

Article

Synanthropic Process Evaluation (with Factors Affecting Propensity to Parasitism) and Host Range within the Genus *Ganoderma* in Central Europe

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Abstract: *Ganoderma* P. Karst. is a genus of wood decaying fungi with complicated taxonomy due to morphological variability of their basidiomata. Although a wide range of host plants is assumed for the genus as a whole, there is a need for revision of the host specificity of individual species. Based on revision of mycological collections across the Czech Republic we analyzed the ecological trends of six European species, including host preferences and propensity to parasitism. Individual *Ganoderma* species were sampled differentially along vegetation categories, with *G. adspersum* (Schulzer) Donk prevailing in habitats with high anthropogenic factors and *G. applanatum* (Pers.) Pat. in natural vegetation with limited anthropogenic influence, differing also in average altitude of sampling. The number of host species of individual *Ganoderma* spp. did not reach an asymptote, suggesting an open host plasticity and great potential for finding new host associations in future. Very distinct host compositions were found for individual *Ganoderma* species, at the genus level, with *G. applanatum* being the least host specific. Individual *Ganoderma* species differ also in their tendency to parasitic life strategy. The proportion of parasites increases with decreasing vegetation category and it is therefore higher in urban than natural environment, especially on hardwood trees.

Keywords: fungal pathogens; host specificity; forest trees; vegetation categories; wood-decay



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1. Introduction

The genus *Ganoderma* P. Karst. includes wood-rotting basidiomycetes with laccate and non-laccate pilei. Historically, laccate taxa were referred to as the *G. lucidum* (Curtis) P. Karst. complex (*Ganoderma lucidum* s.l.), and non-laccate species as the *G. applanatum* (Pers.) Pat. complex. With expansion of molecular methods, the phylogenetic analyses became beneficial for assessing taxonomic complexity of this genus [1–8]. Authors use multilocus phylogeny which generated robust species identification and differentiation in the last decade. Additionally, basidiospore shape and size, geographic location, and host preference were found to aid in species identification [9].

From six species present in the Czech Republic (*G. applanatum* s.str., *G. adspersum*, *G. lucidum* s.str., *G. resinaceum*, *G. carnosum*, *G. pfeifferi*), the above-mentioned applies especially to two of them, *G. adspersum* (Schulzer) Donk and *G. applanatum* (Pers.) Pat. which are clearly distinguishable based on spore size only [10–12]. *Ganoderma adspersum* might be also mistaken for *G. pfeifferi* Bres. but the latter species has resinous layer on pileus surface. *Ganoderma resinaceum* Boud. possesses also a resinous layer on pileus surface but in contrast to *G. pfeifferi* the color of the context is significantly lighter [13]. *Ganoderma lucidum* (Curtis) P. Karst. is a part of *Ganoderma lucidum* complex. It has a laccate pileus and vivid colors, often with stipes. *Ganoderma carnosum* Pat. can be identified

based on the host substrate which should be a coniferous tree in majority of cases [14,15]. However, as aforementioned, the knowledge of host specificity of *Ganoderma* species may be distorted by the difficult taxonomy of the group and common misidentifications [16]. Additionally, genus *Ganoderma* is famous for its many uses in traditional Chinese medicine and for its beneficial properties for human health [17,18], especially *G. lucidum* but due to the phenotypic plasticity, molecular methods play a vital role in characterizing the species within the *G. lucidum*-complex [19]. DNA sequences also proved to be an accurate and rapid way for identification of the causal agents of wood rot in trees [20] including *Ganoderma* spp. which can cause danger in urban environments by falling and disrupting city infrastructure.

Kotlaba [21] and Gáper [22] recorded occurrence of some *Ganoderma* species in habitats highly influenced by humans and Gáperová [23] described (non)synanthropic characters in *Ganoderma* spp. with exception of *G. carnosum* due to lack of data for significant conclusions. The last extensive revisions of mycological collections with focus on *Ganoderma* species in the Czech Republic were conducted mainly by prestigious Czech mycologist František Kotlaba from 1971 to 1980. Therefore, the aim of the present study was to extend revisions to a new material in collections and to: (i) evaluate ecological trends of the species particularly focusing on their occurrence in different vegetation category (to detect synanthropization processes), (ii) determine the host specificity of studied species and their propensity to parasitism.

2. Materials and Methods

We conducted a revision of mycological collections in the Czech Republic during 2014 and 2015, in museums in Prague (PRM), Brno (BRNM), Ostrava (OSM), České Budějovice (CB), Frýdek-Místek (FMM), Hradec Králové (HR), Olomouc (OLM), Pardubice (MP), Valašské Meziříčí (VM), Znojmo (MZ), Jihlava (MJ), Bruntál (OVMB), Rokycany (MBH) and Zlín (GM). Firstly, based on modern literature [10,11,13,24–28], we created an identification key for *Ganoderma* spp. which we used for revision of less ambiguous samples where spore measurement was not needed. For identification of more unclear specimen we measured spore size with maximum magnification (with immerse objective 100×) using light microscopes available at the site or MOTIC light microscope (Motic Company, Wetzlar, Germany).

Specimen's information collected from museums included species name, date of collection, location, substrate, altitude, coordinates, map quadrat (used in Europe and the most common in the Czech Republic is the KFME method—Kartierung der Flora Mitteleuropas—the map field measures 10 min longitude and 6 min latitude). This field is identified by a four-digit numeric code, e.g., 6365. As a result, “63” in this case means a row, numbered from north to south, and “65” means a column, from west to east. This basic map field can be further divided into quarters, marked with letters a, b, c, d [29], assumed life strategy (parasitic or saprotrophic), collector and determiner names. Missing altitude data were completed according to location description on specimen tag with help of Google Earth using radius of proximal area and counting average altitude. Similarly, for map quadrat we used a tool for conversion of coordinates freely accessible on BioLib [30]. Herbarium-based study shows that habitats of *Ganoderma* species in the Czech Republic range from heavily managed town and city centers, to the natural reserves in strictly protected areas. For evaluation of preference of the type of vegetation we created eight categories as follows (modified after Jeffrey [31]): 1. Central areas (areas with high anthropogenic influence): town or city center. Paved spaces with woody plants, such as tree-lined alleys, promenades and squares are often found in these centers; 2. Suburban areas (areas with medium to high anthropogenic influence): areas surrounding towns or city centers, including residential sites, suburban public parks and gardens, mixed used sites, as well as industrial and commercial sites. Suburban areas are heavily managed for particular amenity-based uses. High application rates of agrochemicals, especially herbicides and fertilizers is common; 3. Peri-urban areas (areas with lower anthropogenic influence): urban

periphery areas characterized by combination of fragmented urban and rural features rich in ruderal sites and agricultural management, but sometimes abandoned; 4. Rural areas (areas with medium to high anthropogenic influence): villages and agricultural areas that are located outside towns and cities. These areas have a low population density and small settlements; 5. Quasi-natural habitats associated with engineered features (areas with low anthropogenic influence): mainly linear features along roads or railways with maintenance of adjacent greenery for transport safety; 6. Nearly natural habitats (areas with limited anthropogenic influence): secluded housing surrounded by forests without engineered features. People management achieve balance between forest protection and their amenity; 7. Green areas (areas with limited anthropogenic influence): forests, mainly wood industry forests, according to FAO (Food and Agriculture Organization of the United Nations) defined as a land area spanning more than 0.5 hectares with trees higher than 5 m and a canopy cover of more than 10%, or trees able to reach these thresholds in situ. The management must be carried out according to forest management plans; 8. Natural reserves and protected areas (areas with minimal or no anthropogenic influence): national parks and landscape areas according to Act no. 114/1992 Coll. on Nature and Landscape Protection defined as large areas with a harmoniously shaped landscape, characteristic relief, a significant proportion of natural forest ecosystems and permanent grasslands. The management must be carried out according to the zones of graded protection, so as to preserve and improve the natural conditions preserve and create the optimum ecological functions of these territories. Recreational use shall be admissible, provided that it does not damage the natural values of the protected landscape area. The protection regime in these areas is therefore looser than in the case of national parks. All studied specimens were of herbarium origin and division into vegetation categories was according to location of each specimen.

2.1. Temporal and Spatial Sampling Trends of *Ganoderma* Species

We analyzed data in R 3.4.3 using packages “MASS” [32], “MuMIn” [33], “car” [34], “sciplot” [35], “sm” [36], “vegan” [37] and “rareNMtests” [38], in Canoco 5.01 [39]. To analyze which explanatory variables are associated with differences in individual *Ganoderma* species presence patterns, we assumed each sample as the presence of a given species and the absence of other species (in a given space and time). Then, we used binomial generalized linear mixed models with multivariate normal random effects, using Penalized Quasi-Likelihood, with presence/absence data as dependent variable and *Ganoderma* species, year, altitude, vegetation category, type of environment, host type, and type of trophism as explanatory variables. The random effects were ID of sample and rank of sampling quadrates in longitudinal and latitudinal direction. For the full model, we tested the possible collinearity between variables calculating variance-inflation factor function (VIF), with the aim to sequentially remove the variables with highest VIF, till all VIFs were less than five [40]. The full model was simplified to a final one by backward selection. To compare temporal trends in sampling of individual species in more detail, we used the comparison of individual species univariate density estimates during years [41]. For differences among *Ganoderma* species in sampling years, latitude (N), longitude (E) and altitude, we used only presence data, applying Generalized linear models with Poisson, Gamma and negative binomial distributions, respectively.

2.2. Host Specificity Differences among *Ganoderma* Species

To depict trends in revealing new host tree species during years, we used species accumulation curves with method “collector” adding years in the order they happen, with pooling the few samples before 1920 together. To find the best taxonomical simplification of *Ganoderma* species specificity, we created set of binomial generalized linear models with the previously introduced dependent variable, (i.e., each sample as the presence of a given species and the absence of other species) with different taxonomic levels of host trees (species, genera, families, orders or phyla) as explanatory variables, and we compared

those models by model selection function using Akaike information criterion (AICc). To test the differences in the host-range among *Ganoderma* species (on the host genus level), we used biogeographical null model tests for comparing rarefaction curves [38] tested on 1000 permutations, and we depicted those differences by genera accumulation curves of individual samples with the “Coleman” method [42]. To test, if there are differences among the *Ganoderma* species in host specificity at genus level, we used Canonical correspondence analysis (CCA) with species of *Ganoderma* as explanatory variable and testing the analysis with Monte-Carlo permutational test using 1000 permutations. The host genera with less than five observations were pooled to “rare deciduous trees” and “rare coniferous trees” categories.

2.3. Propensity of *Ganoderma* Species to Parasitism

For identifying trophism patterns for *Ganoderma* species and other trends, we used only presence data. For propensity to parasitism we used binomial generalized linear model with *Ganoderma* species, year, altitude, vegetation category, type of environment and host type as possible explanatory variables and we used also their interactions. On full model we tested the possible collinearity between variables calculating variance-inflation factor function (VIF), with the aim to sequentially remove the variables with highest VIF, till all VIFs were less than five [40]. The model was simplified to the final version by backward selection. Similar approach was applied in Figure S3 for revealing trends in distribution of samples from different vegetation categories using GLMs with binomial distribution.

3. Results

3.1. Temporal and Spatial Sampling Trends of *Ganoderma* Species

Overall, we collected herbarium data on 784 specimens from six species. The six *Ganoderma* species were sampled in differential proportions ($\chi^2 = 357.96$, $p < 0.001$) with *G. applanatum* being the most, and *G. pfeifferi* the least sampled species. Although the samples were quite uniformly distributed across the vegetation category gradient ($\chi^2 = 2.13$, $p = 0.145$), separate species were sampled distinctly along this gradient ($\chi^2 = 85.08$, $p < 0.001$). Whereas *G. adspersum* strongly declined with increasing vegetation category, *G. applanatum* increased (Figure 1).

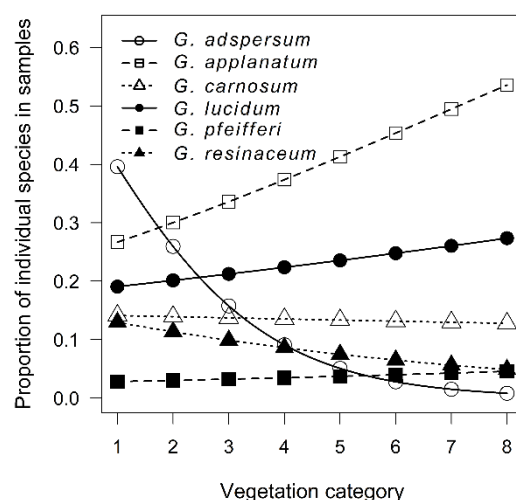


Figure 1. Proportion of individual *Ganoderma* species along the vegetation category gradient. The positions of points are predicted from the binomial generalized linear mixed model.

The *Ganoderma* species also differed in the period, when they were mostly sampled ($F = 9.54$, $p < 0.001$), with median of *G. applanatum* being 1970, whereas *G. resinaceum* median being 1990. The sampling pattern of individual *Ganoderma* species during the years was distinct ($p < 0.001$) with *G. adspersum*, *G. applanatum*, and *G. lucidum* sampling culminating between 1960–1970, *G. carnosum* sampling culminating around 1980, *G. resinaceum* sampling

culminating shortly before 2000, and *G. pfeifferi* with most sampling events in 1960–1970 and in the new century (Supplementary Figure S1).

The species differed also in average latitude ($F = 16.48$, $p < 0.001$) and longitude ($df = 769$, $F = 3.33$, $p = 0.006$) of sampling with *G. lucidum* samples being the most south shifted, *G. adspersum* most north and west shifted and *G. applanatum* most east shifted species. There were significant differences among average altitude of samples of individual *Ganoderma* species ($\chi^2 = 102.97$, $p < 0.001$), partially caused by the fact that *Ganoderma* samples from coniferous trees had higher average altitude than samples from broadleaf trees ($\chi^2 = 17.84$, $p < 0.001$), but on coniferous trees, only three species of *Ganoderma* were present. There were also differences in this pattern among individual *Ganoderma* species ($\chi^2 = 14.64$, $p < 0.001$), e.g., whereas *G. lucidum* samples on broadleaf trees had the second lowest average altitude, on coniferous trees they had the highest average altitude (Figure 2).

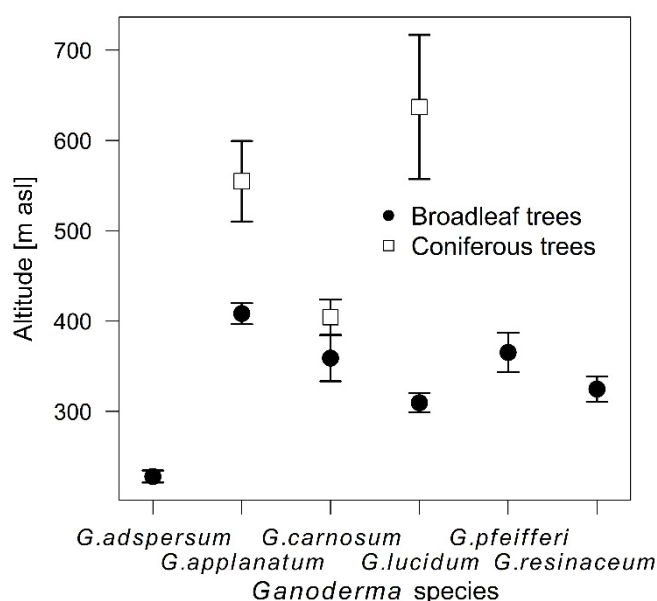


Figure 2. Average altitude of samples of individual *Ganoderma* species on broadleaf and coniferous trees (mean \pm SE).

3.2. Host Specificity Differences among *Ganoderma* Species

Regarding host specificity, during years the increase in number of tree species associated with individual *Ganoderma* species did not reach an asymptote, even for the *G. pfeifferi* and *G. resinaceum* with low host-range (Figure 3). The best simplification of pattern of *Ganoderma* species host specificity can be based on host genus level (Table 1), with significant differences between host tree genera ($\chi^2 = 828.92$, $p < 0.001$) (Supplementary Figure S2). CCA analysis confirmed great differences in host genus specificity among *Ganoderma* species ($F = 7.8$, $p = 0.001$) (Figure 4). *Ganoderma lucidum* and *G. resinaceum* were highly associated with *Quercus* followed by *G. adspersum* which also showed preference of *Quercus*. *Ganoderma pfeifferi* was found mostly on *Fagus*, *G. carnosum* on *Picea* and *Abies* (i.e., coniferous trees), whereas *G. applanatum* was least host specific, frequently associated with *Quercus*, *Fagus*, *Tilia*, *Acer*, *Populus*, and *Picea*, and less frequently associated with the other 24 tree genera. Biogeographical null model tests revealed that there were significant differences in level of host specificity among *Ganoderma* species ($Z_{sim} = 2681.25$, $p = 0.009$), with difference among the group of less host specific *G. adspersum*, *G. applanatum* and *G. carnosum* and more specialized group of *G. lucidum*, *G. pfeifferi* and *G. resinaceum* (Figure 5). Host preferences for each *Ganoderma* species are shown in Table 2.

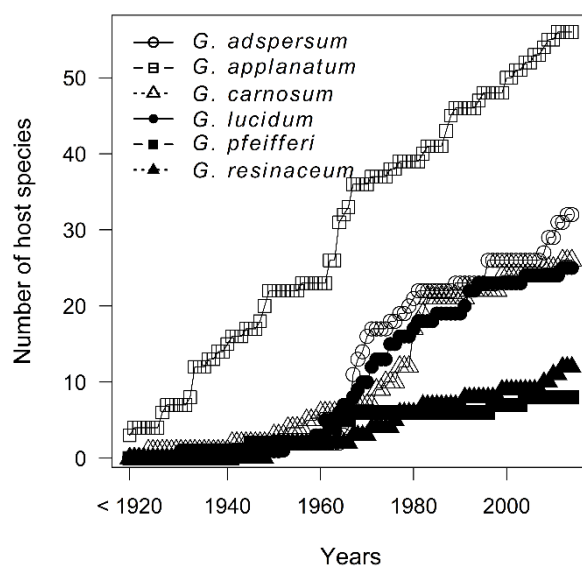


Figure 3. Species accumulation curves of host tree species for individual *Ganoderma* species created with method “collector” adding the years in the order they happen to be in the data.

Table 1. Comparison of GLM models with presence of given *Ganoderma* species as dependent variable and varying resolution of host identity as explanatory variable. Host level: taxonomic level of host used as explanatory variable; Df: degrees of freedom used in the model; LogLik: log-likelihood; AICc: the value of the Akaike information criterion; AICc Δ : difference in information criterion between the model and the best model with lowest AICc.

Host Level	Df	LogLik	AICc	AICc Δ
Genus	216	−995.025	2450.5	0.00
Order	66	−1180.481	2495.5	45.01
Family	108	−1136.384	2495.7	45.17
Species	510	−823.424	2840.6	390.13
Phyllum	12	−1446.361	2916.8	466.28

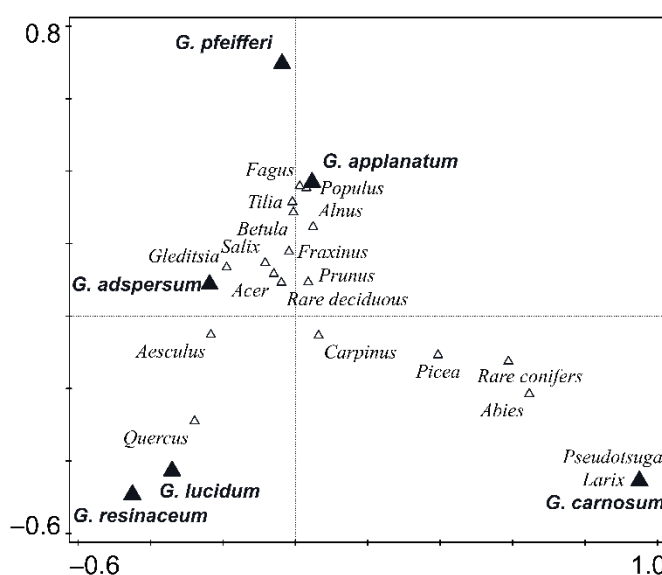


Figure 4. CCA analysis plot showing the differences in host tree composition among *Ganoderma* species and affiliation of them to host genera.

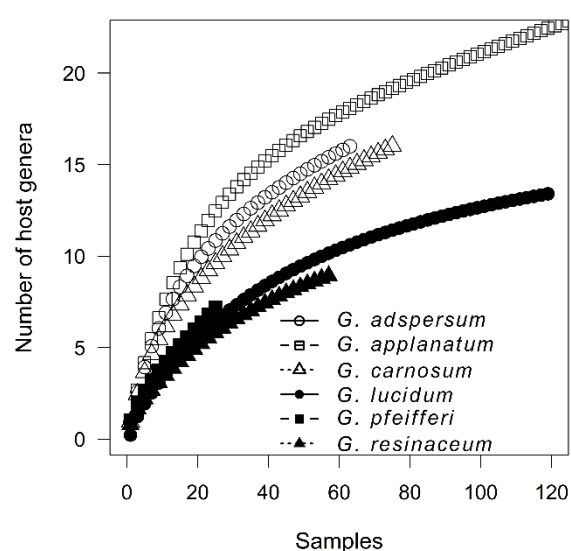


Figure 5. Genera accumulation curves showing the level of host specificity of individual *Ganoderma* species. The axes shortened for clarity.

Table 2. Number of records for individual *Ganoderma* species associated with different host genera (ranked by appearance).

Host Genera	<i>G. adspersum</i>	<i>G. applanatum</i>	<i>G. carnosum</i>	<i>G. lucidum</i>	<i>G. pfeifferi</i>	<i>G. resinaceum</i>
<i>Quercus</i>	16	20	4	79	1	43
<i>Fagus</i>	2	39	2	4	17	1
<i>Tilia</i>	7	36	0	1	1	0
<i>Acer</i>	8	16	2	7	3	1
<i>Picea</i>	0	15	16	5	0	0
<i>Abies</i>	0	9	21	1	0	0
<i>Prunus</i>	6	12	3	2	0	1
<i>Carpinus</i>	0	11	4	7	0	1
<i>Salix</i>	2	14	0	3	0	2
<i>Aesculus</i>	6	4	0	4	1	4
<i>Populus</i>	1	17	0	0	0	0
<i>Alnus</i>	0	13	1	2	1	0
<i>Fraxinus</i>	3	9	1	0	1	2
<i>Betula</i>	1	11	0	1	0	0
<i>Pseudotsuga</i>	0	0	11	0	0	0
<i>Gleditsia</i>	5	1	0	0	0	0
<i>Larix</i>	0	0	5	0	0	0
<i>Pyrus</i>	1	2	1	0	0	0
<i>Robinia</i>	0	2	0	2	0	0
<i>Juglans</i>	2	1	0	0	0	0
<i>Platanus</i>	0	0	0	0	0	3
<i>Ulmus</i>	0	2	0	1	0	0
<i>Corylus</i>	1	1	0	0	0	0
<i>Malus</i>	1	0	1	0	0	0
<i>Pinus</i>	0	1	1	0	0	0
<i>Spiraea</i>	1	1	0	0	0	0
<i>Ailanthus</i>	0	1	0	0	0	0
<i>Cedrus</i>	0	0	1	0	0	0
<i>Cydonia</i>	0	1	0	0	0	0
<i>Davidia</i>	0	1	0	0	0	0
<i>Frangula</i>	0	1	0	0	0	0
<i>Hibiscus</i>	0	1	0	0	0	0
<i>Juniperus</i>	0	1	0	0	0	0
<i>Lonicera</i>	0	1	0	0	0	0
<i>Pterocarya</i>	0	1	0	0	0	0
<i>Taxus</i>	0	0	1	0	0	0

3.3. Propensity of *Ganoderma* Species to Parasitism

The proportion of parasitic samples differed strongly among *Ganoderma* species ($\chi^2 = 100.36$, $p < 0.001$) (Figure 6), decreased with increasing vegetation category ($\chi^2 = 9.88$, $p = 0.002$) (Figure 7), was lower in natural than urban environment ($\chi^2 = 6.90$, $p = 0.009$), and was lower for coniferous than deciduous trees ($\chi^2 = 7.32$, $p = 0.007$) (Figure 8). Toward the north, *Ganoderma* samples were sampled in decreasing vegetation categories ($\chi^2 = 11.70$, $p < 0.001$) with much stronger trend for parasitic than saprotrophic strategy ($\chi^2 = 10.13$, $p = 0.001$) (Supplementary Figure S3). Parasitic *Ganoderma* samples were also shifted more to the west, than saprotrophic ones ($F = 13.75$, $p < 0.001$) (Supplementary Figure S4). The proportion of parasitic specimens of *Ganoderma* sampled on individual host genera is shown in Supplementary Figure S5.

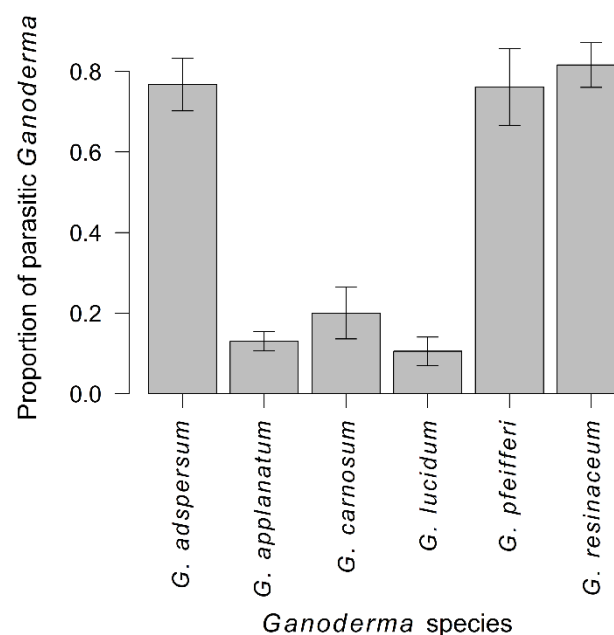


Figure 6. Proportion of parasitic samples in individual *Ganoderma* species (mean ± SE).

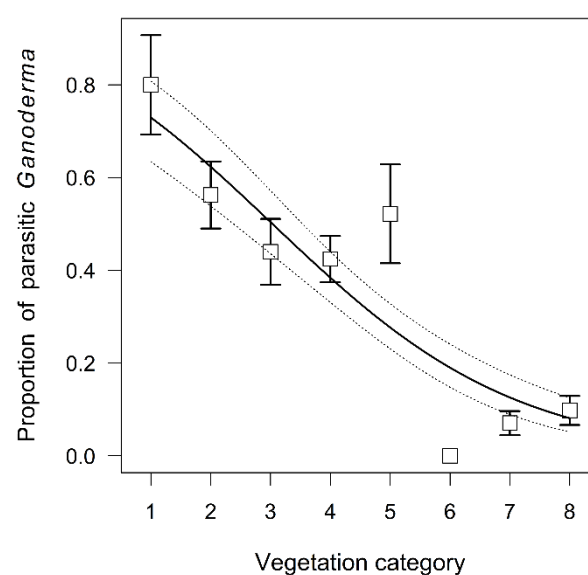


Figure 7. Proportion of parasitic *Ganoderma* samples along the vegetation category gradient (mean ± SE), the trend is predicted from binomial generalized linear model.

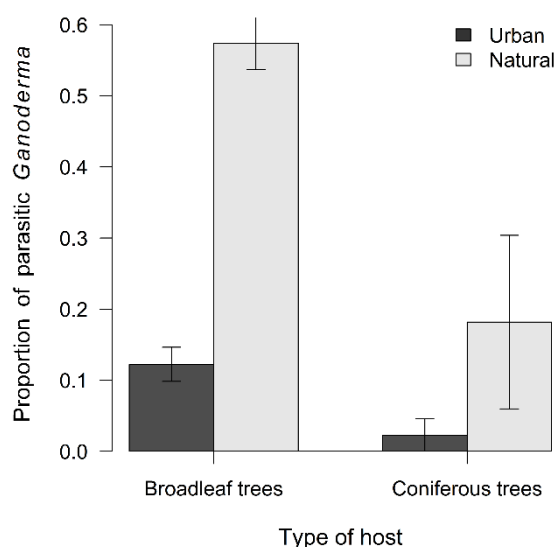


Figure 8. Proportion of parasitic *Ganoderma* samples in urban or natural environment and on broadleaf or coniferous trees (mean \pm SE).

4. Discussion

4.1. Temporal and Spatial Sampling Trends of *Ganoderma* Species

Six studied species within *Ganoderma* genus were represented in herbaria collections differently, which might reflect their real abundances in nature but also sampling bias, as the specimens were not collected according to stratified random sampling protocol required in rigorous ecological study [43]. Sampling for museum natural collections is probably often carried out dependably on what is needed to enrich the collection or led by pure interest of the collector who is attracted by shape, color, size or overall appearance of the specimen [44,45]. Such non-representative collecting strategies play an important role in museum's data recording and due to this fact, the records are limited by spatial and temporal biases which can lead to a limitation of tracking real abundance [46,47]. We need to keep in mind there are four major biases in records data which were identified by Isaac et al. [48]: (1) uneven recording intensity over time, (2) uneven spatial coverage, (3) uneven sampling effort per visit and (4) uneven detectability across space and time. That proves in most situations the sampling in nature is not perfect, moreover when some species are easier to spot than others [49] which may be strongly influenced by vegetation structure or successional change [50] or species location occurrence e.g., near roadsides [51]. Another bias during our study was presented by using presence-only data. For aforementioned reasons, in our research we focused on analyses of species proportion that are always in interaction to other environmental variables or on analyses of trends in those environmental variables and its interpretation to overcome this drawback. Despite the limitations, the interactions should not be dependable on collector sampling directly and thus we can consider them as authentic.

Synanthropization of some *Ganoderma* species is documented [11,21,23,52–55] but with no respect to different types of vegetation. All analyzed species are common with exception of *G. pfeifferi* which was found in the least number of samples, corresponding to the consideration of being rare in the Czech Republic [56,57]. None of the findings of *G. pfeifferi* were from the category level one, central areas or historic city center (areas with high anthropogenic influence) but according to Sokół [58], *G. pfeifferi* should be synanthropic species growing on old oaks in parks. Other authors recorded its growth in natural old beech forests in Europe [28,59]. The proportion of *G. adspersum* strongly increases toward lower-level of vegetation categories. Within the first and the second vegetation category level (with high and medium anthropogenic factors) were included 17.5% and 37.5% of all *G. adspersum* findings, respectively. In the categories with limited or almost no anthropogenic influence there were only 5% of all findings of this species. *Ganoderma*

adpersum is considered to be synanthropic and a common species [21,27,54,58,60,61] but more detailed evaluation from different types of urbanized vegetation is lacking. The proportion of *G. resinaceum* also slightly increases toward lower vegetation categories, therefore we can consider it synanthropic. Most of the findings was from fourth vegetation category level, from rural areas. According to other authors, its occurrence was recorded in parks, gardens or along roadsides [21–23,58] but it can be also found in forests in southern Europe similarly as *G. adpersum* [62].

Relatively to other *Ganoderma* species, *G. lucidum* increases towards the higher vegetation categories, e.g., with decreasing human impact, in accordance with literature stating that this species occurs in Europe mainly in forests, but can be also found in parks and botanical gardens on old hardwoods [58,63]. We found that samples of *G. carnosum* were quite uniformly distributed across the vegetation category gradient, despite the fact that Kotlaba [21] recorded them mainly from synanthropic areas.

In our analyses each species had slightly different sampling peak throughout years. This might, except for aforementioned matters, reflect ecological trends e.g., environment quality. It is well known that environment and its global changes during the past century show human impacts which are reflected in natural collections [64–67].

4.2. Host Specificity Differences among *Ganoderma* Species

For the complex of studied species, we revealed a very broad host-range including at least 69 host species (belonging to 36 genera). Moreover, from species accumulation curves it can be expected, that in the next years, more host association could be observed. At species level we can observe a major change in the number of newly discovered associated tree species from the 1960s to 1980s which might have been caused by (i) a new law that entered in 1959 which led to a dynamic increase in enriching museum's collections during those years or (ii) it might be connected to declining quality of environment when *Ganoderma* species had more opportunities to colonize new host trees. Host expansion tendency was previously observed for example in mistletoe [68] which may happen through introduction of new hosts to a new area or as a result of evolutionary pressures [69,70] originating from habitat and climate changes [71,72]. There are also several studies that focused on diversity of wood fungi under varying environmental factors and their influence on host plant [73–75]. Based on AICc of set of models, we found that the best simplification of host preference is at the genus level. According to the range of attacked tree genera we can split *Ganoderma* species into two groups, those with: (i) lower host plasticity including *G. resinaceum*, *G. lucidum* and *G. pfeifferi* and (ii) with higher host plasticity including *G. applanatum*, *G. adpersum* and *G. carnosum*, showed also by genera accumulation curves.

The occurrence of *G. carnosum* on hardwood trees should be rare [13,14]. Ryvarden and Melo [13] recorded *G. carnosum* on four hardwood genera only. In contrast, our analyses showed that *G. carnosum* preferably colonizes not only softwood trees, but frequently also hardwood trees of at least nine genera. Compared to literature [11,13,15,21,25,28,56,58,60,63,76,77] we recorded *Cedrus* as a new host genus for *G. carnosum*. *G. lucidum* and *G. resinaceum* should be specialized on *Quercus* spp. In former Czechoslovakia, 58% of the findings of *G. resinaceum* were from *Quercus* spp.-*Q. robur*, *Q. palustris*, *Q. petraea*, *Q. rubra*, and 71% records of *G. lucidum* were from *Quercus* spp. [21]. It corresponds to our findings that these species strongly prefer oaks. However, *G. resinaceum* was also found on eight other hardwood genera, and *G. lucidum* was found on other 11 hardwood and two softwood genera. Kotlaba and Pouzar [61] recorded *G. adpersum* mostly on oak trees (*Quercus* spp.), lime trees (*Tilia* spp.) and horse chestnut (*Aesculus hippocastanum*) but compared to other author's findings [11,13,15,20,21,23,25,58,60,63,77–79] we discovered *Corylus* and *Malus* as two more new host genera. *G. applanatum* is the most common species and has a much wider range of host tree genera than *G. adpersum* [11,14,25,63], in former Czechoslovakia Kotlaba [21] documented 53 host species, occasionally including conifers such as *Abies* and *Picea*. Two new uncommon host genera were recorded during our analyses—*Gleditsia* and *Ailanthus*

which were not previously mentioned [11,13,21–23,25,28,56,58,60,76,77,80]. *G. pfeifferi* was not previously recorded on *Tilia* sp. [13,17,21,28,56,58,60,63,76,77,81].

Ganoderma samples from softwoods had higher average altitude than samples from hardwoods. This could be obviously caused by the fact that softwood and hardwood trees vary in their abundances in relation to altitude and thus, uneven chance to sample coniferous and deciduous trees along the altitudinal gradient could be expected.

4.3. Propensity of *Ganoderma* Species to Parasitism

Parasitic life strategy was more common among samples towards lower vegetation category which means more common in urbanized environment and areas under anthropogenic influence. This could be caused by sampling bias. In urban areas, greater sampling effort would be expected and thus much earlier detection of *Ganoderma* fungi on the trees, at a time when they are still growing parasitically. In other words, in more distant non-urban areas, artificially higher proportion of saprotrophic specimens would be caused by later discovery of fungi. From an ecological point of view, there are more opportunities for parasitism in urban areas due to higher traffic and more intense human activities. We also observed higher rates of parasitism on hardwood trees which is consistent with that of Krah et al. [82] in which most white rot fungi are broadleaf trees specialists. Moreover, in urban environment conifers are less prone to be parasitized in contrast to broadleaf trees which are much more affected. This may be connected to different structure and content of lignin comparing conifers and broadleaf trees [83]. However, this was in contrast to our expectation to observe more parasitic species on conifers due to slower dying of needles and therefore identifying them as parasites while they are actually already saprotrophs. Authors should discuss the results and how they can be interpreted from the perspective of previous studies and of the working hypotheses. The findings and their implications should be discussed in the broadest context possible. Future research directions may also be highlighted.

5. Conclusions

We revealed that all studied *Ganoderma* species have broad host-range, which is increasing during many decades without apparent slowing. Some of the specimens show synanthropization processes in different vegetation categories with higher or lower anthropogenic factors, particularly *G. adspersum*, and great propensity to parasitism, which increases toward urban areas, and is more frequent on hardwood trees. As ornamental greenery is often formed by a large diversity of tree species in the cities, which are stressed by the pollution of the environment and gradually age, we can assume, based on our data, that there are great possibilities to discover newly associated host tree species for *Ganoderma* genus in the upcoming years. As *Ganoderma* species may act as serious tree pathogens, their still expanding host-range should be considered.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12111437/s1>, Figure S1: Temporal trends in *Ganoderma* species sampling. The sampling pattern of individual *Ganoderma* species during the years was very distinct ($p < 0.001$), Figure S2: Whittaker rank-abundance plot for host tree genera of individual *Ganoderma* species, Figure S3: Average vegetation category along the latitudinal gradient for saprotrophic and parasitic *Ganoderma* samples. *Ganoderma* samples were sampled along latitudinal gradient in decreasing vegetation categories ($df = 442$, $\chi^2 = 11.70$, $p < 0.001$) and parasitic *Ganoderma* samples are from lower vegetation categories than saprotrophic ones ($df = 442$, $\chi^2 = 93.29$, $p < 0.001$). The slope of decrease of vegetation category along latitudinal gradient differs strongly between parasitic and saprotrophic *Ganoderma* samples ($df = 442$, $\chi^2 = 10.13$, $p = 0.001$), whereas there is a strong relationship for parasitic ones, the saprotrophic ones decrease gently, Figure S4: E coordinates for parasitic and saprotrophic trophic category (mean \pm SE). Saprotrophic *Ganoderma* samples has in average higher east coordinates (they are shifted east), than parasitic *Ganoderma* samples ($df = 444$, $F = 13.75$, $p < 0.001$), Figure S5: Proportion of parasitic specimens of *Ganoderma* sampled on individual host genera. Suppl. 1: Key to *Ganoderma* species.

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