



The diverse habitats of *Hygrocybe* – peeking into an enigmatic lifestyle

Halbwachs H^{1*}, Karasch P² and Griffith GW³

¹ Bavarian Mycological Society, Danzigerstr. 20, D-63916 Amorbach, Germany

² Bavarian Mycological Society, Taubenhüller Weg 2A, D - 82131 Gauting, Germany

³ Institute of Biological, Environmental and Rural Sciences, Cledwyn Building, Aberystwyth University, Penglais, Aberystwyth, Ceredigion SY23 3DD Wales, gwg@aber.ac.uk

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Abstract

The genus *Hygrocybe* (Fr.) P. Kumm. is globally distributed. Certain taxa occur on different continents, even in the northern and the southern hemisphere. In Europe grassland is the preferred habitat. The trophic ecology is still unclear. In this review studies and internet sources of about 65 locations distributed from high to low latitudes across all continents in which 16 *Hygrocybe* species (typically found in Europe) occur have been analysed with regard to habitat types, vegetation and soil properties. The analysis shows that several of the selected *Hygrocybe* species can cope with a very wide range of habitats. They appear to prefer soils with low fertility, grassland over forests and temperate/boreal climates. Most significantly, waxcaps are found in forest habitats in the absence of grasses, and in grasslands where woody hosts are absent. Mosses are not obligately associated. Their host associations are extremely flexible. A biotrophic lifestyle should be considered.

Keywords – biotrophy – distribution – ecozones – grassland – mosses – soil – trophic ecology – waxcaps – woodland

Introduction

The genus *Hygrocybe* (Fr.) P. Kumm. has a worldwide distribution (Beisenherz 2000, Krieglsteiner & Gminder 2001, Boertmann 2010), except for arid ecozones (Beisenherz 2000). *Hygrocybe* (waxcaps) are found in forests, grassland, marshes, fens and bogs (Boertmann 2010). Typically, European waxcaps occur on extensively managed grassland and meadows (Boertmann 2010).

It has been argued that European grassland environments may be ersatz habitats, and that the primary habitats would be forests (Homola et al. 1985, Krieglsteiner 2004.). To our knowledge, conclusive evidence for this assumption has not been scientifically documented. In contrast, Vera (2000) proposed that during the early post-glacial, large herbivores (e.g. deer, bison, aurochs and wild horses) had been important in maintaining an open landscape including grassland (see also Griffith et al. 2004).

The nutritional mode of waxcaps is uncertain (Bresinsky 2008: 37f). To date they are mostly classified as saprotrophic (e.g. Knudsen & Vesterholt 2012: 265), and more specifically being dependent on humic compounds in the soil (Arnolds 1981). However, as noted by Seitzman et al. (2011), many related taxa within the family Hygrophoraceae exhibit biotrophic nutritional

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Corresponding Author: Hans Halbwachs – e-mail – halb.wax@onlinehome.de

strategies, including ectomycorrhizas (*Hygrophorus*) and lichenised taxa (*Lichenomphalia*) which is supported by the stable isotope signatures of waxcaps (Griffith et al. 2002, Seitzman et al. 2011). The latter authors have also suggested that waxcaps might be associated with bryophytes as hosts. All waxcaps share one clear-cut property – they cannot be grown under axenic laboratory conditions (Griffith et al. 2002, Halbwegs unpublished data), which is a hallmark of most biotrophic fungi, e.g. obligate parasites (Cooke 1979: 39).

Trophic modes are to a certain extent related to habitats. Ectomycorrhizal fungi for example, are untypical for grasslands, because they only rarely harbour specific host plants (cf. Eriksen et al. 2002). The spectrum of habitats “European” waxcaps inhabit has not been analysed to date in a systematic manner. To shed more light onto the question, whether the range of habitats can tell us something about the nutritional lifestyle of (European) waxcaps, we analysed in this review 65 studies and internet-based sources about sites in Europe, the Americas, Africa, Macaronesia, Asia, the Arctic and Antarctic, Australia and New Zealand.

Methods

To compare habitats, we focused on *Hygrocybe* spp. *sensu* Boertmann (2010). These included the ten most common species and species complexes in Europe: *H. ceracea*, *H. chlorophana*, *H. coccinea* s.l., *H. conica* s.l., *H. insipida*, *H. pratensis* s.l., *H. psittacina* s.l., *H. punicea*, *H. quieta* and *H. virginea* s.l., based on the total number of records for each species on the Field Records Database of Britain and Ireland (BMS 2012) and which correlated well with occurrence in Germany (Bresinsky 2008), as well as six less common species, which nevertheless are widely distributed (*H. aurantiosplendens*, *H. flavipes*, *H. fornicata*, *H. miniata* s.l., *H. mucronella*, *H. nitrata*).

We attempted to compare as many diverse habitats as possible where common European *Hygrocybe* taxa occur. This turned out to be amazingly difficult, because important habitat information about climatic characteristics, associated vegetation and soil properties are either rarely recorded, or not recorded in a systematic and consistent manner. Nevertheless, we were able to compare 65 waxcap sites worldwide (Fig. 1) by using additional sources, such as data banks and internet-based site descriptions providing data on vegetation and soil. To compare the climatic influence we assigned the sites to ecozones as defined by FAO (2001). We included data from two German sites and from a site on La Palma (Canaries), which we had compiled personally in 2011 and 2005 (unpublished data).

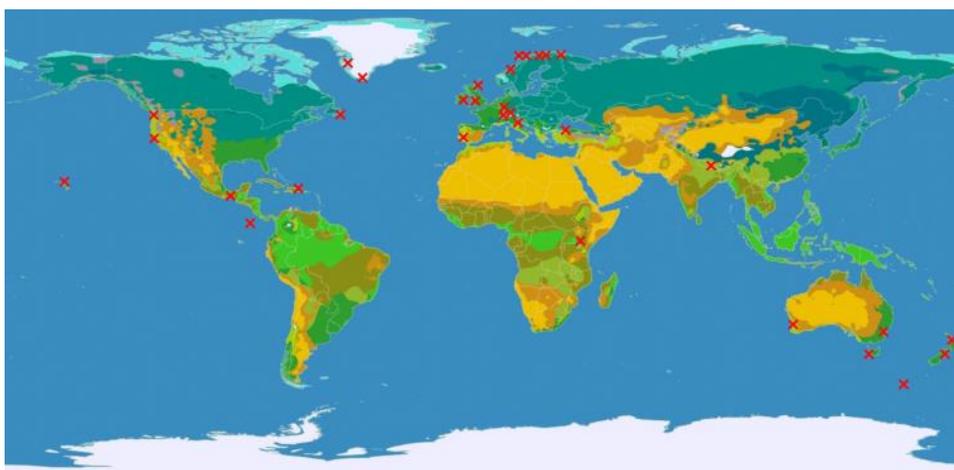


Fig. 1 – Map with simplified eco-zones according to Köppen (1931), showing the global distribution of sites for which *Hygrocybe* spp. data were obtained. Red X indicate the waxcap site areas covered by the study. Map source: Wikimedia Commons 2007; author LordToran. Legend: ■ tropical rainforest, ■ savannah, ■ steppe, ■ desert, ■ humid temperate, ■ humid subtropical, ■ humid continental, ■ transsiberian, ■ dry-cold summer, ■ tundra, ■ glaciated-polar.

There are clearly more data for Europe than for other regions, in large part due to higher human density and long history of mycological study, so care was taken to select sites across all ecozones of the continent. In this way a possible selection bias was minimised. The data we compiled comprised ecozones, habitat descriptions, associated vegetation and soil properties (see master table in table 1).

Climate zones were recorded according to the ecozone concept, as it has been developed by various authors (e.g. Köppen 1931, Walter & Breckle 1999, Schultz 2008). We chose the climate-centred modified Köppen-Trewartha scheme, which is used by FAO (2001). This has been found to exhibit a good correspondence between its sub-zones or climatic types and the natural climax vegetation types and soils within them (Bailey 1996; Kehl 2011). This approach allows a standardised evaluation of the climatic bandwidth, in which the selected waxcap species occur. If not already stated in the source data, elevation and geographical coordinates were determined with Google Maps.

Vegetation, if not sufficiently mentioned in the source, was determined by internet-based national vegetation charts or in some cases site descriptions where waxcap sites were located within protected areas. Of particular interest were data about woodland and grassland types characterising the various habitats.

For additional information about vegetation preferences of waxcaps we analysed 220 internet images from 17 countries in Asia, Australasia, Europe, North and Central America. Typical images are shown in Figure 2.



Fig. 2 – Examples of internet images used for determining the main plant groups associated with waxcaps. A: *H. conica* (Florida USA, © Richard Kneal – common domain); B: *H. psittacina* (California USA, © Erin Page Blanchard - common domain); C: *H. punicea* (Derbyshire UK, © Malcolm Storey – courtesy of M. Storey); D: *H. virginea* (Black Forest Germany, © Georg Müller – courtesy of G. Müller).

Image sources: http://mushroomobserver.org/observer/observation_search?pattern=hygrocybe, <http://www.bioimages.org.uk/>, <http://www.wildaboutbritain.co.uk/fungi>, <http://www.in2.dk/svampe/svpic/frame1.htm>, <http://www.mycology.com/>, <http://www.pilzepilze.de/>, <http://www.pilzbestimmung.de/>

Table 1 – Master table showing the investigated sites (column 2), their corresponding ecozones according to FAO (2001) (Column 1), habitat descriptions (column 3), predominant vegetation (column 4), soil types according to IUSS (2006) (column 5) and the primary sources (column 6).

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Boreal Coniferous Forests (Ba): Boreal Plains	Canada Labrador, Avalon Peninsula, Cape St. Mary's Park Reserve (46.83, -54.18) 100 m	Maritime Barrens Ecoregion (Southeastern)	heathlands, yellow birch (<i>Betula alleghaniensis</i>)	orthic podzols, dystric gleysols, dystric histosols, lithosols (50, 30, 10, 10)	DFRA 2002, Voitk 2005
Boreal Coniferous Forests (Ba): Boreal Plains	Canada Labrador, Avalon Peninsula, La Manche Provincial Park (47.18, -52.89) 80 m	Maritime Barrens Ecoregion (Southeastern), Avalon Forest Ecoregion	balsam fir (<i>A. balsamea</i>), yellow birch (<i>B. alleghaniensis</i>)	orthic podzols, dystric gleysols, dystric histosols, lithosols (50, 30, 10, 10)	DFRA 2002, Voitk 2005
Boreal Mountain Systems (BM): Atlantic dwarf shrub heaths	Norway Andøy, Høyvik (69.24, 15.87) 100 m	natural grassland near beach	<i>Poaceae</i>	dystric histosol, cambic arenosol, lithosol (70, 20, 10)	NBIC 2011
Boreal Mountain Systems (BM): Atlantic dwarf shrub heaths	Norway Andøy, Kobbedalen, Øverdalsplassen (69.02, 15.6) 11 m	natural grassland	<i>Poaceae</i>	dystric histosol, cambic arenosol, lithosol (70, 20, 10)	NBIC 2011
Boreal Mountain Systems (BM): Atlantic dwarf shrub heaths	Norway Nordland, Alstahaug, Tjøtta (65.83, 12.43) 5 m	meadows, small birch, salt marsh	<i>Poaceae</i> , herbs	lithosol, dystric regosol, cambic arenosol (60, 20, 20)	NBIC 2011
Boreal Mountain Systems (BM): Atlantic dwarf shrub heaths	Norway Nordland, Dønna, Sandstrak (66.06, 12.39) 0-40 m	meadow in saltmarsh, heathland, birch forest	birch, <i>Dryas</i> , juniper	lithosol, dystric regosol, cambic arenosol (40, 40, 20)	NBIC 2011
Boreal Mountain Systems (BM): Atlantic dwarf shrub heaths	Norway Nordland, Evenes, Evenesmarka (68.50, 16.76) 80 m	natural grassland on calcareous soils	<i>Poaceae</i>	eutric cambisols, lithic leptosols, haplic podzols, dystric fluvisols, umbric gleysols (40, 20, 20, 10, 10)	NBIC 2011
Boreal Mountain Systems (BM): Atlantic dwarf shrub heaths	Norway Troms, Lyngen, Lyngsdalen, Trange (69.44, 20.12) 130 m	stony grassland	<i>Poaceae</i>	haplic podzols, dystric regosols, lithic leptosols, gleyic podzols (40, 30, 20, 10)	NBIC 2011
Boreal Mountain Systems (BM): Atlantic dwarf shrub heaths	Norway Troms, west of Harstad (68.80, 16.45) 160-200 m	grassy slope	<i>Poaceae</i>	orthic podzols, dystric regosol, lithosol, gleyic podzol (40, 30, 20, 10)	NBIC 2011
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Finnmark, Alta, Vassbotndalen v. Bjørnelva (69.99, 22.85) 75 m	grassy trail	<i>Poaceae</i>	dystric regosol, orthic podzols, lithosol (40, 40, 20)	NBIC 2011

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Finnmark, Sør-Varanger, Melkefoss (upstream river Pasvik, plot gg4) (69.40, 29.76) 40 m	former pasture on sandy soils	<i>Poaceae</i>	orthic podzols, dystric regosol, dystric histosol, gleyic podzol (50, 20, 20, 10)	NBIC 2011
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Finnmark, Sør-Varanger, Noatun, courtyard (69.16, 29.25) 50 m	grassland with birch and pine	<i>Poaceae, Betula, Pinus</i>	orthic podzols, dystric regosol, dystric histosol, gleyic podzol (50, 20, 20, 10), glacial river deposits	NBIC 2011
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Nordland, Evenes, Botn (68.49, 17.11) 7 m	grassland with trees	birch, alder, aspen, pine, willow, <i>Poaceae</i>	haplic podzols, dystric regosols, lithic leptosols, gleyic podzols (40, 30, 20, 10)	NBIC 2011
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Nordland, Sortland: Holmstaddalen (68.71, 15.31) 160 m	natural meadow (forest meadow)	birch, alder, aspen, pine, willow, <i>Poaceae</i>	lithosols, dystric regosols, cambic arenosols (60, 20, 20)	NBIC 2011
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Troms, Bardu, Øverland (68.70, 18.10) 250 m	between herbs on gravelroad shoulder	herbs, downy birch (<i>Betula pubescens</i> subsp. <i>tortuosa</i>)	dystric regosol, orthic podzols, lithosol (40, 40, 20)	NBIC 2011, Stabursvik 2007
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Troms, Kåfjord, Kåfjorddalen, Ankerlia (69.43, 20.97) 120-180 m	subalpine birch forest	<i>Betula</i>	dystric regosols, haplic podzols, lithic leptosols (40, 40, 20)	NBIC 2011
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Troms, Nordreisa, Sappen, near school (69.56, 21.29) 74 m	pine forest	<i>Pinus</i>	haplic podzols, dystric regosols, fibric histosols, gleyic podzols (50, 20, 20, 10)	NBIC 2011
Boreal Mountain Systems (BM): Western boreal and montane birch forests, with pine	Norway Troms, Storfjord, Skibotn, near Kurssenter (69.39, 20.27) 1-10 m	oligotrophic pine forest	pine	dystric fluvisol, cambic arenosol (60, 40)	NBIC 2011

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Boreal Tundra Woodland (Bb)	Canada Labrador, Avalon Peninsula, Salmonier Nature Park (47.26, -53.28) 130 m	Maritime Barrens Ecoregion (Southeastern), Avalon Forest Ecoregion	<i>Abies balsamea</i> , <i>Betula alleghaniensis</i> , heathlands	orthic podzols, dystric gleysols, dystric histosols, lithosols (50, 30, 10, 10)	DFRA 2002, Voitek 2005
Cascade Mixed Forest-Coniferous Forest-Alpine Meadow (TeM / M242)	USA Cooper Point Rd. NW and 68th Ave. NW, Olympia, Washington (47.13, -122.93) 50 m	in abundance under Western red cedar	<i>Thuja plicata</i>	humic acrisols, haplic phaeozems, humic cambisols (60, 20, 20)	TOA 2011a, Bailey 1995
Polar Arctic Tundras (P), Boreal Subarctic Tundras (Ba)	Greenland Fredericshab, head of Eqaqut fjord (61.99, -49.53) 20 m	herb and grassland slopes	<i>Alchemilla</i> , <i>Setaria glauca</i> , <i>Juniperus</i>	Gelic regosols	Borgen & Arnolds 2004
Polar Arctic Tundras (P), Boreal Subarctic Tundras (Ba)	Greenland Igaliku (60.98, -45.43) 40 m	grassland slope, grazed by sheep	<i>Poaceae</i> , <i>Betula glandulosa</i> , <i>Setaria glauca</i>	Gelic regosols	Borgen & Arnolds 2004
Polar Arctic Tundras (P), Boreal Subarctic Tundras (Ba)	Greenland Nasarsuaq, Kiattuut Qaqqaat, North of main river (61.21, -45.37) 150 m	rather dry, semi-natural grassland slopes	<i>Poaceae</i>	Gelic regosols	Borgen & Arnolds 2004
Polar Arctic Tundras (P), Boreal Subarctic Tundras (Ba)	Greenland Nasarsuaq, near harbour (61.15, -45.43) 10-60 m	among grasses, lichens and mosses, dwarf-shrub copse	<i>Thalictrum</i> , <i>Cyperaceae</i>	Gelic regosols	Borgen & Arnolds 2004
Polar Arctic Tundras (P), Boreal Subarctic Tundras (Ba)	Greenland Nuuk (Godthåb), Qooqqut (Qôrqut) (64.27, -50.90) 50 m	acidic, seminatural grassland slope, on mesic to dry soil on old river banks	<i>Carex</i> , <i>Empetrum</i> , <i>Salix herbacea</i> , <i>Bryophyta</i>	Gelic regosols	Borgen & Arnolds 2004
Polar, Antarctic Tundras (P)	Antarctica Macquarie Island (-54.58, 158.88) 100 - 200 m	tundra lacking woody plants (closed short herb vegetation)	<i>Poaceae</i> , <i>Acaena</i> , <i>Luzula</i> , <i>Bryophyta</i>	(mollic) andosols (on pillow basalt)	Selkirk et al. 1990, Selkirk & Adamson 2011
Subtropical Dry Forest (SCs): Mediterranean Division	USA San Pablo Reservoir, Contra Costa Co., California (37.92, -122.25) 170 m	woodland	<i>Arbutus menziesii</i>	chromic luvisols, dystric fluvisols, mollic gleysols (60, 30, 10)	CDMR 2011
Subtropical Dry Forest (SCs): Mediterranean sclerophyllous forests and scrub	Italy Tuscany, Arezzo, Alpe de la Luna (43.64, 12.17) 600 - 1500 m	coppices and transitory high forests of broad-leaved trees	<i>Fagus</i> , <i>Crataegus monogyna</i> , <i>Laburnum alpinum</i> , <i>Quercus cerris</i> , <i>Sorbus aria</i> , <i>Taxus baccata</i> , <i>Ilex aquifolium</i> , <i>Carpinus betulus</i> , <i>Cardamine enneaphyllos</i>	eutric cambisols, haplic luvisols, rendzic leptosols (45, 30, 25) (sandstones and marls)	Salerni & Perini 2007

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Subtropical Dry Forest (SCs): Mediterranean sclerophyllous forests and scrub	Portugal Alentejo, Parque de Natureza de Noudar (38.18, -7.04) 215 m	under <i>Cistus</i> in <i>Quercus</i> forest	<i>Cistus ladanifer</i> , <i>Quercus rotundifolia</i>	eutric regosols, eutric cambisols, dystric regosols, lithic leptosols, haplic luvisols, haplic acrisols, rock outcrops (35, 20, 15, 15, 5, 5, 5)	Louro et al. 2009
Subtropical Dry Forest (SCs): Mediterranean sclerophyllous forests and scrub	Turkey Giresun, Görele, Ardic (40.95, 39.01) 440 m	on lawns	<i>Poaceae</i>	orthic acrisols, rankers, humic cambisols, dystric cambisols, lithosols (30, 20, 20, 20, 10)	Sesli 2007
Subtropical Dry Forest (SCs): Mediterranean sclerophyllous forests and scrub	Turkey Gümüşhane, Kürtün, Kizilot (40.72, 39.09) 730 m	amongst grass	<i>Poaceae</i>	orthic acrisols, rankers, humic cambisols, dystric cambisols, lithosols (30, 20, 20, 20, 10)	Sesli 2007
Subtropical Dry Forest (SCs): Mediterranean sclerophyllous forests and scrub	Turkey Trabzon, Macka, Karakaban (41.00, 39.73) 70 m	in pasture	<i>Poaceae</i> , <i>herbs</i>	orthic acrisols, rankers, humic cambisols, dystric cambisols, lithosols (30, 20, 20, 20, 10)	Sesli 2007
Subtropical Dry Forest (SCs): Swan Coastal Plain (SWA)	Australia Perth, Whiteman Park (-31.89, 115.96) 5 m	natural bushland, heathlands, growing in mosses	<i>Banksia</i> , <i>Eucalyptus</i> , <i>Melaleuca</i> , <i>Nutsya</i> , <i>Xanthorrhoea</i> , <i>Hibbertia</i> , <i>Acacia</i> , <i>Verticordia</i> , <i>Bryophyta</i>	dystric regosols, eutric regosols, cambic arenosols, calcaric regosols (50, 20, 20, 10)	Bougher et al. 2006, WP 2011
Subtropical Humid Forest (SCf): Northland Temperate Forest	New Zealand Waikato, Mt Pirongia, W. Scott F.R (-38.07, 175.09) 200-280 m	broadleaved-podocarp forest	<i>Podocarpus</i>	dystric cambisols, ochric andosols (70, 30)	LRNZ 2011
Subtropical Humid Forest (SCf): Northland Temperate Forest	New Zealand Wellington, Rimutaka Forest Park, Orongorongo River track (-41.36, 175.00) 100-400 m	broadleaved-podocarp forest	<i>Podocarpus</i>	dystric cambisols, rankers (90, 10)	LRNZ 2011
Subtropical Humid Forest (SCf): Northland Temperate Kauri Forest	New Zealand Northland, Waipoua State Forest, Te Matua Ngahere Track (-35.65, 173.56) 100 m	kauri forest	<i>Agathis australis</i>	humic acrisols, eutric cambisols, gleyic acrisols (50, 20, 20)	LRNZ 2011
Subtropical Humid Forest (SCf): Subtropical Hygrothermophilous mixed deciduous broad-leaved forests	Canaries La Palma, Los Tilos (28.79, -17.80) 510 m	laurel forest („Laurisilva“)	<i>Laurus novocanariensis</i> , <i>Persea indica</i> , <i>Myrica faya</i> , <i>Erica arborea</i> , <i>Ilex canariensis</i> , <i>Viburnum rigidum</i> , <i>Hypericum grandifolium</i> , herbs, ferns, no mosses	chromic luvisols, ochric andosols, orthic luvisols, dystric fluvisols, lithosols (40, 20, 20, 10, 10)	Karasch 2006, Castro pers. comm.

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Subtropical Humid Forests (SCf): Sydney Basin	Australia Sidney, Lane Cove Bushland Park, core zone along the Gore Creek catchment (-33.82, 151.18) 15 m	warm-temperate wet sclerophyll gallery forest	<i>Eucalyptus</i> , <i>Angophora</i> , <i>Ceratopetalum apetalum</i> , <i>Poaceae</i> , <i>Lepidozia</i>	humic podzols, orthic podzols, gleyic podzols, planosols, dystric regosols, calcareic regosols (30, 20, 20, 10, 10, 10)	Kearney & Kearney 2007, Lepp 2001
Temperate Continental Forest (TeDc): Montane coniferous forests, partly with broadleaved trees	Switzerland Merishausen (Uff der Grate, Gratental) (47.76, 8.62) 570-710 m	grassland at ≤ 1 swathe per year	Medicagini falcatea -, Dauco-Salvio -, Seselio libanotidis - Mesobrometum	orthic rendzina, eutric cambisol (60, 30, 10)	Brunner 1987
Temperate Continental Forests (TeDc): forest steppes	Germany Amorbach-West, „Vordere Äcker“ (49.65, 9.20) 200 m	mesotrophic, herb-rich sheep meadow, 2-3 swathes per year	<i>Rhytidiadelphus squarrosus</i> , <i>Festuca rubra</i> , <i>Trifolium pratense</i> , <i>Agrostis capillaris</i> , <i>Leontodon hispidus</i> , <i>Cirriphyllum piliferum</i> , <i>Plantago lanceolata</i> , <i>Lotus corniculatus</i> plus 36 species with low abundance	dystric cambisols, leptic podzols, stagno-gleyic cambisols (60, 20, 20)	Kaiser pers. comm., Halbwachs pers.obs.
Temperate Continental Forests (TeDc): forest steppes	Germany Hartschimmel / Ammersee, Goaslweide (47.94, 11.18) 720 m	oligotrophic, extant woodland pasture including a calcereous fen	<i>Agrostis capillaris</i> , <i>Anemone nemorosa</i> , <i>Brachypodium rupestre</i> , <i>Briza media</i> , <i>Bromus erectus</i> , <i>Calluna vulgaris</i> , <i>Cynosurus cristatus</i> , <i>Carex</i> (5 species), <i>Festuca</i> (4 species), <i>Carlina acaulis</i> , <i>Centaurea scabiosa</i> , <i>Dactylis glomerata</i> , <i>Danthonia decumbens</i> , <i>Hippocrepis comosa</i> plus roughly 300 more species, including trees such as <i>Quercus robur</i> , <i>Fagus sylvatica</i> , <i>Fraxinus excelsior</i> , <i>Abies alba</i>	orthic luvisols, eutric cambisols, eutric regosols, stagno-gleyic luvisols (70, 20, 5, 5)	Karasch 2001
Temperate Continental Forests (TeDc): forest steppes	UK Cardiff, Llanishen Reservoir Embankment, Radyr Cricket Ground / junction fields (51.52, -3.18) 20 m	grassland	<i>Poaceae</i> , herbs	urban	Grantham et al. 2009
Temperate Continental Forests (TeDc): forest steppes	UK Wales, Dinefwr Park (51.88, -4.00) 65 m	estate parkland	<i>Poaceae</i>	dystric cambisols, ferric podzols, dystric gleysols, umbric leptosols, rock outcrops (65, 10, 10, 10, 5)	Rotheroe 1999

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Temperate mountain systems (TM)	Nepal Solu-Khumbu, Khunde, Sagarmatha National Park (27.82, 86.71) 3900 m	on moist soil in birch - rhododendron forest	<i>Betula utilis</i> , <i>Rhododendron campanulatum</i> , <i>R. campylocarpum</i>	lithosols, rock outcrops, rankers, humic cambisols (25, 25, 25, 25)	Giri 2007
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Alp Schera (46.64, 10.19) 2000 m	clearings in alpine forests, alpine grassland	<i>Pinus</i> , <i>Poaceae</i> , herbs	orthic podzols, dystric podzoluvisols, ranker (45, 40, 15)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Fuorn, Murteras da Grimmels (46.68, 10.19) 2500 m	alpine grassland	<i>Poaceae</i> , herbs	orthic podzols, dystric podzoluvisols, ranker (45, 40, 15)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Mot dal Gajer (46.71, 10.33) 2600 m	climbing beyond tree-line, alpine grassland	<i>Poaceae</i> , herbs	lithosol, dystric regosol (60, 40)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Piz Starlex (46.66, 10.38) 2650 m	alpine grassland	<i>Poaceae</i> , herbs	lithosols, dystric regosols (60, 40)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Plateau de San Jon (46.79, 10.31) 1450 (2550) m	grassy plateau (climbing beyond tree-line), no soil preferences, alpine grassland	<i>Poaceae</i> , herbs	orthic podzols, dystric podzoluvisols, ranker (45, 40, 15)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, S-chanf, Alp Griatschouls (46.63, 9.97) 1700 m	dry gravelly slope	<i>Calamintha alpina</i> , <i>Petasites paradoxus</i> , <i>Gypsophila repens</i>	orthic podzols, dystric podzoluvisols, ranker (45, 40, 15)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Stabelchod (46.66, 10.24) 1900 m	alpine coniferous forests, alpine grassland	<i>Pinus mugo</i> , <i>Poaceae</i> , herbs	orthic podzols, dystric podzoluvisols, ranker (45, 40, 15)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Susch, Sandögna (46.73, 10.08) 1450 m	alpine grassland	<i>Poaceae</i>	dystric podzoluvisols, dystric cambisols, orthic podzols (40, 30, 30)	Favre 1960

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Val Laschadura (46.70, 10.16) 2350 m	beyond treeline, alpine grassland	<i>Poaceae</i> , herbs	orthic rendzina, calcareic gleysols, humic cambisol, eutric podzoluvisols (30, 30, 20, 20)	Favre 1960
Temperate Mountain Systems (TM): Alpine vegetation and Montane steppes	Switzerland Engadin, Swiss National Park, Val Trupchun (46.62, 10.02) 1800 m	dry calcereous gravelly slope	<i>Calamintha alpina</i> , <i>Petasites paradoxus</i> , <i>Gypsophila repens</i>	orthic podzols, dystric podzoluvisols, ranker (45, 40, 15)	Favre 1960
Temperate Mountain Systems (TM): Australian Alps	Australia Tasmania, Mt. Field, Newdegate Pass (-42.65, 146.56) 1280 m	Tasmanian bolster heath	<i>Dracophyllum minimum</i> , <i>Donatia novae-zelandiae</i> , lilies, daisies, grasses, herbs, sedges	chromic cambisols, regosols, lithosols, dystric histosols, humic cambisols (40, 20, 20, 10, 10)	McMullan-Fisher et al. 2003, FPA 2007
Temperate Oceanic Forest (TeDo)	Ireland The Curragh, Kildare (53.16, -6.83) 100 m	acidic, semi-natural grassland	<i>Poaceae</i> , herbs, <i>Ulex</i>	orthic luvisol, eutric cambisol, eutric gleysols, terric histosols (50, 25, 20, 5)	McHugh et al. 2001
Temperate Oceanic Forests (TeDo): Southland Temperate Forest	New Zealand Nelson, Murchison cemetery (-41.80, 172.34) 150 m	cemetery	grass	dystric cambisols, orthic podzols, lithosols (60, 30, 10)	LRNZ 2011
Temperate Oceanic Forests (TeDo): Southland Temperate Forest	New Zealand North Canterbury, Glentui Bush (-43.20, 172.25) 400 m	beech-broadleaved forest	<i>Nothofagus</i>	eutric cambisols, orthic luvisols, gleyic luvisols (60, 20, 20)	LRNZ 2011, Te Ara 2011
Temperate Steppe (TeBSk): coastal dune vegetation	UK Aberdeenshire, Blairton Links (57.26, -2.04) 10 m	fixed acidic dune with grassland	<i>Salix repens</i> , <i>Poaceae a.o.</i> <i>Corynephorus canescens</i> , <i>Empetrum nigrum</i>	dystric regosols, sand	Holden 2007, BFN 2004
Tropical Mountain Systems (TM): Albertine Rift Montane Forest Ecoregion	Congo Bukavu, slopes of Mt. Kahuzi (-2.47, 28.80) 1850 m	savannah	<i>Hyparrhenia</i>	humic ferralsols, humic nitisols (60, 40)	McGINLEY 2009
Tropical mountain systems (TM): Hispaniolan Pine Forest	Dominican Republic Santiago, San José de Las Matas (19.34, -70.94) 520 m	pine forest, on soil	<i>Pinus occidentalis</i>	eutric cambisols, haplic acrisols, chromic cambisols, eutric leptosols (40, 15, 30, 15)	TOA 2011b

Ecozone FAO	Site	Habitat	Vegetation	Soil	Sources*
Tropical Mountain Systems (TM): Tropical Central American Sierra Madre and Chiapas highlands	Mexico Chiapas, municipio de Ocozocoautla de Espinosa, Parque Educativo Laguna Béglica (16.88, -93.46) 1000 m	(Acahual) Selva Mediana subperennifolia (disturbed evergreen seasonal forest)	<i>Brosimum alicastrum</i> , <i>Bursera simaruba</i> , <i>Cedrela odorata</i> , <i>Chamaedorea ernesti-augusti</i> , <i>Cordia alliodora</i> , <i>Ficus involuta</i> , <i>Pseudolmedia oxyphyllaria</i> , <i>Terminalia amazonia</i> , <i>Cecropia</i> , <i>Croton draco</i> , <i>Heliocarpus donnellsmithii</i> , <i>Piper auritum</i> , <i>Trema micrantha</i> , <i>Trichospermum mexicanum</i>	haplic luvisols, rendzic leptosols (70, 30)	Chanona-Gomez et al. 2007, Escobar-Ocampo & Ochoa-Gaona 2007
Tropical Mountain Systems (TM): Tropical medium elevation subhumid	Kenya Mt. Kenya, Naro Moru track (-0.18, 37.15) 2450 m	Podocarpus forest, plant debris	<i>Podocarpus</i>	humic lithosols, umbric andosols (60, 40)	Kost 2002
Tropical rain forest (TAr)	Hawaiian Islands Moloka'i, Kamakou Forest Preserve, Kamoku Flats (21.12, -156.92) 1110 m	in soil under introduced Monterey Cypress	<i>Cupressus macrocarpa</i>	lithosols, humic andosols (50, 50)	Desjardin & Hemmes 1997
Tropical Rain Forest (TAr): Tropical moist forest (marine association)	Costa Rica Cocos Island, Cerro Iglesias (5.53, -87.08) 280(?) m	moist tropical forest, among mosses	<i>Bryophyta</i>	humic lithosols, dystic gleysols, ferralic cambisols (50, 25, 25)	Gómez 1983, Damobrosio 2001

Due to the lack of comparable records about soil properties, we had to rely on the FAO World reference base for soil resources (IUSS 2006) for the classification of the soil types, and on the Harmonized World Soil Database (FAO & ISRIC 2009) for the identification of the soil types. The latter database works with geographical coordinates for pinpointing any location worldwide with a precision of two decimals (ca. 1.1 km). From the findings we extracted a measure about the soil types waxcaps prefer. For this we calculated a preference index by scaling the ratio between the number of sites and the global surface area of a specific soil type between 0 and 100).

Results and Discussion

As is the case with most biodiversity distribution data there is a bias towards Europe (Fig. 1), and this needs to be kept in mind when assessing our quantitative analyses.

The term *Hygrocybe* is widely used especially in Europe to refer to the waxcap species found in grassland, as described by Boertmann (2010). However, it is now recognised that this genus is polyphyletic with members of the component taxa spread across the family Hygrophoraceae (cf. Seitzman et al. 2011), a recognition that is not reflected by the results of our analysis. Since there is a lack of fungal molecular data corresponding to the sources investigated, we were not able to look into genetic variations of the selected taxa. It would theoretically be desirable to match molecular data with specific sites. Practically the considerable effort to generate DNA-based data from all the specimens mentioned by our sources would probably not pay off, because the overall trends found within the realm of this review would probably not be affected by genotypic variations.

The comparison of the 65 waxcap sites ranging from the tropical to the polar zones, where one or more of the 16 waxcap species occur, show a broad ecological amplitude (Table 1). For temperate habitats this has already been shown by Bresinsky (2008: 47) who recorded a distribution over almost all habitats in Germany. All 16 species occurred in temperate and boreal habitats, 7 at polar, 9 at subtropical and 3 at tropical locations. *H. conica* and *H. miniata* show the greatest latitudinal distribution (poles to tropics), whereas *H. chlorophana* and *H. mucronella* are restricted to temperate and boreal climates (Fig. 3).

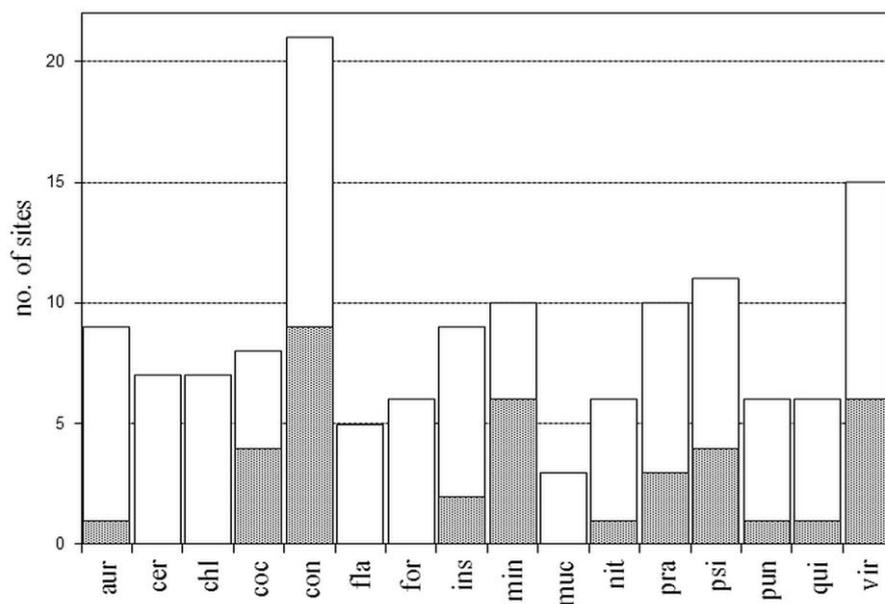


Fig. 3 – Occurrence of the 16 *Hygrocybe* species in woodland and grassland. The y-axis shows the number of sites, the x-axis the species, both as defined in our data set. Shaded: woodland, unshaded: grassland. Species abbreviations: aur – *aurantiosplendens*, cer – *ceracea*, chl – *chlorophana*, coc – *coccinea*, con – *conica*, fla – *flavipes*, for – *forficata*, ins – *insipida*, min – *miniata*, muc – *mucronella*, nit – *nitrata*, pra – *pratensis*, psi – *psittacina*, pun – *punicea*, qui – *quieta*, vir – *virginea*.

Waxcaps occur in association with a great variety of plant communities and plant species (table 1). Looking at the distribution in forests relative to grass/heathland (Table 2, Fig. 3), a diverse species-related pattern emerges from the locations investigated. The overall distribution between forests and grass/heathland of the 65 locations follows a proportion of ca. 1:2.6 in favour of the latter. The internet image analysis arrived at comparable results (fig. 4)

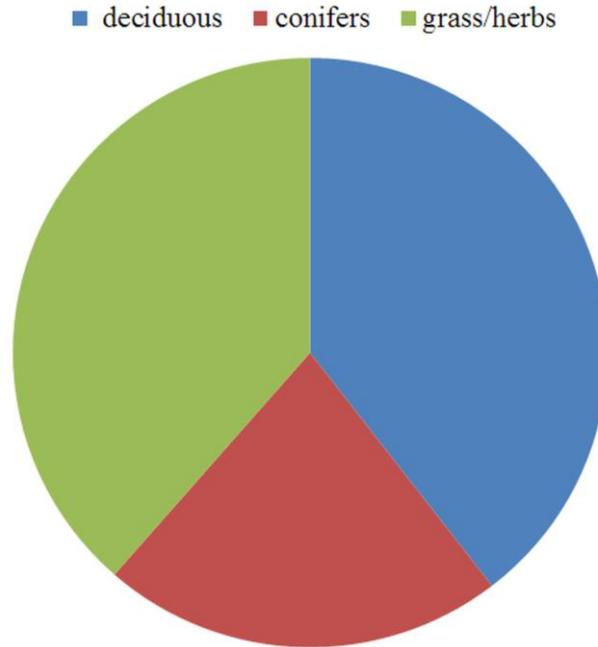


Fig. 4 – Total distribution of the major vegetation types with images of waxcaps out of the 16 selected taxa in Europe and North America. The distribution between forests and grass/heathland follows in Europe a proportion of ca. 1:4.1, in North America the proportion is reversed with ca. 6.5:1. In addition, the analysis showed associations with bryophytes for ca. 50% of the images

Table 2 – Ecozone ranges of the 16 *Hygrocybe* species in our data set. The ecozones in the first column on the left are defined according to FAO (2001). The second column shows the number of sites in each ecozone. Species abbreviations in the column headers: aur – *aurantiosplendens*, cer – *ceracea*, chl – *chlorophana*, coc – *coccinea*, con – *conica*, fla – *flavipes*, for – *fornicata*, ins – *insipida*, min – *miniata*, muc – *mucronella*, nit – *nitrata*, pra – *pratensis*, psi – *psittacina*, pun – *punicea*, qui – *quieta*, vir – *virginea*.

	sites	aur	cer	chl	coc	con	fla	for	ins	min	muc	nit	pra	psi	pun	qui	vir
Tropical rain forest	2					x											
Tropical mountain systems	4					x				x							
Subtropical humid forest	14				x	x		x	x			x	x	x		x	x
Subtropical dry forest	12					x				x			x	x			x
Temperate oceanic forest	7	x				x		x		x		x			x	x	
Temperate continental forest	9		x	x		x	x				x		x	x			x
Temperate steppe	6		x			x			x				x	x			x
Temperate mountain systems	16	x		x	x	x		x	x	x		x	x	x	x	x	x
Boreal coniferous forest	4					x									x	x	x
Boreal tundra woodland	1									x							
Boreal mountain systems	16	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Polar	9		x			x			x	x			x	x			x

The diversity of waxcaps and of the associated vegetation appear not to be connected (cf. Öster 2006, 2008). The notion that poor grassland is an ersatz habitat for forests in Europe seems to be plausible, at first glance. In North America most waxcap locations are reported to be forests (e.g. Hesler & Smith 1963: 32), contrary to many European countries. But it should be noted that this can partly be attributed to an under-sampling of grassland in the USA (Griffith & Roderick 2008). Also, one important difference between the two geographical areas concerns the eutrophication status. In North America vast old-growth forest areas still have a natural or semi-natural status (FAO 2006; Greenpeace 2006). In Central Europe most forested areas have undergone intense management activities and suffer from soluble nitrogen, phosphorus and sulphur deposition, leading to eutrophication and acidification (Lorenz et al. 2006, Simpson et al. 2006). Moreover, there is no reason to assume that in European forests waxcap mycelium is present below ground and that the fruiting is inhibited at the same time. One should remember that open woodland and vast areas of grassland existed after the last glaciation, all natural habitats where waxcaps could have thrived. Ungulates kept the vegetation cover short (Svenning 2002, Kirby 2004, Johnson 2009), which encourages the fruiting of waxcaps, as grazing or mowing grassland does (Griffith et al. 2011). An obligate association with mosses can be excluded, because *Hygrocybe* species colonise moss-free habitats according to our findings, e.g. the laurel forests on La Palma (see also fig. 2). The often observed co-occurrence of waxcaps and mosses could be due to the fact that moss also have a preference for low nutrient soils and an absence of rank vegetation. The extremely broad spectrum of the vegetation associated with waxcaps (see table 1) and the fact that they occur in habitats with low or high diversity of vegetation, clearly show the independence of waxcaps from specific plant taxa or communities.

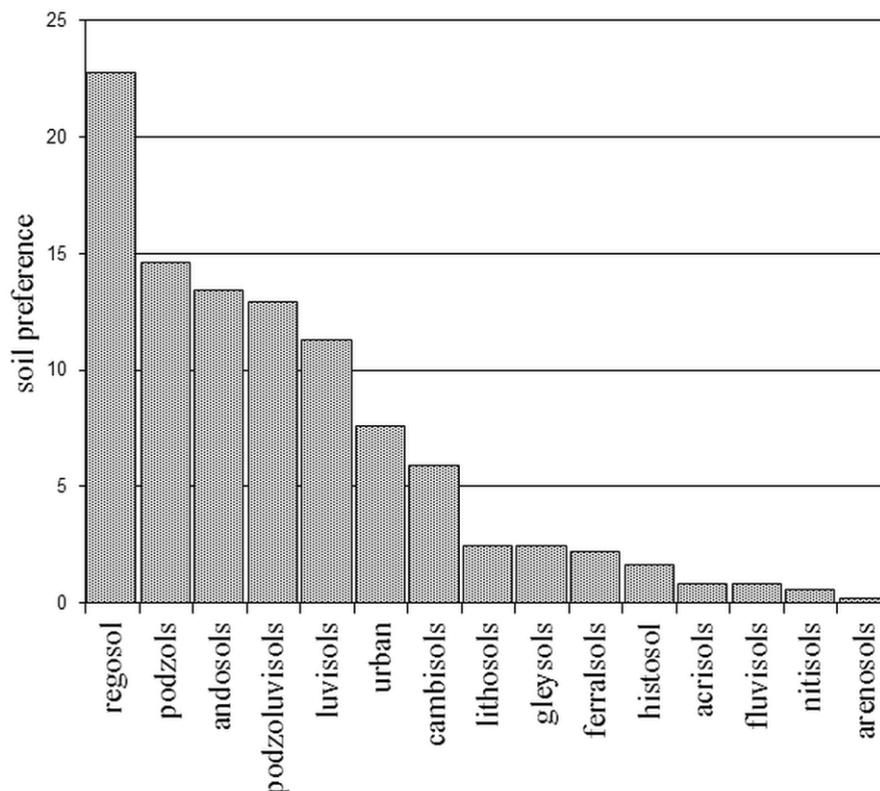


Fig. 5 – Soil preferences of the 16 *Hygrocybe* species in our data set. The y-axis shows the preferences weighed by the land areas covered by the soil types on the x-axis (source: FAO 2006).

Regosols, podzols, andosols, podzoluvisols and luvisols were the preferred soil types (see Fig. 5). More than two thirds of the waxcap sites have soils of low fertility (dystric). Looking at the

specific soil requirements of the waxcaps investigated, *H. conica*, *H. virginea* and *H. psittacina* appear to be able to cope with a great variety of soil types.

Most restricted are *H. flavipes*, *mucronella* and *quieta* (Fig. 6). We are aware that the FAO World reference base for soil resources (IUSS 2006) provides a limited resolution which does not reflect possible small-scale variations. Nevertheless, the results appear to be in line with previous appraisals.

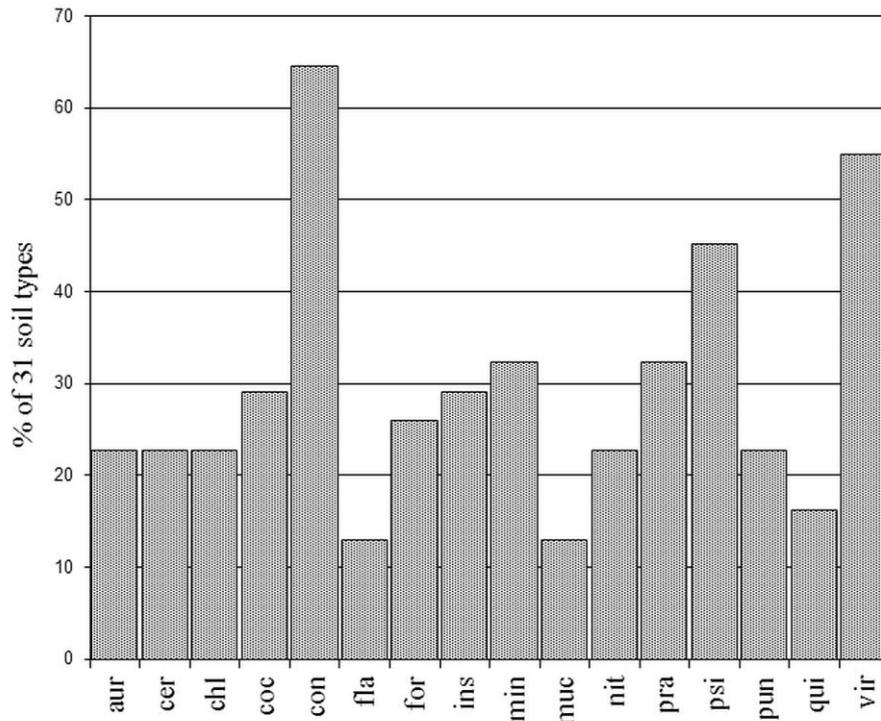


Fig. 6 – Range of soil types by *Hygrocybe* species. Percentage of the 31 FAO soil types identified (y-axis) where the 16 *Hygrocybe* species of our data set (x-axis) were found. Species abbreviations: aur – *aurantiosplendens*, cer – *ceracea*, chl – *chlorophana*, coc – *coccinea*, con – *conica*, fla – *flavipes*, for – *fornicata*, ins – *insipida*, min – *miniata*, muc – *mucronella*, nit – *nitratata*, pra – *pratensis*, psi – *psittacina*, pun – *punicea*, qui – *quieta*, vir – *virginea*.

The high tolerance of *H. conica*, *H. virginea* and *H. psittacina* in regard to soil types may be the main reason for their widespread distribution. But overall the selected *Hygrocybe* species show a marked preference for regosols and other dystric soils. Some species (e.g. *H. conica* and *H. virginea*), often appear as first waxcap species in formerly disturbed habitats, such as dunes (cf. Holden 2007), new highway embankments and green roofs (authors’ observations), and roadsides (Beisenherz 2000).

Our review thus confirms at a broader ecological scale the suggestions of other authors (e.g. Griffith et al. 2002, Young 2005, Boertmann 2010: 19) that low fertility, namely in terms of mineralised phosphorus and nitrogen levels, is a prerequisite for most of the 16 waxcap species. Soil organic matter, including humic compounds, seems not to have discriminating effects.

Nutritional considerations

The small scale associations of several *Hygrocybe* species (Schweers 1949), also observed by the authors (data not shown), indicate a non-combative lifestyle (cohabitation, see Tuininga 2005). On the other side, the persistence of waxcaps at established, stable sites as often observed by the authors is more typical for a combative c-strategy. The appearance at primary succession sites, such as dunes, new highway embankments and green roofs favours an r-selected strategy. The

occurrence of waxcaps under extreme environmental conditions would be an expression of a stress-tolerant lifestyle (s-selected, see Andrews 1992). These seemingly contradictory traits may be an indication of a high adaptability by changing strategies (Pugh & Boddy 1988) and/or of the use of a widely distributed nutritional source.

Most of the species in our data set prefer grass- or heathland over woodland, which may be interpreted as avoidance of ectomycorrhizal fungi (hosts) which is corroborated by our observations that waxcaps are less abundant in grassland with the ectomycorrhizal *Helianthemum* or *Dryas* (cf. Harrington 1996, 2003). Though the waxcaps in southern Canada and northern USA are predominantly found in ectomycorrhizal forests (Hesler & Smith 1963: 35), it should be noted that temperate and boreal forests also hold endo-mycotrophic plants e.g. *Taxus baccata* or forbs such as *Pulsatilla* (Öpik et al. 2006). Moreover, ectomycorrhizal fungi in forests may be suppressed by shrubs colonised with arbuscular mycorrhizae (McHugh & Gehring 2006). From Germany it is well known that some waxcaps are often associated with *Fraxinus* and *Acer* (Bresinsky et al. 2007, Krieglsteiner 2004), both being predominantly colonised by arbuscular fungi (Wang & Qiu 2006). The dominant tree of the waxcap locations in Macaronesian laurel forests is *Laurus novocanariensis*, a species which is closely related to *Laurus nobilis*, also colonised by endophytic mycorrhizae (Maremmani et al. 2003). Unfortunately, waxcap habitat descriptions from the Americas only rarely consider the accompanying vegetation in sufficient detail. It seems that *Hygrocybe* avoids habitats where ectomycorrhizal fungi dominate. This could be interpreted as an avoidance of competition, which could imply a biotrophic mode on the side of the waxcaps as also suggested by Seitzman et al. (2011), corroborated by the reluctance of waxcaps to grow axenically (see introduction).

Conclusion

There are clear commonalities of the habitats investigated. “European” waxcaps prefer weakly developed soils of low fertility, temperate and boreal ecozones and grassland, without mosses being obligate associates. Still, some *Hygrocybe* species in our data set are widely distributed over almost every ecozone of our planet, occupying extremely diverse habitats. This and the peculiar nutritional behaviour is in line with a biotrophic mode as suggested by Bresinsky (2008) and Seitzmann et al. (2011). Further research on the trophic lifestyle of waxcaps is needed, including histological investigations and barcoding of substrates and associated plants.

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