probability of *Goodyera repens* across forest land in Östergötland county, southeastern Sweden (a), with independent validation records (purple triangles: *G. repens*; black circles: other species of conservation concern) from the Swedish Species Observation System (Artportalen). Panel (b) shows the location of the study area within Europe; panels (c–e) show zoomed-in examples of predicted probabilities and validation records; and panel (f) shows *G. repens* with its evergreen leaf rosette and flowering inflorescence. The prediction model was developed using occurrence records from the Swedish National Forest Inventory covering the main distribution of *G. repens* in Sweden (Johansson et al., 2026), with all explanatory variables derived from publicly available geodata. Europe basemap: © OpenStreetMap contributors, © CARTO. Photos: V. Johansson.

nitrogen from its fungal partners even as a photosynthetic adult (Cameron et al., 2006). *Goodyera repens* primarily associates with saprotrophic rhizoctonia-forming fungi (*Tulasnella* and *Ceratobasidium*) that decompose organic matter in the forest floor (Liebel et al., 2015), making the species dependent on the stable microclimate and well-developed humus layers characteristic of mature coniferous forests. Throughout its range, *G. repens* is typically found in mature coniferous forests with old-growth characteristics (Widenfalk and Weslien, 2009; Lõhmus and Kull, 2011; Johnson, 2014).

2.2. Modelling occurrence probability based on open geodata

Occurrence data for *Goodyera repens* were obtained from the Swedish National Forest Inventory (NFI; Fridman et al., 2014), a nationwide field-based monitoring programme conducted on permanent circular sample plots (10 m radius) systematically distributed across Sweden. The inventory records a long list of forest variables and species, but in this study we used only the occurrence data (presence/absence) of *G. repens*, since our aim was to build a model based solely on publicly available predictors. Plot coordinates are not publicly available for confidentiality reasons. Our analysis used data covering the primary distribution of *G. repens* in Sweden (Johansson et al., 2026) over a 10-year period (2013–2022), resulting in 4805 inventory plots. For plots with multiple inventories, only the most recent was retained.

Three predictor variables, basal area, forest age, and soil moisture, were derived from openly available geodata at 10 × 10 m resolution, matching variables shown to be important for explaining the occurrence of the species in more detailed analyses (Johansson et al., 2025). First, basal area (m^2/ha) was obtained from the Swedish Forest Agency's nationwide raster (Skogsstyrelsen, 2025), which is modelled from airborne laser scanning data combined with National Forest Inventory plot measurements as training data. Second, soil moisture index was obtained from the Swedish National Land Cover Database (NMD). This wall-to-wall topographic index combines Depth to Water and a Soil Topographic Wetness Index, derived from a high-resolution elevation model integrated with soil data, providing a continuous estimate of soil moisture conditions across Sweden (Klein, 2019). For each NFI plot, values were extracted using a 10 m buffer around the plot centre. Third, the proportion of old forest in the surrounding landscape was calculated from tree age rasters for pine (*Pinus sylvestris* L.) and spruce (*Picea abies* (L.) H. Karst.), provided by the Swedish University of Agricultural Sciences (SLU Skogsdatalabbet, 2025). These are wall-to-wall modelled raster data combining NFI plot measurements with satellite imagery, rather than direct field measurements. The two age rasters were combined by taking the maximum value for each pixel, representing the age of the oldest coniferous trees present. This raster was converted to a binary raster where pixels above an age threshold were assigned 1 and younger pixels 0. The proportion of old forest was then calculated as the focal mean within a circular moving window. Different age thresholds (60–130 years) and buffer radii (100–5000 m) were tested, and the combination resulting in the lowest AIC (≥80 years within 100 m) was selected (Appendix A, Fig. A1). The 100 m radius represents the smallest scale tested, as smaller radii would largely overlap with the focal stand itself rather than capture the surrounding landscape context.

Occurrence probability was modelled using logistic regression (generalised linear model with binomial distribution) with the presence/absence (1/0) of *G. repens* as the response variable and basal area, soil moisture, and the proportion of old (≥80 years) forest in the surrounding landscape as predictors. Each predictor was first evaluated individually against a null model, and all three improved model fit. They were then combined in a multivariate model, where AIC-based selection retained all three as their removal would have increased AIC by more than 2 units. ΔAIC values in Table 1 indicate the relative contribution of each predictor in the full model. The fitted model was then used to predict *G. repens* occurrence probability across the landscape at the 10 × 10 m resolution of the predictor rasters.

Table 1
Parameter estimates from the final occurrence model for *Goodyera repens*. Estimates are standardized coefficients. SE = standard error; ΔAIC = increase in Akaike Information Criterion when removing each variable from the full model; NMD = the Swedish National Land Cover Database.

Variable	Estimate (β)	SE	z	p	ΔAIC
Basal area (m^2/ha)	1.01	0.13	7.63	<0.001	61.5
Proportion old forest (100 m)	0.61	0.10	5.78	<0.001	30.5
Soil moisture index (NMD)	−0.37	0.14	−2.63	0.009	5.5

2.3. Model validation and transferability

Model performance was evaluated using 928 independent occurrence records of *Goodyera repens* from the Swedish Species Observation System (SLU ArtDatabanken, 2025) from a 10,000 km^2 in south-eastern Sweden (the county of Östergötland, Fig. 1a). To ensure spatial independence, occurrence points were thinned to a minimum distance of 400 m, which is twice the distance at which 100 m buffers used for calculating proportion old forest (see below) no longer overlap. This resulted in 227 spatially independent validation points (Fig. 1). Model discrimination was assessed using the Area Under the Receiver Operating Characteristic Curve (AUC), comparing predicted probabilities at occurrence locations with 2320 random background points. AUC values range above 0.8 indicate good performance.

Model transferability was evaluated using independent occurrence records of 42 conifer-associated species of conservation concern (Nitare, 2019) from the Swedish Species Observation System (SLU ArtDatabanken, 2025) across Östergötland. Species were selected based on their ecological association with spruce and pine forests, including mycorrhizal fungi, wood-decay fungi, lichens, bryophytes, vascular plants, and saproxylic insects (Appendix A). To ensure spatial independence, occurrence points were thinned to a minimum distance of 400 m, and a maximum of five records per species were retained to prevent common species from dominating the validation. This resulted in 126 spatially independent validation points from 34 species (Fig. 1). Model discrimination was assessed using the Area Under the Receiver Operating Characteristic Curve (AUC). This threshold-independent metric assesses the model's ability to distinguish between presence records and background locations, where an AUC of 0.5 indicates performance no better than random and 1.0 represents perfect discrimination (Swets, 1988). Specifically, we compared the predicted probabilities at independent occurrence locations with 1260 random background points (pseudo-absences) to characterize the model's performance across the landscape (Elith et al., 2006).

To further assess model transferability across a larger geographic gradient, we evaluated the model on independent occurrence data from central and northern Sweden, in the counties of Västmanland, Hälsingland and Ångermanland (spanning latitudes 59.3° to 64.4° N). Occurrence records of *G. repens* and of the conifer-associated indicator species were obtained from the Swedish Species Observation System (SLU ArtDatabanken, 2025). Occurrence points were thinned to a minimum distance of 400 m, following the same procedure as in the Östergötland validation. For *G. repens*, we randomly subsampled 500 occurrence points and 5000 random background points. For the indicator species, a maximum of five records per species were retained (resulting in 162 occurrence points) and these were compared against 1620 random background points (10:1 ratio). Model discrimination was assessed using AUC in both cases.

3. Results

The occurrence probability of *Goodyera repens* increased with basal area and the proportion of old forest within 100 m, and decreased with soil moisture (Fig. 2, Table 1). Basal area had the strongest positive effect, followed by proportion of old forest (≥80 years) within 100 m,

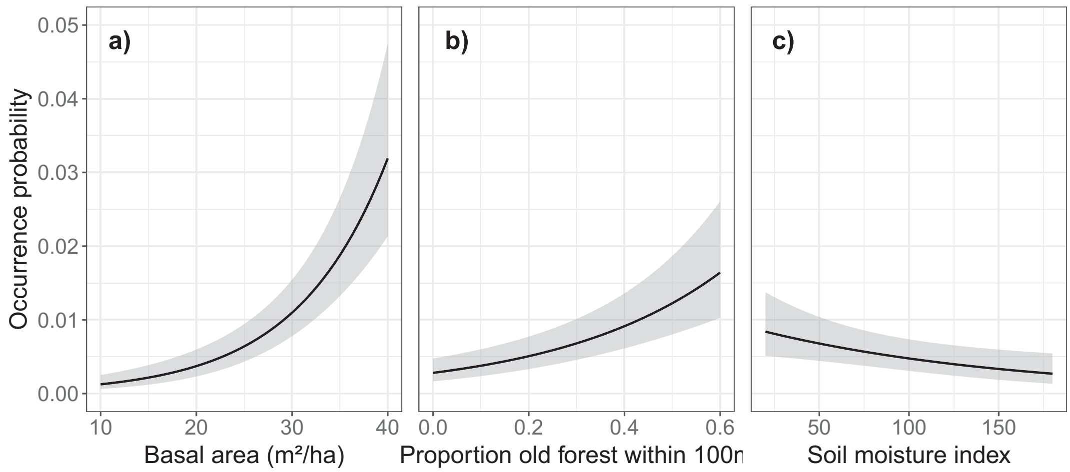

Fig. 2. The occurrence probability of *Goodyera repens* in relation to a) basal area, b) proportion of old forest (≥80 years) within 100 m, and c) soil moisture. Predictions are from a binomial GLM (parameter estimates are shown in Table 1) with other variables held at their mean values. Shaded areas represent 95% confidence intervals.

while soil moisture index had a weaker negative effect. The best model (lowest AIC) used an age threshold of 80 years and a buffer radius of 100 m (Appendix A, Fig. A1). Variable importance, assessed by the increase in AIC when removing each variable from the final model, indicated that basal area contributed most to model fit (ΔAIC = 61.5), followed by proportion old forest (ΔAIC = 30.5) and soil moisture index (ΔAIC = 5.5).

3.1. Model validation

Predicted occurrence probabilities at locations where *Goodyera repens* had been reported in Swedish Species Observation System (Fig. 1a with zoomed-in examples in Fig. 1c–e) were approximately 12 times higher than at random points across the landscape (median 0.040 vs 0.0034; Fig. 3a). The model achieved an AUC of 0.88. Across all forest pixels in Östergötland, the predicted occurrence probability followed a heavily right-skewed distribution, with a median of 0.003 and a mean of 0.009. Predicted probabilities exceeding 0.05 and 0.1 were restricted to 3.3% and 1.1% of the pixels, respectively.

Predicted occurrence probabilities at locations where conifer-associated species of conservation concern had been reported were approximately 5 times higher than at random points (median 0.016 vs 0.0033; Fig. 3b). The model achieved an AUC of 0.79.

Predictive performance was comparable to that in Östergötland (Fig. A2) and consistent across the three northern regions. For *G. repens*, AUC ranged from 0.89 to 0.93 (Västmanland: 0.93, Hälsingland: 0.89, Ångermanland: 0.91), and for indicator species from 0.75 to 0.81 (Västmanland: 0.81, Hälsingland: 0.75, Ångermanland: 0.77).

4. Discussion

Our study demonstrates that the occurrence of *Goodyera repens* can be predicted with good accuracy using publicly available geodata. The model achieved an AUC of 0.88, indicating ‘excellent’ discriminatory ability according to the classification by Swets (1988). Furthermore, the predicted occurrence probabilities at independent validation locations were nearly 12 times higher than at random background points, confirming the model's high precision in identifying suitable habitat across the landscape. Moreover, the model showed acceptable transferability to other conifer-associated species of conservation concern (AUC = 0.79), with predicted probabilities approximately 5 times higher at occurrence locations of than at random points, suggesting that it captures general characteristics of high-quality conifer forest habitat.

Predicting species distributions efficiently across large areas remains

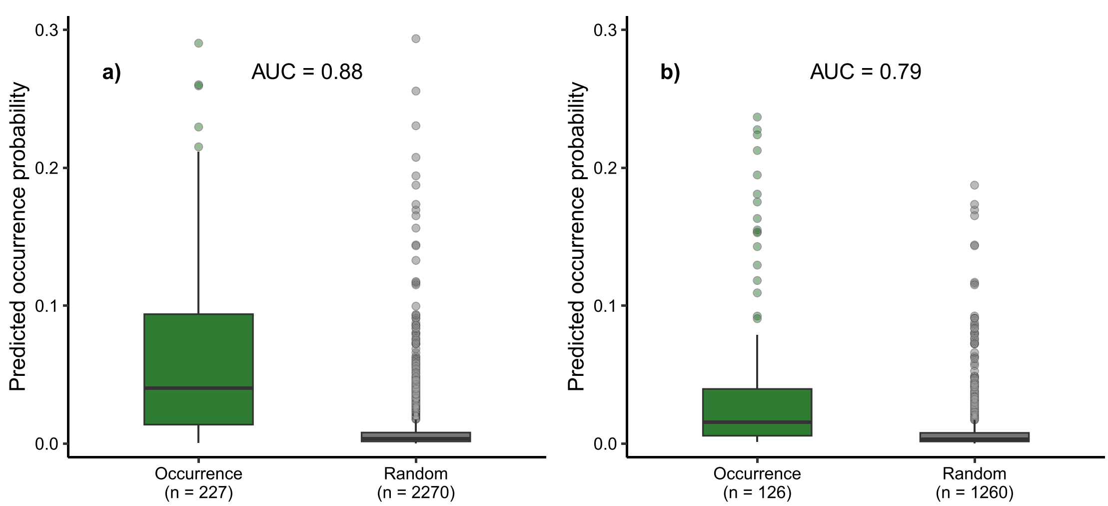

Fig. 3. Predicted occurrence probability at independent validation locations compared to randomly sampled background locations. (a) Validation against *Goodyera repens* occurrences from Artportalen (n = 227) compared to random points (n = 2270). (b) Validation against 36 conifer-associated species of conservation concern from Artportalen (n = 126) compared to random points (n = 1860). AUC = Area under the receiver operating characteristic curve.

a central challenge in conservation biology, particularly in production landscapes where land-use decisions must balance economic and ecological objectives (Margules and Pressey, 2000; Guisan et al., 2013). While species distribution models have become essential tools for conservation planning, their application is often constrained by the need for detailed environmental data that are costly or difficult to obtain at relevant scales (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). Our results show that publicly available relatively simple raster data on forest structure can provide sufficient predictive power for practical applications, even for a species with specialized habitat requirements. This finding supports the growing recognition that remotely sensed data can complement or even substitute for field-based measurements in distribution modelling (He et al., 2015). The approach is readily transferable to other regions with similar geodata infrastructure and could potentially be applied to other forest-dwelling species with known associations to stand structure and forest age.

Basal area emerged as the strongest predictor of *G. repens* occurrence, consistent with field-based studies identifying it as the most important predictor across models of occurrence, colonization, and extinction (Johansson et al., 2026). High basal area creates closed-canopy conditions that maintain stable humidity (Vesala et al., 2005) while reducing competition from light-demanding species (Reich et al., 2012; Hekkala et al., 2023). However, high basal area alone is probably not sufficient to identify suitable *G. repens* habitat, as the general densification of Swedish forests has increased basal area without compensating for the loss of old-growth characteristics that accumulate only with stand age (Johansson et al., 2026; Kyaschenko et al., 2022). Truly suitable stands therefore combine high basal area with mature forest structure, including well-developed moss layers and stable microclimatic conditions that this orchid requires (Johansson et al., 2026). The positive effect of proportion old forest within 100 m likely reflects both stand structure and landscape context. A high proportion of surrounding old forest indicates that occurrences are situated within larger, continuous forest patches rather than at edges, reducing exposure to wind, desiccation, and microclimatic fluctuations that negatively affect forest interior specialists. Additionally, proximity to existing populations may facilitate colonization, although the species' extremely low colonization rates, only 0.7% over approximately 10 years (Johansson et al., 2026), suggest that edge effects on habitat quality may be more important than dispersal limitation at this spatial scale. The small radius at which this variable was most predictive (100 m) has practical implications for retention forestry, suggesting that maintaining larger, contiguous old forest patches could be more effective than preserving small, isolated remnants (Gustafsson et al., 2012; Fedrowitz et al., 2014). The 80-year threshold that best predicted occurrence is biologically meaningful in the context of Swedish forestry, where current rotation periods typically range from 65 to 100 years (Felton et al., 2017). Forests ≥80 years are unlikely to have been clear-cut, and have therefore had time to develop the closed canopy, continuous moss layers, and stable humidity that *G. repens* depends on, features also reflected in the strong basal area effect. The negative relationship between soil moisture and occurrence probability reflects the species' preference for mesic conditions. *G. repens* is typically associated with well-drained coniferous forests with feather moss carpets, avoiding waterlogged sites where *Sphagnum* mosses dominate (Lõhmus and Kull, 2011). However, soil moisture had a notably weaker effect than basal area ($\Delta AIC = 5.5$ vs 61.5 for basal area), suggesting that *G. repens* is relatively tolerant of moisture variation as long as the broader stand conditions are suitable.

The model's ability to predict occurrences of other conifer-associated species of conservation concern suggests that the environmental variables captured—basal area, proportion old forest, and soil moisture—represent fundamental characteristics of high-quality conifer forest habitat that benefit multiple taxa (Jokela et al., 2018). The 34 indicator species used for validation included fungi, bryophytes, lichens, and vascular plants, among which many depend on mature forest conditions with structural complexity (Nordén et al., 2013; Nirhamo et al., 2025). The lower but still acceptable AUC (0.79) compared to the focal species validation (0.88) is expected, as these species have varying habitat requirements and ecological niches. Nevertheless, this finding indicates that the model has broader conservation utility beyond *G. repens* alone, potentially serving as a general tool for identifying high-value conifer forest habitats.

A key strength of this study is the use of entirely open geodata, making the approach reproducible and scalable across Sweden and potentially other Nordic countries with similar data infrastructure (He et al., 2015; Lehtomäki et al., 2015). The Swedish Forest Agency's basal area raster and the National Land Cover Database provide standardized, nationally consistent data that enable large-scale habitat mapping without the need for costly field surveys. This is particularly valuable given the ongoing decline of *G. repens* populations (Johansson et al., 2026) and the need for efficient tools to identify remaining habitat. The model provides a practical tool for prioritizing areas for field verification and conservation attention (Guisan et al., 2013; Mikkonen et al., 2023). Given that field surveys for *G. repens* are time-consuming and the species can be difficult to detect without systematic searching, geodata-based predictions can help focus survey efforts on locations with higher occurrence probability. This is particularly relevant in the context of forest management planning, where identifying potential *G. repens* habitat before logging operations could help avoid conflicts and ensure compliance with species protection legislation (Pecchi et al., 2019). The demonstrated transferability to other conifer-associated species further enhances the model's practical value, as high-scoring areas may harbour multiple species of conservation concern (Edenius and Mikusiński, 2006).

Whether this approach would perform equally well in other parts of *G. repens'* wide European range remains an open question. The model would likely transfer well to other Fennoscandian countries (Norway, Finland) with similar boreal forest ecosystems, production forestry, and open geodata. However, in more diverse temperate or mountain forest landscapes of Central and Southern Europe, where *G. repens* may be constrained by additional factors such as soil chemistry (Tsiftsis et al., 2012), additional predictors may be required.

In conclusion, our results demonstrate that open geodata can predict *G. repens* occurrence with sufficient accuracy to be useful for conservation planning. The model's transferability to other conifer-associated indicator species suggests it captures general characteristics of high-quality conifer forest habitat, extending its utility beyond the focal species. The importance of basal area and surrounding old forest confirms findings from field-based research and reinforces that this species—and other old-growth specialists—are fundamentally dependent on mature forest conditions that are systematically removed under current forestry practices. As the decline of old-growth specialists continues in managed boreal forests (Johansson et al., 2026; Gustafsson et al., 2025), efficient tools for habitat identification will become increasingly critical for conservation efforts.

CRediT authorship contribution statement

Victor Johansson: Writing – original draft, Supervision, Methodology, Formal analysis, Conceptualization. **Matilda Jansson:** Writing – review & editing, Formal analysis, Data curation. **Karl-Olof Bergman:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

Acknowledgments

The study was funded by Stiftelsen Skogssällskapet (grant number: 2024-1264) and Stiftelsen Extensus. We thank two anonymous reviewers for valuable comments on an earlier version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111915.

Data availability

The authors do not have permission to share data.

References

Bergman, K.-O., Petersen, R., Johansson, V., Westerberg, L., Milberg, P., Jansson, N., 2025. From clear-cuts to nature reserves: saproxylic beetle diversity and deadwood availability in Norway spruce (*Picea abies* L.) stands in southern Sweden. Ann. For. Sci. 82, 37. https://doi.org/10.1186/s13595-025-01307-5.

Bergman, K.-O., Viding, R., Johansson, V., 2026. Lower deadwood quality and cryptogam diversity in boreal production forests compared to nature reserves. For. Ecol. Manag. 602, 123416. https://doi.org/10.1016/j.foreco.2025.123416.

Bradshaw, C.J., Warkentin, I.G., Sodhi, N.S., 2009. Urgent preservation of boreal carbon stocks and biodiversity. Trends Ecol. Evol. 24, 541–548. https://doi.org/10.1016/j.tree.2009.03.019.

Cameron, D.D., Leake, J.R., Read, D.J., 2006. Mutualistic mycorrhiza in orchids: evidence from plant–fungus carbon and nitrogen transfers in the green-leaved terrestrial orchid *Goodyera repens*. New Phytol. 171, 405–416. https://doi.org/10.1111/j.1469-8137.2006.01767.x.

Dahlberg, A., Genney, D.R., Heilmann-Clausen, J., 2001. Developing a comprehensive strategy for fungal conservation in Europe: current status and future needs. Fungal Ecol. 4, 359–367. https://doi.org/10.1016/j.funeco.2009.10.004.

Edenius, L., Mikusiński, G., 2006. Utility of habitat suitability models as biodiversity assessment tools in forest management. Scand. J. For. Res. 21 (S7), 62–72. https://doi.org/10.1080/14004080500486989.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.

Elith, J., Graham, C.H., Anderson, R.P., et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

FAO, 2020. Global Forest Resources Assessment 2020: Main Report. Food and Agriculture Organization of the United Nations, Rome.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. J. Appl. Ecol. 51, 1669–1679. https://doi.org/10.1111/1365-2664.12289.

Felton, A., Sonesson, J., Nilsson, U., Lämås, T., Lundmark, T., Nordin, A., Ranius, T., Roberge, J.-M., 2017. Varying rotation lengths in northern production forests: implications for habitats provided by retention and production trees. Ambio 46, 324–334. https://doi.org/10.1007/s13280-017-0909-7.

Franklin, J., 2010. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge.

Fridman, J., Holm, S., Nilsson, M., Nilsson, P., Ringvall, A.H., Ståhl, G., 2014. Adapting National Forest Inventories to changing requirements – the case of the Swedish National Forest Inventory at the turn of the 20th century. Silva Fennica 48 (3), 1095. https://doi.org/10.14214/sf.1095.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. Science 349, 819–822. https://doi.org/10.1126/science.aaa9092.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. https://doi.org/10.1111/ele.12189.

Gustafsson, L., Perhans, K., 2010. Biodiversity conservation in Swedish forests: ways forward for a 30-year-old multi-scaled approach. Ambio 39, 546–554. https://doi.org/10.1007/s13280-010-0071-y.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. BioScience 62, 633–645. https://doi.org/10.1525/bio.2012.62.7.6.

Gustafsson, L., Andersson, J., Jonsson, F., Jönsson, M., Jonsson, M., Nordin, U., Strengbom, J., Johansson, V., 2025. Long-continuity forests are essential for sustaining epiphytic biodiversity in boreal production forest landscapes. J. Appl. Ecol. 68, 1929–1938.

Halpern, C.B., 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70, 704–720. https://doi.org/10.2307/1940221.

He, K.S., Bradley, B.A., Cord, A.F., Rocchini, D., Tuanmu, M.-N., Schmidtlein, S., Turner, W., Wegmann, M., Pettorelli, N., 2015. Will remote sensing shape the next generation of species distribution models? Remote Sensing Ecol. Conserv. 1, 4–18. https://doi.org/10.1002/rse2.7.

Heithecker, T.D., Halpern, C.B., 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. For. Ecol. Manag. 248, 163–173. https://doi.org/10.1016/j.foreco.2007.05.003.

Hekkala, A.M., Jönsson, M., Kärvemo, S., Strengbom, J., Sjögren, J., 2023. Habitat heterogeneity is a good predictor of boreal forest biodiversity. Ecol. Indic. 148, 110069. https://doi.org/10.1016/j.ecolind.2023.110069.

Hylander, K., Weibull, H., 2012. Do time-lagged extinctions and colonizations change the interpretation of buffer strip effectiveness? – a study of riparian bryophytes in the first decade after logging. J. Appl. Ecol. 49, 1316–1324. https://doi.org/10.1111/j.1365-2664.2012.02218.x.

IPBES, 2019. Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn, Germany.

Johansson, V., Wikström, C.J., Hylander, K., 2018. Time-lagged lichen extinction in retained buffer strips 16.5 years after clear-cutting. Biol. Conserv. 225, 53–65. https://doi.org/10.1016/j.biocon.2018.06.016.

Johansson, V., Erbs, C., Bergman, K.-O., 2025. The indicator value of a debated orchid: can *Goodyera repens* predict forests of high conservation potential? Scand. J. For. Res. 40, 273–281.

Johansson, V., Jansson, M., Bergman, K.-O., 2026. A 30-year population decline of a threatened forest orchid associated with old growth forests. Biol. Conserv. 316, 111765.

Johnson, S., 2014. Retention Forestry as a Conservation Measure for Boreal Forest Ground Vegetation. Swedish University of Agricultural Sciences, Uppsala (Doctoral thesis).

Jokela, J., Juutilainen, K., Korpela, L., Kouki, J., Kuntsi, S., Koivula, M., Siitonen, J., 2018. Cross-taxon congruence and relationships to stand characteristics of vascular plants, bryophytes, polyporous fungi and beetles in mature managed boreal forests. Ecol. Indic. 85, 137–145. https://doi.org/10.1016/j.ecolind.2017.10.036.

Klein, J., 2019. Rikstäckande information om markens fuktighet. Kart. Bildteknik. 16–20.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S., Uotila, A., 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scand. J. For. Res. 16 (S3), 27–37. https://doi.org/10.1080/028275801300090564.

Kuuluvainen, T., Tahvonen, O., Aakala, T., 2015. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. Ambio 44, 519–533. https://doi.org/10.1007/s13280-012-0289-y.

Kyaschenko, J., Strengbom, J., Felton, A., Aakala, T., Staland, H., Ranius, T., 2022. Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: the effect of three decades of biodiversity-oriented forest policy in Swedish forests. J. Environ. Manag. 313, 114993. https://doi.org/10.1016/j.jenvman.2022.114993.

Lehtomäki, J., Tuominen, S., Toivonen, T., Leinonen, A., 2015. What data to use for forest conservation planning? A comparison of coarse open and detailed proprietary forest inventory data in Finland. PLoS One 10, e0135926. https://doi.org/10.1371/journal.pone.0135926.

Liebel, H.T., Bidartondo, M.I., Gebauer, G., 2015. Are carbon and nitrogen exchange between fungi and the orchid Goodyera repens affected by irradiance? Ann. Bot. 115, 251–261. https://doi.org/10.1093/aob/mcu240.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445. https://doi.org/10.1016/j.biocon.2006.02.019.

Lõhmus, A., Kull, T., 2011. Orchid abundance in hemiboreal forests: stand-scale effects of clear-cutting, green-tree retention, and artificial drainage. Can. J. For. Res. 41, 1352–1358. https://doi.org/10.1139/x11-047.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253. https://doi.org/10.1038/35012251.

Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E., 2016. Biodiversity: the ravages of guns, nets and bulldozers. Nature 536, 143–145. https://doi.org/10.1038/536143a.

Mikkonen, N., Leikola, N., Lehtomäki, J., Halme, P., Moilanen, A., 2023. National high-resolution conservation prioritisation of boreal forests. For. Ecol. Manag. 541, 121079. https://doi.org/10.1016/j.foreco.2023.121079.

Nirhamo, A., Aakala, T., Kouki, J., 2025. Forest biodiversity in boreal Europe: species richness and turnover among old-growth forests, managed forests and clearcut sites. Biol. Conserv. 306, 111147. https://doi.org/10.1016/j.biocon.2025.111147.

Nitare, J., 2019. Skyddsvärd skog -Naturvårdsarter och andra kriterier för naturvärdesbedömning. Skogsstyrelsen (in Swedish).

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J. Ecol. 101, 701–712. https://doi.org/10.1111/1365-2745.12085.

Nordén, B., Dahlberg, A., Brandrud, T.E., Fritz, Ö., Ejrnaes, R., Ovaskainen, O., 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: a review. Écoscience 21, 34–45. https://doi.org/10.2980/21-1-3667.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24, 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x.

Pecchi, M., Marchi, M., Giannetti, F., Ferrara, C., Chirici, G., Spinoni, J., Marcolin, E., Scotti, R., Ferretti, F., Salvati, L., Corona, P., 2019. Species distribution modelling to support forest management. A literature review. Ecol. Model. 411, 108817. https://doi.org/10.1016/j.ecolmodel.2019.108817.

Reich, P.B., Frelich, L.E., Voldseth, R.A., Bakken, P., Adair, E.C., 2012. Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. J. Ecol. 100, 539–545. https://doi.org/10.1111/j.1365-2745.2011.01942.x.

Skogsstyrelsen, 2025. https://www.skogsstyrelsen.se/laddanergeodata.

SLU ArtDatabanken, 2025. Artportalen. https://www.artportalen.se.

SLU ArtDatabanken, 2026. Rödlistade arter i Sverige 2025 [The Swedish Red List 2025]. SLU, Uppsala.

SLU Skogsdatalabbet, 2025. https://gis.slu.se/data/skogsdatalabbet/SLU_skogsalder_2025/.

Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science 240, 1285–1293. https://doi.org/10.1126/science.3287615.

Tsiftsis, S., Tsiripidis, I., Papaioannou, A., 2012. Ecology of the orchid *Goodyera repens* in its southern distribution limits. Plant Biosyst. 146, 857–866. https://doi.org/10.1080/11263504.2011.642416.

Vesala, T., Suni, T., Rannik, Ü., Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, S., Kulmala, M., Ilvesniemi, H., Ojansuu, R., Uotila, A., Levula, J., Mäkelä, A., Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., Nikinmaa, E., Hari, P., 2005. Effect of thinning on surface fluxes in a boreal forest. Glob. Biogeochem. Cycles 19, GB2001. https://doi.org/10.1029/2004GB002316.

Widenfalk, O., Weslien, J., 2009. Plant species richness in managed boreal forests—effects of stand succession and thinning. For. Ecol. Manag. 257, 1386–1393. https://doi.org/10.1016/j.foreco.2008.12.010.