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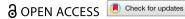
Victor Johansson, Charlotte Erbs & Karl-Olof Bergman

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The indicator value of a debated orchid: can Goodyera repens predict forests of high conservation potential?

Victor Johansson, Charlotte Erbs and Karl-Olof Bergman

Department of Physics, Chemistry and Biology (IFM), Linköping University, Linköping, Sweden

ABSTRACT

Indicator species require empirical validation for reliable conservation assessment. We evaluated the effectiveness of Goodyera repens, a threatened and legally protected orchid in Sweden, as an indicator of forests with high conservation potential. We surveyed conifer-dominated stands: 40 containing G. repens, 20 similar-aged stands without it ("old stands" 88-171 years), and 20 randomly selected stands of various ages in Östergötland, southeastern Sweden. We measured habitat heterogeneity scores (HHS), dead wood volumes, tree diameters, stand age, and presence of conservation concern species. Stands with G. repens contained significantly more species of conservation concern (mean 2.9) than old stands (1.85) and random stands (0.55), and showed higher habitat heterogeneity and dead wood volumes. Habitat heterogeneity was the strongest predictor of species richness, while stand age best predicted red-listed species occurrence. G. repens abundance showed no correlation with conservation species richness at stand level but correlated significantly at plot level (50 × 50 m), making the species potentially useful for identifying retention areas during logging. While G. repens can indicate forests with conservation value, direct assessments of habitat heterogeneity and stand age provide more reliable biodiversity predictions. We recommend combining species-based indicators with structural habitat measurements for more effective identification of high-value forests in human-dominated landscapes.

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KEYWORDS

: Boreal forest; conservation planning; dead wood; forest structure; habitat heterogeneity; stand age

Introduction

Current species extinction rates are estimated to be 100-1000 times higher than natural background rates, with habitat degradation and land-use changes serving as primary drivers (Maxwell et al. 2016; IPBES 2019). Forest ecosystems, which harbour approximately 80% of terrestrial biodiversity, are particularly affected by anthropogenic activities (FAO 2020). This impact is especially pronounced in boreal forests, which represent nearly one-third of global forest cover and provide essential ecosystem services, including climate regulation, carbon sequestration, and biodiversity maintenance (Bradshaw et al. 2009 Gauthier et al. 2015). Intensive forestry practices have substantially simplified these once-heterogeneous landscapes into structurally uniform stands with reduced habitat complexity, resulting in altered microclimates and diminished refuges for species sensitive to environmental change (Halpern 1989; Heithecker and Halpern 2007; Gustafsson and Perhans 2010; Paillet et al. 2010).

The identification and protection of forests with high conservation value has emerged as a critical strategy for biodiversity conservation in managed forest landscapes (Lindenmayer et al. 2006). Various approaches have been developed to assess forest conservation value, including the quantification of important habitat structures such as dead wood volume, large living trees, and structural heterogeneity (Tikkanen et al. 2006; Gao et al. 2015; Hekkala et al. 2023). Recent research has shown that habitat heterogeneity is a particularly strong predictor of red-listed species abundance in southern boreal regions (Hekkala et al. 2023). Additionally, indicator species have been widely employed to signal the presence of other species of conservation concern and reflect ecosystem conditions that are otherwise difficult or impractical to measure (Niemi and McDonald 2004; Lindenmayer and Likens 2011; Siddig et al. 2016). Indicator species remain widely used as cost-effective, field-based cues about hard-tomeasure ecosystem attributes, yet their reliability must be rigorously evaluated before implementation in

CONTACT Victor Johansson 🔯 victor.a.johansson@liu.se 🗈 Department of Physics, Chemistry and Biology (IFM), Linköping University, SE-581 83 Linköping, Sweden

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conservation planning, as their predictive power can vary across different contexts and scales (Jonsson and Jonsell 1999 Lõhmus 2016; Siddig et al. 2016).

In Fennoscandian boreal forests, intensive forestry practices have led to significant declines in old-growth forests and associated biodiversity (Kouki et al. 2001; Löfman and Kouki 2001 Kuuluvainen et al. 2015). In Sweden, where production forestry dominates the landscape, more than 10% of forest-associated species are now red-listed, with many populations declining and becoming increasingly fragmented (Hansen et al. 2014). Previous studies have demonstrated that logging negatively affects various taxonomic groups, including vascular plants, bryophytes, lichens, and fungi (Dahlberg et al. 2001; Lõhmus and Kull 2011 Hylander and Weibull 2012; Johansson et al. 2018). To identify remaining forests of high biodiversity the Forestry Agency have established long lists of indicator species.

One species that has gained particular attention in Swedish forestry debates is Goodyera repens, a small orchid classified as vulnerable on the national Red List. This species is legally protected under the Species Protection Ordinance (Naturvårdsverket 2007), and its presence can halt planned logging operations, making it a contentious topic in forest management debates (Widenfalk and Weslien 2009 Johnson 2014). G. repens is reported to be associated with old-growth coniferous forests and demonstrate high sensitivity to environmental changes, particularly those caused by clearcutting (Lõhmus and Kull 2011). Its reliance on stable habitats and mycorrhizal fungi suggests that its presence might indicate forests of high ecological continuity and value (Nordén et al. 2014). However, despite its significant influence on forestry operations and widespread use as an indicator of valuable forest habitats, empirical evidence regarding its effectiveness as a predictor of other threatened species remains limited.

The aim of this study was to evaluate the effectiveness of G. repens as an indicator species, assessing its ability to predict the presence of other species of conservation concern. Moreover, we examined how well its occurrence relates to overall structural heterogeneity (Hekkala et al. 2023) and to deadwood volume, tree dimensions, and stand age, and how these variables in turn relate to the richness of other species of conservation concern. Additionally, we explored whether the indicator value of G. repens improves as the number of observed rosettes increases. Our findings will offer evidence-based insights that can guide conservation planning and promote sustainable forest management in boreal landscapes, thereby contributing to a more balanced integration of production goals with biodiversity conservation (Mori et al. 2017; Felton et al. 2020).

Methods

Study species

Goodyera repens (L.) R. Br. (Figure 1) is an orchid in the family Orchidaceae, that is found across northern Europe, Asia, and North America, primarily in coniferous forests. This evergreen, rhizomatous species disperses both vegetatively and by seeds, and depends on mycorrhizal fungi for nutrient uptake during early life stages (Cameron et al., 2006). It is associated with old-growth forests in late successional (Widenfalk & Weslien, 2009, Lõhmus & Kull, 2011, Ståhl, 2012, Johnson, 2014).

In Sweden, G. repens is listed as Vulnerable (VU) on the Swedish Red List (SLU ArtDatabanken 2020), though it is categorized as Least Concern (LC) at the European level (Bilz et al., 2011). Protected under the Swedish Species Protection Ordinance (SFS 2007:845), which prohibits damaging or removing plants, its legal status can halt clear-cutting operations, sparking debate in the forestry sector. However, knowledge about its habitat requirements and its reliability as an indicator of high-conservation forests with other threatened species remains limited.

Study site, stand selection and sampling

The study was conducted in 2024 in south-eastern Sweden, Östergötland county (58.0°N, 15.7°E, Figure 1). Study forest stands were selected from the stand register of the forest company Boxholms Skogar. A total of 40 stands were chosen where Goodyera repens had previously been recorded, along with 20 stands of the same age as the G. repens stands (randomly selected, aged between 88 and 171 years), and 20 stands randomly selected from the entire database (0-358 years) of Boxholms Skogar. All selected stands were conifer dominated (mean > 90%). Within each of the selected stands, with no previous record of G. repens, three sampling points were randomly allocated. In the stands with G. repens, one point was centred on a previous G. repens record, while the other two were placed at random. To reduce edge effects, all sampling points were located at least 10 m from the stand boundary.

At each sampling point, plots of three different sizes $(20 \times 20 \text{ m}, 50 \times 50 \text{ m}, \text{ and } 50 \times 100 \text{ m})$ were established. In the 20×20 m plots, all living trees were measured, with species and diameter recorded. In the 50×50 m plots, all indicator species (including red-listed species) of mosses, lichens, fungi, vascular plants, and beetles were recorded (Nitare 2019). Deadwood with a diameter >10 cm was also measured within the 50×50 m plots, following the methodology of Wijk (2016). We recorded diameter at breast height (1.3 m), length (for lying

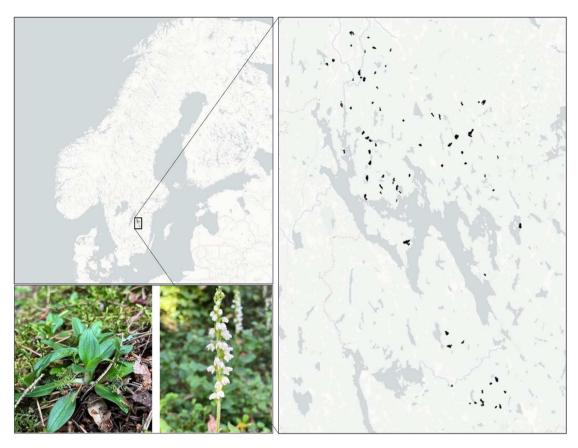


Figure 1. The study area in south-eastern Sweden with the 80 sampled stands (black polygons) and the study species *Goodyera repens* (with evergreen leaf rosettes and flowering inflorescences). Photo: Victor Johansson.

deadwood), height (for standing deadwood), and top circumference (if the tree was not intact). In the $50 \times$ 100 m plots, different habitat structures were documented based on the protocol outlined in Swedish by Drakenberg and Lindhe (1999) and translated to English by Hekkala et al. (2023). In short, it includes site characteristics (topography, soil conditions, water features), disturbance processes (fire signs, natural regeneration), habitat structures (age distribution, dead wood, tree microhabitats), and vegetation features (ground cover, tree composition, structural diversity). According to the developers, the method can be used in any type of forest to measure its conservation value based on structures without having specialized species knowledge. The number of structures was summarized at the stand level in the field (i.e. from all three plots together covering 1.5 ha in total) to get a stand level "Habitat Heterogeneity Score" (HHS, Hekkala et al. 2023).

Statistics

All statistical analyses were conducted using R version 4.2.2. To compare stand types when it comes to habitat heterogeneity score (HHS), dead wood

volumes, stand age and dbh we used ANOVAs with Tukey's post hoc-test for pair-wise comparisons between stand categories. To analyse the number of species of conservation concern in relation to stand category, HHS, dead wood volumes, and mean tree diameter we used generalized linear models (GLM) with a Poisson distribution and log-link. For pair-wise difference between stand categories we used the "glht function" from the R package multcomp (Bretz et al., 2010). To assess the relative importance of explanatory variables, we employed a systematic variable selection approach using AIC comparison. Starting with a null model (intercept only), we individually added each of the four explanatory variables to create separate single-predictor models. We then compared the AIC values of these models to identify which variable provided the greatest improvement in model fit (lowest AIC) relative to the null model. The occurrence probability of red-listed species in relation to the explanatory variables above was analysed using GLMs with a binomial distribution and logit link function (logistic regression). Neither the number of species of conservation concern nor red-listed species occurrence exhibited significant spatial autocorrelation (Moran's I, p > 0.18). To



test the relation between the number of G. repens rosettes and the number of species of conservation concern we used Spearman rank correlation both at the stand and the plot level.

Results

In total there were 26 nature value indicator species (other than Goodyera repens) found across all stands, of which six were red-listed (as NT), see Supplementary material, Table S1. Apart from the 40 stands selected based on the occurrence of G. repens, the species was also found in two of the old stands, while it was not found in the random stands from the entire age distribution. The total count of leaf rosettes was 2512, ranging from 3 to 240 at the stand level and 1-188 at the plot level (50 × 50 m plots). Dead-wood volumes ranged 0.39-121.77 (mean = 27.83) m³/ha and the number of alive trees ranged 17-136 (mean = 74.7). Stand age ranged from 1 to 171 years (mean 106.6 years).

The habitat heterogeneity score (HHS) differed significantly between all three stand types, with the highest HHS in G. repens stands, followed by old and random stands. Dead wood volumes were significantly higher in G. repens stands, while old and random stands did not differ. The mean diameter was significantly larger in G. repens compared to the random stands, but not compared to old stands. Stand ages did not differ between G. repens stands and old, while the age of random stands was significantly lower (Figure 2). There were strong correlations between the HHS, dead wood volumes, and stand age (rho between 0.60 and 0.82), while mean tree diameter was less correlated to the other variables (rho between 0.16 and 0.34).

The number of nature value indicator species differed significantly between the three stand types. On average 2.9 (SE = 0.24) species of conservation concern was found in stands with Goodyera repens, 1.85 (SE = 0.29) in old stands, and 0.55 (SE = 0.17) in the randomly selected stands (Figure 3). The number of species increased significantly with increasing HHS, total dead wood volume and stand age (Figure 3), but there was no significant relationship with mean tree diameter. Based on AIC, species richness was best explained by HHS (AIC = 252.5), followed by stand age (AIC = 254.2), stand category (AIC = 256.4), and dead wood volumes (AIC = 260.2).

No red-listed species were found in the random stands. There was no significant difference in the occurrence probability of red-listed species between the two other stand categories (p = 0.14), and there were no significant relationships with mean tree diameter and dead wood volumes. However, the occurrence probability significantly increased with the habitat heterogeneity score and stand age (Figure 4), where the latter had the best explanatory power based on AIC, 88.3 compared to 90.0.

Among stands with G. repens there was a statistically significant correlation between rosette abundance of G. repens and the number of species of conservation concern (rho = 0.21, p = 0.021) at the plot level. However, we found no significant correlation between rosette abundance and the number of species of conservation concern at the stand level (p = 0.22). Rosette abundance showed significant correlations with both habitat heterogeneity score (HHS) (r = 0.39, p = 0.011) and dead wood volumes (r = 0.38, p = 0.013), while no significant relationship was detected with mean tree diameter.

Discussion

Our study evaluated the effectiveness of Goodyera repens as an indicator species for forests of high conservation value in boreal landscapes. The results confirmed that G. repens can function as a useful indicator - stands containing this species harboured more species of conservation concern and exhibited significantly higher habitat heterogeneity scores (HHS) and greater dead wood volumes compared to randomly selected stands. This effectiveness as an indicator is consistent with its association to old forests and known sensitivity to disturbances like clear-cutting, which remove the canopy and moss layers it depends on (Widenfalk & Weslien, 2009, Lõhmus & Kull, 2011, Ståhl, 2012, Johnson, 2014, Kirillova et al., 2023). However, even if single species have been shown to be good indicators of general biodiversity (Nilsson et al. 1995), there is caution that single species rarely capture the full complexity of a habitat (Lindenmayer and Likens 2011). This concern is supported by multiple studies showing that groups of coexisting ancient forest species are more reliable indicators of high species diversity and forest biodiversity hotspots than individual species (Stefańska-Krzaczek et al., 2016; Hofmeister et al., 2019). Our analyses support this more nuanced view, showing that habitat heterogeneity and stand age are stronger predictors of biodiversity value than the presence of G. repens alone.

Habitat heterogeneity emerged as the strongest predictor of overall species richness (lowest AIC value), while stand age was the best predictor for red-listed species occurrence. This aligns with Hekkala et al. (2023), who found that habitat heterogeneity strongly predicts red-listed species abundance in southern boreal regions, and with Tikkanen et al. (2006), who demonstrated the importance of structural complexity

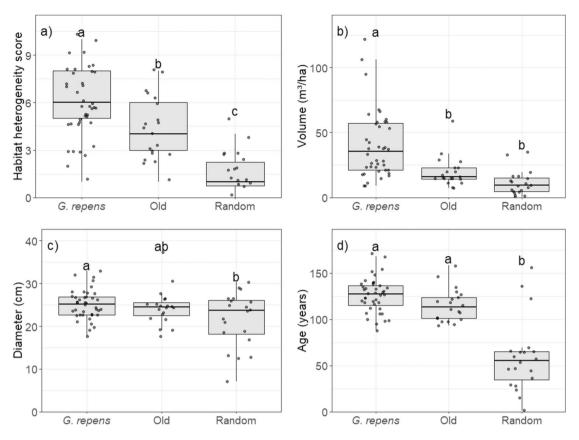


Figure 2. The distribution of the (a) Habitat heterogeneity score (HHS), (b) total volume of dead wood, (c) mean tree diameter, (d) and stand age in *Goodyera repens* stands, old stands, and random aged stands. Letters above boxplots indicate statistical differences.

for biodiversity conservation. Heterogeneity of the forest structure has also been shown to affect the composition of forest specialist species (Smyčková et al. 2024). The strong correlations between HHS, dead wood volumes, and stand age reflect their interdependence in forest ecosystems, where time allows the natural development of structural complexity and resource accumulation critical for biodiversity (Bergeron and Harper, 2009, Angelstam et al., 2011). These findings support the concept of ecological continuity, where temporal stability allows for the accumulation of specialized species and complex forest structures (Nordén et al., 2014). Conversely, mean tree diameter showed weaker correlations, indicating that diameter alone is insufficient for assessing forest conservation value, a finding consistent with previous research showing that structural diversity is more important than tree size for many forest-dwelling organisms (Paillet et al., 2010, Lindenmayer et al., 2011).

The abundance of *G. repens* (number of rosettes) showed no correlation with the number of conservation species at the stand level, suggesting that stands where *G. repens* thrives are not necessarily of higher conservation value than stands with only a few rosettes. This contradicts assumptions that higher abundance indicates

better habitat quality across entire stands (Siddig et al. 2016). However, at a smaller scale (here the plot level) within stands, the abundance of *G. repens* correlated with other species, suggesting that it can be used to pinpoint parts of stands with higher values. This finding could have implications for conservation planning, as it suggests that while *G. repens* presence can indicate valuable stands, abundance provides a compass for prioritizing retention within stands during logging operations (Gustafsson et al., 2012, Fedrowitz et al., 2014).

Our results have significant implications for forest conservation and management. While the legal protection of *G. repens* under the Swedish Species Protection Ordinance appears justified from a biodiversity perspective, relying solely on this species as an indicator is insufficient (Lindenmayer et al., 2011, Siddig et al. 2016). Conservation strategies would benefit from integrating standardized assessments of habitat heterogeneity, dead wood volumes, and stand age into decision-making processes (Moning and Müller, 2009, Gao et al., 2015). Such a combined approach – using both species-based indicators and direct habitat measurements – would provide a more comprehensive basis for identifying forests of high conservation potential, a strategy supported by multiple studies on biodiversity

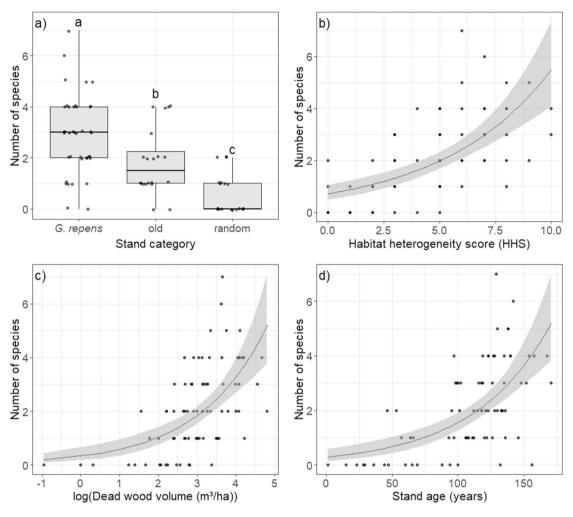


Figure 3. The number of species of conservation concern in relation to (a) stand category, (b) habitat heterogeneity score, (c) dead wood volume and (d) stand age. Letters above boxplots in (a) indicate statistical differences and lines in (b, d) represent model predictions with 95% confidence intervals. Points are raw data.

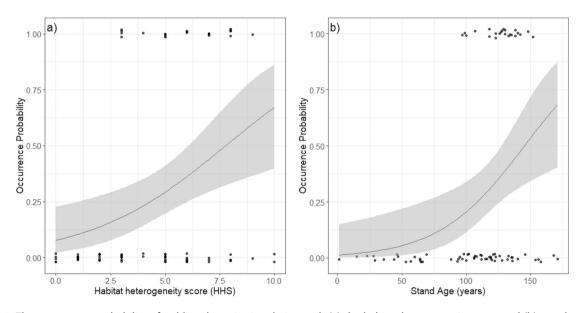


Figure 4. The occurrence probability of red-listed species in relation with (a) the habitat heterogeneity score and (b) stand age. Lines represent model predictions with 95% confidence intervals and points are raw data (with a small scatter to improve visualization).

assessment in managed landscapes (Lindenmayer et al., 2006, Kuuluvainen, 2009). This is what was done in Sweden's Woodland Key Habitat inventory, conducted from 1992 to 2021, which systematically documented ecologically valuable areas before logging operations (Ericsson et al. 2005). With this protocol now discontinued, the presence of Goodyera repens has become one of the few remaining legal mechanisms conservationists can utilize to protect biologically significant forests. This has transformed the orchid into a focal point of intense debate between forestry economic interests and environmental advocates.

Even though we demonstrate that G. repens correlates with habitat structures important for biodiversity, our study does not delve deeply into the species' ecology and long-term population dynamics, which is necessary to fully understand its habitat preferences and population dynamics for effective conservation. Future research should also explore whether its indicator value hold across broader geographical ranges, different management regimes, and longer time scales, as recommended by Lõhmus (2016) for indicator species validation. Additionally, investigating how G. repens relates to specific taxonomic groups could reveal more nuanced patterns of association - an approach that has proven valuable for understanding the complementarity of different indicator taxa (Jonsson and Jonsell, 1999, Juutinen and Mönkkönen, 2004).

In conclusion, our study supports the value of G. repens as one component in assessing forest conservation value, but emphasizes that habitat heterogeneity and stand age may be more reliable predictors of biodiversity. The most effective approach to forest conservation planning likely combines species-based indicators with direct measurements of habitat structures, particularly in increasingly human-dominated landscapes where efficient identification of high-value conservation areas is critical (Mori et al., 2017, Felton et al., 2020). We advocate for the reintroduction of the Woodland Key Habitat inventory or similar assessments to ensure legally secure and systematic identification of ecologically valuable areas deserving conservation protection.

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Disclosure statement

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References

- Angelstam P, Andersson K, Axelsson R, Elbakidze M, Jonsson BG, Roberge JM. 2011. Protecting forest areas for biodiversity in Sweden 1991–2010: the policy implementation process and outcomes on the ground. Silva Fenn. 45(5):1111-1133.
- Bergeron Y, Harper KA. 2009. Old-growth forests in the Canadian boreal: the exception rather than the rule? In: Wirth C, Gleixner G, Heimann M, editors. Old-growth forests. Berlin, Heidelberg: Springer; p. 285-300.
- Bilz M. Kell SP. Maxted N. Lansdown RV. 2011. European red list of vascular. Luxembourg: Publications Office of the European Union. doi:10.2779/8515.
- Bradshaw CJ, Warkentin IG, Sodhi NS. 2009. Urgent preservation of boreal carbon stocks and biodiversity. Trends Ecol Evol. 24(10):541-548. doi:10.1016/j.tree.2009.03.019.
- Bretz F, Hothorn T, Westfall P. 2010. Multiple comparisons using R. New York: Chapman and Hall/CRC.
- Cameron DD, Leake JR, Read DJ. 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. doi:10.1111/j.1469-8137. 2006.01767.x.
- Dahlberg A, Genney DR, Heilmann-Clausen J. 2001. Developing a comprehensive strategy for fungal conservation in Europe: current status and future needs. Fungal Ecol. 4(6):359-367. doi:10.1016/j.funeco.2009.10.004.
- Drakenberg B, Lindhe A. 1999. Indirekt naturvärdesbedömning på beståndsnivå – en praktiskt tillämpbar metod. Skog Forsk. 2:60-66.
- Ericsson TS, Berglund H, Östlund L. 2005. History and forest biodiversity of woodland key habitats in south boreal Sweden. Biol Conserv. 122(2):289-303. doi:10.1016/j.biocon.2004.07.019.
- FAO. 2020. Global Forest Resources Assessment 2020: Main report. Rome.
- Fedrowitz K, Koricheva J, Baker SC, Lindenmayer DB, Palik B, Rosenvald R, Beese W, Franklin JF, Kouki J, Macdonald E, et al. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. J Appl Ecol. 51(6):1669–1679. doi:10. 1111/1365-2664.12289.
- Felton A, Löfroth T, Angelstam P, Gustafsson L, Hjältén J, Felton AM, Simonsson P, Dahlberg A, Lindbladh M, Svensson J, et al. 2020. Keeping pace with forestry: multi-scale conservation in a changing production forest matrix. Ambio. 49(5):1050-1064. doi:10.1007/s13280-019-01248-0.
- Gao T, Nielsen AB, Hedblom M. 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. Ecol Indic. 57:420–434. doi:10.1016/j.ecolind.2015. 05.028.
- Gauthier S, Bernier P, Kuuluvainen T, Shvidenko AZ, Schepaschenko DG. 2015. Boreal forest health and global change. Science. 349(6250):819-822. doi:10.1126/science. aaa9092.
- Gustafsson L, Baker SC, Bauhus J, Beese WJ, Brodie A, Kouki J, Lindenmayer DB, Lõhmus A, Pastur GM, Messier C, et al. 2012. Retention forestry to maintain multifunctional



- forests: A world perspective. BioScience. 62(7):633–645. doi:10.1525/bio.2012.62.7.6.
- Gustafsson L, Perhans K. 2010. Biodiversity conservation in Swedish forests: ways forward for a 30-year-old multiscaled approach. Ambio. 39(8):546–554. doi:10.1007/s13280-010-0071-y.
- Halpern CB. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology. 70(3):704–720. doi:10.2307/1940221.
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, et al. 2014. High-resolution global maps of 21st-century forest cover change. Science. 342(6160):850–853. doi:10. 1126/science.1244693.
- Heithecker TD, Halpern CB. 2007. Edge-related gradients in microclimate in forest aggregates following structural retention harvests in western Washington. For Ecol Manage. 248(3):163–173. doi:10.1016/j.foreco.2007.05.003.
- Hekkala AM, Jönsson M, Kärvemo S, Strengbom J, Sjögren J. 2023. Habitat heterogeneity is a good predictor of boreal forest biodiversity. Ecol Indic. 148:110069. doi:10.1016/j. ecolind.2023.110069.
- Hofmeister J, Hošek J, Brabec M, Hermy M, Dvořák D, Fellner R, Malíček J, Palice Z, Tenčík A, Holá E, et al. 2019. Shared affinity of various forest-dwelling taxa point to the continuity of temperate forests. Ecol Indic. 101:904–912. doi:10. 1016/j.ecolind.2019.01.018.
- 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(6):1316–1324. doi: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 CJ, Hylander K. 2018. Time-lagged lichen extinction in retained buffer strips 16.5 years after clear-cutting. Biol Conserv. 225:53–65. doi:10.1016/j. biocon.2018.06.016.
- Johnson S. 2014. Retention forestry as a conservation measure for boreal forest ground vegetation (Doctoral thesis). Swedish University of Agricultural Sciences, Uppsala.
- Jonsson BG, Jonsell M. 1999. Exploring potential biodiversity indicators in boreal forests. Biodivers Conserv. 8(10):1417–1433. doi:10.1023/A:1008900309571.
- Juutinen A, Mönkkönen M. 2004. Testing alternative indicators for biodiversity conservation in old-growth boreal forests: ecology and economics. Ecol Econ. 50(1–2):35–48. doi:10. 1016/j.ecolecon.2004.02.006.
- Kirillova IA, Dubrovskiy YA, Degteva SV, Novakovskiy AB. 2023. Ecological and habitat ranges of orchids in the northernmost regions of their distribution areas: A case study from Ural mountains, Russia. Plant Divers. 45(2):211–218. doi:10. 1016/j.pld.2022.08.005.
- 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. doi:10.1080/028275801300090564.
- Kuuluvainen T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern

- Europe: the complexity challenge. Ambio. 38(6):309–315. doi:10.1579/08-A-490.1.
- Kuuluvainen T, Tahvonen O, Aakala T. 2015. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. Ambio. 44(5):519–533. doi:10.1007/s13280-012-0289-y.
- Lindenmayer DB, Franklin JF, Fischer J. 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol Conserv. 131(3):433–445. doi:10.1016/i.biocon.2006.02.019.
- Lindenmayer DB, Likens GE. 2011. Direct measurement versus surrogate indicator species for evaluating environmental change and biodiversity loss. Ecosystems. 14:47–59. doi:10. 1007/s10021-010-9394-6.
- Löfman S, Kouki J. 2001. Fifty years of landscape transformation in managed forests of southern Finland. Scand J For Res. 16(1):44–53. doi:10.1080/028275801300004406.
- Lõhmus A. 2016. Habitat indicators for cavity-nesters: The polypore *Phellinus pini* in pine forests. Ecol Indic. 66:275–280. doi:10.1016/j.ecolind.2016.02.003.
- 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(6):1352–1358. doi:10.1139/x11-047.
- Maxwell SL, Fuller RA, Brooks TM, Watson JE. 2016. Biodiversity: The ravages of guns, nets and bulldozers. Nature. 536(7615):143–145. doi:10.1038/536143a.
- Moning C, Müller J. 2009. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (*Fagus sylvatica* L.) dominated forests. Ecol Indic. 9(5):922–932. doi:10. 1016/j.ecolind.2008.11.002.
- Mori AS, Lertzman KP, Gustafsson L. 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. J Appl Ecol. 54(1):12–27. doi:10.1111/1365-2664.12669.
- Naturvårdsverket. 2007. Species Protection Ordinance (Artskyddsförordning, SFS 2007:845). Stockholm: Swedish Environmental Protection Agency.
- Niemi GJ, McDonald ME. 2004. Application of ecological indicators. Annu Rev Ecol Evol Syst. 35:89–111. doi:10.1146/annurev.ecolsys.35.112202.130132.
- Nilsson SG, Arup ULF, Baranowski R, Ekman S. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. Conserv Biol. 9(5):1208–1215. doi:10.1046/j.1523-1739.1995.9051199.x-i1.
- Nitare J. 2019. Skyddsvärd skog Naturvårdsarter och andra kriterier för naturvärdesbedömning. Jönköping: Skogsstyrelsen.
- Nordén B, Dahlberg A, Brandrud TE, Fritz Ö, Ejrnaes R, Ovaskainen O. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: A review. Écoscience. 21(1):34–45. doi:10.2980/21-1-3667.
- Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma RJ, De Bruyn L, Fuhr M, Grandin U, et al. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv Biol. 24(1):101–112. doi:10.1111/j.1523-1739.2009.01399.x.
- Siddig AA, Ellison AM, Ochs A, Villar-Leeman C, Lau MK. 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of



- publication in ecological indicators. Ecol Indic. 60:223-230. doi:10.1016/j.ecolind.2015.06.036.
- SLU Artdatabanken. 2020. Rödlistade arter i Sverige 2020 [the Swedish red list 2020]. Uppsala: SLU.
- Smyčková M, Koutecký T, Ujházyová M, Ujházy K, Verheyen K, Volařík D, Šebesta J, Friedl M, Máliš F, Hofmeister J. 2024. Herb layer species richness declines with heterogeneity of the forest structure in primary beech-dominated forests while proportion of forest specialists increases. For Ecol Manag. 556:121728. doi:10.1016/j.foreco.2024.
- Ståhl P. 2012. Knärot är beroende av gammal skog [status of Goodyera repens in Sweden]. Svensk Bot Tidskr. 106:249-254.

- Stefańska-Krzaczek E, Kącki Z, Szypuła B. 2016. Coexistence of ancient forest species as an indicator of high species richness. For Ecol Manag. 365:12–21. doi:10.1016/j.foreco.2016.01.012.
- Tikkanen OP, Martikainen P, Hyvärinen E, Junninen K, Kouki J. 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Ann Zool Fenn. 43(4):373-383.
- Widenfalk O, Weslien J. 2009. Plant species richness in managed boreal forests-effects of stand succession and thinning. For Ecol Manage. 257(5):1386-1393. doi:10.1016/ j.foreco.2008.12.010.
- Wijk S. 2016. Uppföljning av biologisk mångfald i skog med höga naturvärden: Metodik och genomförande. Skogsstyrelsen, Rapport 2016:1.