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Greenish Warbler (*Phylloscopus trochiloides viridanus*): An overlooked indicator of old-growth forest?

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Effective bioindicators of old-growth forest are important for conservation. The Greenish Warbler (*Phylloscopus trochiloides viridanus*), a forest-dwelling passerine, has been recorded in old-growth forests; however, its precise habitat preferences are poorly studied. We used opportunistic observations collected by citizen scientists and stand descriptions from a forestry database to analyse its habitat preferences in Estonia, with a focus on the characteristics of old-growth forests. The Greenish Warbler preferred productive spruce and black alder stands but also favoured rare broad-leaved stands. Forest stands were older, less drained and contained more standing and fallen dead trees in warbler sites than in control sites. Positive effects of stand age and soil fertility exhibited the highest average relative importance in generalized linear models, drainage was of intermediate importance and the occurrence of dead wood was least important. The terrain at warbler sites was also more often uneven than that at control sites. The preference for old-growth forests observed in our study makes the Greenish Warbler, despite occupying various forest stands suggestive of plasticity, a good candidate for inclusion in a suite of old-growth forest indicators.

1. Introduction

Bioindicators are species that are matched to specific habitat features and are reactive to disturbances and environmental changes, and they indicate general biodiversity in a particular habitat (Rohlf 1991, Lambeck 1997, Paoletti 1999, McCarty *et al.* 2002). Indicators are particularly useful in habitats where inventories are difficult or expensive (Juutinen & Mönkkönen 2004). Many species, including various birds (Juutinen & Mönkkönen 2004), have been used to evaluate biodiversity in old-growth forests, which develop over long periods of time without the influence of human activity (Peterken 1996). Woodpeckers are probably the most well-known indicators of biodiversity in old-growth forests (Mikusiński *et al.* 2001, Roberge *et al.* 2008). In European boreal and hemiboreal old-growth forests, several passerines, such as the Bluetail (*Tarsiger cyanurus*), the Red-breasted Flycatcher (*Ficedula parva*), the Treecreeper (*Certhia familiaris*) and tit species, serve a similar purpose and are abundant and easy to study (Tjernberg 1984, Similä *et al.* 2006, Virkkala & Rajasärkkä 2006, Rajasärkka 2010, Rosenvald *et al.* 2011, Pakkala *et al.* 2014, Lindbladh *et al.* 2020). However, these species may also breed in younger managed forests (Jokimäki & Solonen 2011, Lindbladh *et al.* 2020). This raises a question about their usefulness as an indicator (Lindbladh et al. 2020), suggesting the need for alternatives.

The Greenish Warbler (*Phylloscopus trochiloides viridanus*) is a passerine inhabiting a variety of forests across its breeding range from central Europe to central Asia (BirdLife International 2017). In Europe, the species breeds primarily in the eastern part of the continent but is expanding its range westwards (Thoma & Althaus 2015, BirdLife International 2017). Little is known about habitat requirements of this ground-nesting species. Lapshin (2004) found that in Karelia, north-western Russia, the Greenish Warbler mostly occupies mature spruce and mixed forest stands in humid areas, with rich undergrowth and many wind-fallen trees. Similar forests have also been occupied by the Greenish Warbler in Sweden (Elmberg 1985).

According to Suomalainen (1936), the species initially preferred productive mature mixed stands dominated by spruce and birch after colonizing southern Finland but later spread into less productive forests after population growth (Tiainen 1980). General bird inventories in the same region suggest that the Greenish Warbler prefers old-growth forests (Virkkala & Rajasärkkä 2006, Väli & Laurits 2006, Jokimäki & Solonen 2011, Rosenvald *et al.* 2011, Mononen *et al.* 2018).

The species is also associated with uneven landscapes, such as hills and river valleys (Kumari 1954, Rootsmäe & Veroman 1974, Kuus & Leibak 2018). However, this view is based on limited regional observations and few nest findings (Mikelsaar 1963, Lilleleht 1963), and quantitative studies are lacking.

Despite evidence for associations with mature and old-growth forests, the Greenish Warbler is often not included in lists of species typical to this habitat (e.g. Paal 2007) or species of conservation importance (e.g. Lõhmus *et al.* 2001). At the European scale, it is considered a species of least conservation concern, with no current significant threats (BirdLife International 2017). This might be explained by geographical variation in habitat preferences, including more opportunistic habitat use in the core of the distribution where the Greenish Warbler is rather abundant (Dementev & Gladkov 1954). However, it may also reflect the scarcity of studies on habitat requirements and the lack of sufficient data.

Citizen science, the involvement of citizens from the non-scientific community in research, provides extensive data that are difficult to obtain by professional researchers. A network of amateurs has contributed substantially to bird conservation science (Greenwood 2007). The past few decades have witnessed the expansion of citizen science owing to technological developments (Dickinson *et al.* 2012).

While typical projects involving citizen scientists mainly involve reporting species distributions and counts, extensive datasets increasingly allow explorations of correlative relationships (Dickinson *et al.* 2010, McKinley *et al.* 2017; Pocock *et al.* 2018). For example, Weisshaupt & Rodríguez-Pérez (2017) recently used citizen data to compare the habitat use of the Wood Warbler (*Phylloscopus sibilatrix*) during spring migration and the breeding season, Mononen *et al.* (2018) relied on observations of birdwatchers together with airborne laser scanning data to determine the habitat preferences of forest birds.

We used opportunistic observations of the Greenish Warbler collected by citizen scientists to analyse its habitat preferences with a particular focus on characteristics of old-growth forests in Estonia, at the western margin of species' distribution range. We predicted that sites where the Greenish Warbler has been recorded (hereafter, referred to as warbler sites) would exhibit characteristics consistent with those of old-growth forests (old age, lack of drainage, large volume of dead trees), compared with randomly located sites (hereafter, control sites). We also evaluate the view that warbler sites exhibit steeper slopes than those of control sites.

2. Material and methods

2.1. Compilation of observations

Publicly available occurrence records of singing Greenish Warblers in Estonia (57°30'–59°40'N; 21°45'–28°10'E; Supplementary Figure 1) in 2003–2017 deposited by voluntary citizen scientists in the biological data management platform PlutoF (https://plutof.ut.ee/; Abarenkov *et al.* 2010) were obtained via the online portal eBiodiversity (https://elurikkus.ee/en). Records with a precision of ≤ 200 m between 1st May and 31st July were used. To avoid pseudoreplication, when there were multiple observations within 400 m, only one was retained. The dataset was supplemented with 17 precise records obtained by ÜV in the same period. Analyses of forest characteristics were based on 225 total records; terrain unevenness was analysed at 119 warbler sites.

The Estonian population of the Greenish Warbler consists of 7,000–15,000 pairs (Elts *et al.* 2019) with a sparse distribution across the country (Kuus & Leibak 2018). The abundance and distribution differs between years due to influence of weather conditions during spring migration. The species arrives in Estonia in May, and the main migration probably occurs in late May and early June (Kuus & Leibak 2018), although detailed analysis of migration is lacking. Similar arrival dates have been recorded in Karelia, where laying occurs soon after arrival, mostly in the first half of June (Lapshin 2004).

Hence, it is impossible to separate local birds from migrants in late May and early June. In the current study, 59% of records were made in that period (Supplementary Figure 2) and repeated observations in well-studied locations revealed breeders arriving at their territories already in May (see also Lilleleht 1963). Therefore, all records were retained, including potential records of singing migratory individuals. In any case, the exclusion of singing migrants is impossible in most ornithological inventories and thus their inclusion here is justified given our main aim, i.e., determining the value of the Greenish Warbler as an indicator species.

Typical to bird inventories, it was also not possible to separate breeding pairs from single individuals, which are expected to account for a substantial proportion of Greenish Warblers in some years, especially at range margins (Lapshin 2004, Thoma & Althaus 2015, Kuus & Leibak 2018). Such single individuals have been observed in atypical habitats close to geographical barriers (e.g. sea coasts) and their singing period lasts until late summer (Lilleleht 1963, Mikelsaar 1963, Kuus & Leibak 2018). Data used in the current study were recorded in early summer across the country and records somewhat concentrated only at sites with high birding activity (Supplementary Figures 1 and 2).

2.2. Habitat analysis

The size of the breeding territory of the Greenish Warbler is estimated as 0.5–0.8 ha (Cramp 1992). In this study, a circle with a radius of 50 m (0.78 ha) was used as a proxy for the breeding territory where habitats were described. Habitats were also described in a 200 m radius (12.56 ha). The larger circle could be considered a reference for surrounding available habitat, and the difference between the circles with radii of 50 and 200 m would indicate the habitat preference at a local level. However, bird locations are not always correctly estimated by observers in opportunistic datasets. Moreover, the bird moves around in the territory, and the actual nest site and exact borders of the territory were not known. Therefore, the 200 m radius should be considered a less precise proxy of breeding territory, rather than a control showing habitat availability. For comparisons between warbler sites and available habitat, a control sample was composed of 349 randomly located sites across forest land in Estonia, using the same spatial scales of 50 and 200 m radii for habitat descriptions.

For every warbler site and control site, the following forest characteristics were estimated in the two radii at the stand compartment level using the Estonian Forest Register (Metsaportaal 2020): area, dominant tree species, age of the dominant species, soil fertility (site quality class; between 1 (very high) and 5 (very low)), existence of drainage, volume of fallen dead trees and volume of standing dead trees. The unevenness of the terrain was estimated by two methods. First, the difference between minimal and maximal values of elevation contour lines (isohypses) passing through each site was determined. An elevation map with 2.5 m differences between contour lines was used (Maa-amet 2018). Second, the mean slope was obtained from European Digital Elevation Model v.1.1 with 25 m resolution (European Environment Agency 2016).

2.3. Data analysis

The data analysis was conducted in the statistical environment R v.4.0.0 (R Core Team 2020) and all analyses were conducted separately for sites with a 50 m or 200 m radius. Forest parameters in both ra-

Table 1. Best generalized linear models (ΔAICc < 2) describing the importance of widespread, dominant tree species in warbler sites compared with control sites in radii of 50 and 200 m. R^2, coefficient of determination; *AICc*, Akaike information criterion corrected for small values; ΔAICc, difference in AICc values of the best model; *w*, model weight; + and –, direction of the effect of explanatory variables. Parameter estimates ± standard error (se) of explanatory variables, relative importance values (RIV), z-statistic and significance (*P*) are obtained from a conditional average over the models.

Model	Pine	Spruce	Birch	Grey Alder	Black Alder	Aspen	R^2	AICc	ΔAICc	*w*
50 m										
1		+					0.029	422.96	0.00	0.24
2		+			+		0.033	423.38	0.42	0.19
3		+				–	0.032	424.02	1.07	0.14
4		+	–				0.031	424.45	1.49	0.11
5		+			+	–	0.036	424.53	1.58	0.11
6	+	+					0.030	424.56	1.60	0.11
7	+	+			+		0.035	424.84	1.89	0.09
Estimate	31.43	163.15	–32.68		213.13	–145.79				
± SE	± 44.47	± 53.14	± 44.95		± 172.23	± 158.99				
RIV	0.20	1.00	0.11		0.40	0.25				
Z	0.70	3.07	0.72		1.23	0.91				
P	0.479	0.002	0.467		0.215	0.362				
200 m										
1	–		–	–	+		0.029	569.26	0	0.24
2	–		–	–			0.023	569.73	0.47	0.19
3			–	–	+		0.022	570.15	0.90	0.16
4			–	–			0.016	570.83	1.57	0.11
5			–		+		0.016	570.98	1.72	0.10
6	–		–		+		0.019	571.12	1.86	0.10
7	–	0	–	–	+		0.029	571.18	1.93	0.09
Estimate	–6.03	1.74	–8.75	–19.56	33.57					
± SE	± 3.69	± 4.80	± 4.29	± 11.13	± 21.46					
RIV	0.66	0.09	1.00	0.82	0.72					
z	1.63	0.36	2.04	1.76	1.56					
P	0.102	0.717	0.041	0.078	0.117					

dii were determined using weighted averages, taking the area of the stand compartment as the weight. Continuous variables were first analysed using univariate tests (*t*-test for age and Mann–Whitney–Wilcoxon test for other variables). Several predictors were intercorrelated with each other as indicated by the Spearman rank correlation matrix (calculated using package *Hmisc* v. 4.4-0; Supplementary Table 1).

Therefore, we used an information-theoretical approach and multi-model inference (Burnham & Anderson 2002) to analyse the significance and relative importance of forest characteristics. Generalized linear models were used when warbler sites and control sites were binary dependent variables and forest characteristics were independent predictors. Prior to model fitting, continuous predictors were standardized (scaled) using the *mutate* function in the package *dplyr* v.0.8.3 (Wickham *et al.* 2020).

Models were ranked using the Akaike information criterion corrected for small sample size (AICc) using the *dredge* function in the package *MuMIn* v.1.40.4 (Bartoń 2013). The best models were selected according to ΔAICc values (equals $AICc_i – AICc_{min}$, where $AICc_{min}$ is the best model in the set). Finally, model averaging was used to obtain parameter estimates and relative importance values (RIV) for explanatory variables (according to a conditional average model). RIV of each explanatory variable was estimated by summing normalized Akaike weights across all models that contained the variable (Burnham & Anderson 2002).

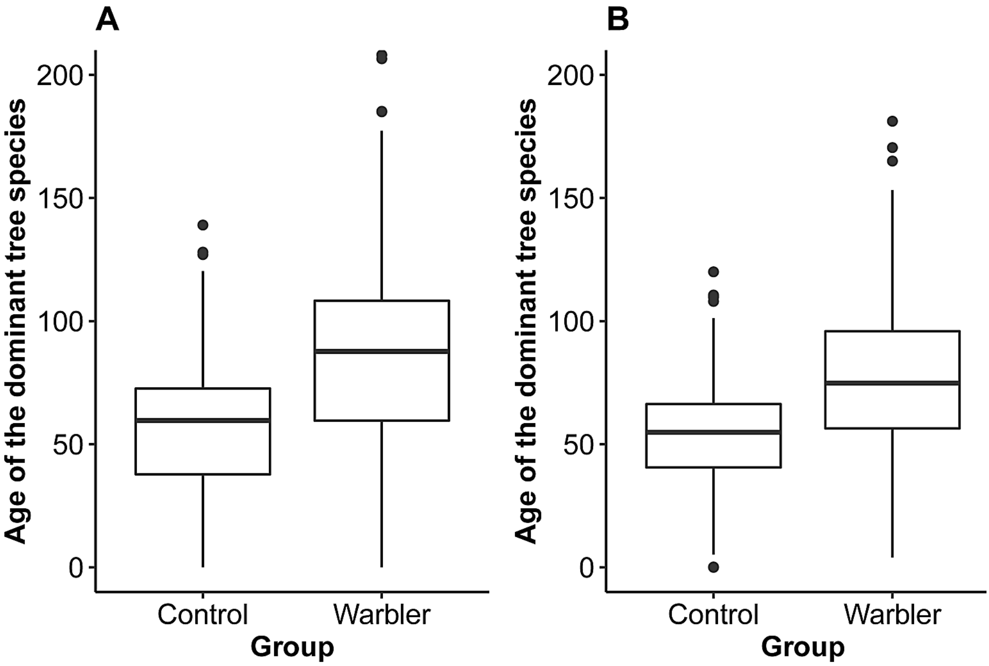

Fig. 1. Mean age of forest stands in control sites and warbler sites in a 50 m radius (A) and 200 m radius (B). Thick line indicates median, box indicates quartiles, whiskers indicate 1.5 times the interquartile range and dots represent outliers.

3. Results

We obtained 192 models with high support (ΔAICc < 2) describing the importance of 14 main tree species recorded in a 50 m radius around warbler sites (Supplementary Table 2). All of the models indicated that spruce is the most abundant species (RIV = 1.00). Broad-leaved species (ash, RIV = 0.88; linden, RIV = 0.60; elm, RIV = 0.60) were also important, while black alder was of intermediate importance (RIV = 0.47). RIV values for other tree species did not exceed 0.20. However, all models had very low weights (≤ 0.01), and only the average estimate for spruce was significant (z = 3.21, P = 0.001). We then developed models including only the seven most widespread tree species. The seven best models (ΔAICc < 2; Table 1) confirmed the importance of spruce, as it was included in all of these models with high significance, and the best model contained only spruce. Although black alder was not a significant factor, it still had moderate importance and was included in the second-best model with spruce.

In a 200 m radius, all 101 models of all tree species with ΔAICc < 2 (Supplementary Table 3) included birch and linden, and high importance was also recorded for willow (RIV = 0.91, due to four occurrences only in control plots), followed by two alder species (RIV = 0.62 and 0.64). However, only the avoidance of birch was significant (z = 2.04; P = 0.04). The seven best models including six widespread tree species (Table 1), confirmed avoidance of birch. The averaged model also suggested avoidance of grey alder and pine as well as a preference for black alder, but these factors were only close to significance limit (Table 1).

Greenish warblers were recorded in stands of all ages, but the mean age of warbler sites was significantly higher than that of control sites in both a 50 and 200 m radius (Fig. 1, Table 2). The proportion of warbler sites was higher than that of control sites in forests >90 years, whereas the opposite pattern was observed in younger stands. Additionally, the proportion of drained stands was significantly lower in bird sites than in control sites (Table 2). Despite the larger proportion of sites

Table 2. Mean values ± standard deviation (SD) of the quantitative forest characteristics and test statistics (*t* in age, *W* in others) and significance (*P*) for univariate tests.

	50 m				200 m			
	Warbler site	Control site	Test statistic	*P*	Warbler site	Control site	Test statistic	*P*
Age (years)	90 ± 42	57 ± 27	7.57	0.001	78 ± 31	54 ± 20	8.75	0.001
Soil fertility (site quality class)	2.15 ± 1.12	2.24 ± 1.17	12,776	0.385	2.12 ± 0.95	2.24 ± 1.02	22,756	0.304
Proportion of drained stands (%)	14 ± 31%	27 ± 42%	13,938	0.005	13 ± 28%	24 ± 34%;	26,263	<0.001
Fallen trees (m^3/ha)	13.3 ± 48.0	7.9 ± 32.2	10,188	0.009	10.8 ± 35.7	6.2 ± 22.3	20,127	0.260
Standing dead trees (m^3/ha)	19.7 ± 109.7	7.2 ± 29.2	10,126	0.007	13.7 ± 78.5	5.3 ± 19.6	19,420	0.085
Difference of isohypses (m)	3.07 ± 6.30	0.65 ± 2.21	12,806	<0.001	1.71 ± 4.64	0.65 ± 2.21	15,292	0.009
Mean slope (°)	2.59 ± 2.48	1.72 ± 1.30	13,390	<0.001	2.33 ± 1.67	1.69 ± 0.87	13,383	<0.001
Maximum slope (°)	3.92 ± 3.86	2.57 ± 1.82	13,458	<0.001	6.44 ± 4.65	4.56 ± 2.51	13,351	<0.001

Table 3. Best generalized linear models (ΔAICc < 2) describing the importance of variables describing old growth and landscape roughness in warbler sites compared with control sites at radii of 50 and 200 m. Abbreviations are similar to those in Table 1.

Model	Age	Soil fertility	Drainage	Laying dead wood	Standing dead wood	R^2	AICc	ΔAICc	*w*
50 m									
1	+	–	–			0.21	354.10	0.00	0.31
2	+	–	–	–		0.21	354.94	0.84	0.20
3	+	–	–	–	+	0.22	355.56	1.46	0.15
4	+	–		–		0.20	356.03	1.92	0.12
5	+	–				0.20	356.05	1.95	0.12
6	+	–	–		–	0.21	356.16	1.96	0.11
Estimate ± SE	1.06 ± 0.16	–0.34 ± 0.13	–0.24 ± 0.13	–0.20 ± 0.19	0.14 ± 0.27				
RIV	1.00	1.00	0.77	0.46	0.26				
z	6.72	2.58	1.82	1.07	0.52				
P	<0.001	0.010	0.068	0.284	0.602				
200 m									
1	+	–	–	–		0.23	468.58	0	0.25
2	+	–	–			0.22	468.94	0.36	0.21
3	+	–	–	–	+	0.23	469.01	0.43	0.20
4	+	–		–		0.22	469.27	0.69	0.18
5	+	–		–	+	0.22	469.66	1.08	0.15
Estimate ± SE	1.57 ± 0.20	–0.60 ± 0.14	–0.22 ± 0.13	–0.38 ± 0.29	0.43 ± 0.48				
RIV	1.00	1.00	0.67	0.79	0.35				
z	7.76	4.21	1.69	1.33	0.90				
P	<0.001	<0.001	0.091	0.183	0.370				

with very high soil fertility (site quality class 1) among warbler sites (30.2% of forests) than among control sites (25.2%), and the lower proportion of low-fertility (class 4) stands among warbler sites (7.1%) than among control sites (10.9%), no difference between the mean soil fertility class was detected (Table 2).

Most studied forest stands contained <10 m^3/ha standing dead trees; however, there were more stands with a higher volume of standing dead trees in warbler sites (27.3% of the total area within 50 m and 23.3% within 200 m) than in control sites (16.3% and 14.1%, respectively). We detected a similar pattern for fallen dead trees. On average, there were significantly more fallen trees and standing dead trees in warbler sites than in control sites in a 50 m radius; similar non-significant trends were noticed in a 200 m radius (Table 2). Univariate tests were also conducted to evaluate differences between warbler sites of 50 and 200 m radii. The only significant difference was found in the mean age of the dominant tree species ($t = 2.50$, df = 199.9, $P = 0.013$; Fig. 1).

Five models of quantitative forest characteristics in a 50 m radius had high support (ΔAIC < 2; Table 3). The models fitted the data well with evenly spread residuals and similar weights ($R^2 = 0.20$–0.21; w = 0.11–0.30). Stand age and soil fertility were the most important characteristics, as determined by RIV values, and the characteristics of dead wood were less important (Table 3). In contrast to the results of univariate analysis (Table 2), multivariate models suggested a negative association between warblers and laying dead wood (Table 3). Similar results were obtained for a 200 m radius (five models with ΔAIC < 2, w = 0.14–0.25, $R^2 = 0.22$–0.23; Table 3).

The Greenish Warbler preferred uneven terrain, as revealed by the significant difference in the mean difference of isohypses, as well as the significant differences between mean and maximum slopes in warbler sites and control sites (Table 2).

4. Discussion

We analysed Greenish Warbler habitats with a focus on the characteristics of old-growth forests. Greenish Warblers preferred forest stands that were older, less drained, and that contained more dead wood as both standing and fallen trees compared with control sites. Our results are supported by earlier results for Sweden, Finland and Karelia, where the species is also typically found in forests that are older than average (Tiainen 1980, Elmberg 1985, Lapshin 2004). The preference for taller trees based on observations and remote sensing also provides indirect evidence for the importance of older forests (Mononen *et al.* 2018).

In the current study, forest age was the most important determinant of warbler habitats among old-growth characteristics. As age is also the easiest characteristic to determine, and is available in most forest databases, it is probably the most useful variable for surveying the Greenish Warbler and other similar old-growth forest bird species. The difference in age was stronger in the 50 m than in the 200 m radius, further confirming the importance of forest age for the Greenish Warbler. This difference also highlights the importance of proper scale in habitat studies. In the current study, the scales employed were equal to the estimated breeding territory, although most preferences for old-growth characteristics were also evident at larger scales.

Forest age is obviously not of primary importance for birds as such but rather is an indicator of the availability of essential resources, such as food, nest sites, and cover (Jokimäki & Solonen 2011). For example, wind-fallen trees, which are found in old-growth forests, often provide shelter for Greenish Warbler nests (Lapshin 2004). In our study, warbler sites contained more dead trees than control sites. However, importance of standing dead trees was more obvious than that of fallen trees, which had opposite effects in univariate tests and multivariate models. This suggests that the link between dead tree volume and warblers may only be correlative and not functional. In Karelia, nests were also found close to ditches and other water bodies (Lapshin 2004), which corroborates warbler preference for undrained forest stands in Estonia. However, variables describing the volume of dead trees, as well as drainage, had high variance caused by many zero-values in the dataset. This resulted in relatively low importance estimates for these variables in the models, indicating plasticity in habitat use by this species.

The Greenish Warbler preferred productive spruce stands, corroborating earlier results for

Fennoscandia (Tiainen 1980, Elmberg 1985, Lapshin 2004). The strong and specific preference suggests that the species fills a niche that is largely unoccupied by other warbler species in the region (Tiainen *et al.* 1983). We also noticed a preference for broad-leaved trees, which are uncommon in Estonia but used by the warbler in central Europe (e.g. Christen 2015). A shortage of this type of forest might have been compensated by the black alder, which is also rather strongly preferred, especially at the larger spatial scale (200 m). At the larger scale, we also noticed the avoidance of birch and grey alder stands. By contrast, birch stands are preferred in Finland (Tiainen 1980), indicating that there is geographical variation in species preferences. Productive spruce forests were the main habitat after the initial colonization of the country (Suomalainen 1936), with later spread to other forests, such as pine forests (Tiainen 1980), which, at least regionally, seem to determine the current distribution of the species (Mononen *et al.* 2018). Hence, the habitat requirements seem to have relaxed over time in Finland.

Similar relaxation of habitat requirements may also have occurred in Estonia, where earlier literature (Kumari 1954, Lilleleht 1963, Mikelsaar 1963, Rootsmäe & Veroman 1974, Kuus & Leibak 2018) unequivocally linked species with slopes, but contemporary data indicate a broad distribution across flat land. However, we detected a significant preference for uneven terrain. The preference for slopes has been explained by foraging behaviour involving vertical flights (Mikelsaar 1963). This might be associated with interspecific competition, which plays a major role in the division of habitats between different species of *Phylloscopus* warblers (Price 1991, Forstmeier *et al.* 2001). Indeed, the Greenish Warbler flies more often during foraging than the Willow Warbler (*Phylloscopus trochilus*) and Chiffchaff (*P. collybita*) and tends to capture large mobile prey (Batova 2011).

Additionally, a preference for slopes can be explained by a requirement for particular light and wind conditions (Mikelsaar 1963). In fact, similar conditions are created by trees of uneven age and openings in old-growth forests. In such forests, the terrain is also uneven at a microhabitat scale, as it contains mounds and pits created by fallen trees and roots pulled out of the ground, which provides suitable places for nests. However, it is possible that the preference for slopes is indirectly associated with the preference for old-growth forests. Forests growing on slopes might have been historically more difficult to reach and cut; therefore, they are now often protected old-growth forests. However, the lack of correlations between most characteristics of old-growth forests and those of uneven terrain (Supplementary Table 1) does not support this view. Instead, collinearity between soil fertility and terrain unevenness suggests that what is really important is the availability of productive stands on slopes. Forests on slopes tend to be less drained, which may additionally support the preference for slopes by the Greenish Warbler.

Similarly to many other countries, the popularity of birdwatching has increased in Estonia. This has been paralleled by a surge in the number of observations being deposited in open databases, allowing researchers to collect considerable data even on rare species. Obviously, there are also concerns and limitations to using citizen data (Dickinson *et al.* 2010).

First, the limited experience of observers may result in the introduction of erroneous data into datasets. Indeed, misidentification is a potential problem for *Phylloscopus* warblers, which are not easy to identify by plumage alone. However, the possibility to deposit song recordings makes species identification much easier and increases the reliability of the records. Moreover, many observations of Greenish Warblers have been made by well-known and experienced birdwatchers, and the records of less experienced people are verified by experts prior to their acceptance in the PlutoF database, which was the source of the data used the current study.

Second, rare species are often over-reported, compared with common species, but this does not influence the results of the current single-species study. On the other hand, rare habitats such as old-growth forests may be oversampled.

In Estonia, old-growth and mature forests are more widespread than in many European regions, and they are not specifically targeted by birdwatchers. Old-growth forests are also harder to access than managed forests, which are often situated close to settlements and roads. Indeed, higher accessibility leads to oversampling of species in degraded residential forests (Dickinson *et al.*

2010), which may have resulted in higher detection of the Greenish Warbler in managed young stands in the current study.

Unfortunately, most opportunistic citizen data are sporadic and superficial. Observations are usually non-recurrent and therefore it was impossible to separate migrants from breeding individuals in the current study. Moreover, it is impossible to determine without performing detailed observations and nest searches whether the absence of records of the warbler's song means that it had migrated further north or it started to lay eggs. This may have added "noise" to our results of the breeding population, because habitat use during migration is not always similar as that during breeding (Igl & Ballard 1999, but see Colwell & Oring 1988). For example, in a year of exceptional abundance, Wood Warblers showed no preference for habitat features during migration and covered practically all available habitat types from urbanized areas to wetlands and forests in Spain, whereas during breeding the birds tended to prefer forest habitats in Switzerland (Weisshaupt & Rodríguez-Pérez 2017).

Similarly, Greenish Warblers have been recorded in a wide spectrum of habitats in Estonia during invasion years (Mikelsaar 1963). We propose that the "noise" added by migrants in the current study is limited for several reasons. First, only sites covered by the forestry database were included in the analyses of forest characteristics and records in non-forest biotopes were included only in the analysis of terrain unevenness. Secondly, virtually all Greenish Warblers records in the Estonian PlutoF database are spontaneous (playback not used) song records. Greenish Warblers vocally mark territories and defend resources both in breeding and wintering grounds (Price 1981, Katti 2001). Singing, accompanied by various other activities such as rapid flight and wing flicking, is costly for Greenish Warblers (Katti 2001). Therefore, Greenish Warblers probably do not engage much in this type of activity during migration, which may have led to an underrepresentation of migrants in our sample. However, migrants are not excluded from most ornithological inventories. Therefore, given that our main aim was to analyse the value of the Greenish Warbler as an indicator species of a certain habitat type, pooling migrants and breeders should not be considered a drawback but a merit instead, because it confirms the robustness of the Greenish Warbler as an indicator species.

Is the Greenish Warbler a suitable indicator of old-growth forest? On the one hand, the species indeed preferred stands meeting the criteria for natural old-growth forests (old age, large amount of dead wood, no drainage). Hence, the Greenish Warbler would indicate the naturalness of certain types of forests (e.g. old spruce-dominated or broad-leaved productive forests in Estonia). On the other hand, the high variance of studied variables indicates the plasticity of the species, which becomes more obvious as the population grows (Tiainen 1980). For example, a century after colonizing Estonia, the species is no longer associated only with specific stands, as observed in the current study. However, we also showed that such stands are still preferred, suggesting that the value of the species as an indicator is retained. In fact, there is similar mixed support for the effectiveness of the other abovementioned indicator species. The Greenish Warbler should therefore be included in a suite of candidate indicators of old-growth forests.

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Idänuunilintu: vanhojen metsien unohdettu indikaattorilaji?

Vanhojen metsien indikaattorilajit ovat tärkeitä metsien suojelun kannalta. Idänuunilintua on havaittu vanhoissa metsissä, mutta sen elinympäristövaatimukset ovat huonosti tunnettuja. Tässä tutkimuksessa käytettiin harrastajien keräämää havaintodataa ja metsänhoitoaineistoja, erityisesti vanhoista metsistä, idänuunilinnun elinympäristöjen selvittämiseen.

Idänuunilintu suosi kuusimetsiä ja tervaleppämetsiköitä, mutta myös lehtimetsiä. Alueet, joilla havaittiin idänuunilintuja olivat keskimäärin iäkkäämpiä, sisälsivät vähemmän ojitettua metsää, ja enemmän kuolleita puita kuin kontrollialueet.

Metsikön ikä ja maaperän ravinteikkuus olivat parhaiten idänuunilinnun esiintyvyyttä selittäviä tekijöitä, ojittaminen toiseksi merkittävin ja kuolleiden puiden esiintyminen vähiten tärkeä. Alueet, joilla idänuunilintua havaittiin olivat useimmin rinteillä kuin tasamaata. Nämä havainnot tekevät idänuunilinnusta hyvän lisän vanhojen metsien indikaattoreihin.

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Online supplementary material:
Väli & Vaan: Habitat preferences of the Greenish Warbler

The spatial and temporal distribution of analysed records, correlation matrices of variables and lists of models describing the importance of tree species around warbler sites.