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Amanita inopinata, its ecology and expansion in Europe

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Résumé – Amanita inopinata est une espèce intrigante, qui est apparue en Europe en 1976 et s'y propage lentement depuis lors. Au sein du genre Amanita, elle appartient à un petit groupe d'espèces qui sont très originales, notamment parce qu'elles ne sont pas mycorrhiziques, et qui seraient situées à la base de l'arbre phylogénétique du genre. Le présent article présente une synthèse des connaissances accumulées au sujet de l'écologie, de la phénologie et de la distribution d'A. *inopinata*. Son écologie, très souvent située dans des milieux rudéralisés ou aménagés par l'homme, laisse penser qu'elle n'est pas indigène en Europe, et peut-être pas non plus en Nouvelle Zélande, où elle est également observée. L'étude détaillée de sa progression en Europe montre que les accroissements d'aire se font, soit par progression locale (< 30 km), soit par sauts plus importants (50-300 km). Le vent serait le vecteur déterminant pour ces derniers. L'expansion de l'espèce en Europe tend à s'accélérer au cours du temps et on peut donc la qualifier d'invasive. Comme elle reste malgré tout une espèce rare et qu'elle colonise principalement des milieux artificiels, son impact sur la mycoflore locale reste négligeable.

Amanita inopinata / carte de distribution / espèce invasive / expansion / niches

Abstract – *Amanita inopinata* is an intriguing species, which appeared in Europe in 1976 and propagates there slowly since then. Within the genus *Amanita*, it belongs to a small group of species which are very original, a.o. because they are not mycorrhizal, and which would be situated at the base of the genus phylogeny. This study presents an update on the ecology, the phenology and the distribution of *A. inopinata*. Its ecology, very often situated in artificial and more or less ruderalized biotopes, suggests that it is not native to Europe, and maybe not to New Zealand either, where it has also been observed. A detailed study of its progression in Europe shows that its distribution area increases either by local expansion (< 30 km) or by "big jumps" (50-300 km) and that wind would be the main vector for the latter. The expansion of *A. inopinata* in Europe tends to accelerate over time and we can thus consider it as an invasive species. Nevertheless, as it remains a rare species everywhere, that colonizes mainly artificial biotopes, its impact on the local mycoflora remains insignificant.

Amanita inopinata / distribution map / ecology / expansion / invasive species / niches

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INTRODUCTION

On 30.IX.2012, in Mont-sur-Marchienne (S of Charleroi, Belgium), Mr Christian Lambert collected a curious fungus, which he could not connect with a species he knew. He showed it to one of us (MDG) who, since it looked like a *Strobilomyces strobilaceus* (Scop.: Fr.) Berk. seen from above, but resembled *Amanita* as well, identified the collection as *Amanita inopinata*. The collector has not been able to describe precisely the environment in which he picked up the fungus. However, some *Taxus* needles were still attached to the carpophore, which fits well with the ecological range in which the species has been observed, up to now, in Europe.

It is the first time that the species is reported from Wallonia (southern Belgium). We present in this paper a survey of the data concerning the systematics, trophism, ecology, phenology and distribution of the species, as well as its possible invasive character.

TAXONOMY

Amanita inopinata D.A. Reid & Bas, in D.A. Reid, Notes Roy. Bot. Gard. Edinburgh 44 (3): 506 (1987). Figs 1-2

= Aspidella inopinata (D.A. Reid & Bas) Vizzini & Contu, in Vizzini et al., Micol. Veget. Medit. 27 (2): 82 (2012).

= Amanita "sp. 1" ss. G.S. Ridl., Austral. Syst. Bot. 4 (2): 350 (1991).

Holotype: UK, Surrey, Tandridge Hall, 2.X.1983, coll. Mrs Irene Palmer (K).

Illustrations: Figs 1-2 show pictures of collections made, respectively, in Edegem (Belgium) and in the forest of Guines (France). Colour pictures or aquarels of sporophores are also proposed by Taylor (1981, sub "Amanita sp."), Kibby (2000), Ridley (2000), Uljé (2001: 36), Courtecuisse & Moreau (2004), Neville & Poumarat (2004: 884), Kibby (2005), Overall (2010, 2011), Steeman *et al.* (2011), Steeman (2012), Boniface (2011, 2012) and the web-sites of Tulloss¹ and of the *Nederlandse Mycologische Vereniging (NMV)*². Other illustrations are also available on the Internet.

Drawings of microscopic details are presented by Reid (1987), Ridley (1991 and 2000), Uljé (2001), Courtecuisse & Moreau (2004) and Neville & Poumarat (2004: 515-516).

Descriptions: Good descriptions of the species are given by Reid (1987, original description), Ridley (1991: 350, sub "sp. 1"), Ridley (2000), Courtecuisse & Moreau (2004), Neville & Poumarat (2004: 513-514) and Tulloss's web-site.

The species is easily recognized by the following characters (Reid, 1987): cap grey-brown, prominently warted, resembling that of *Strobilomyces floccopus* from above [or a dark variant of *Leucoagaricus macrorrhizus* Locq., fide Courtecuisse & Moreau, 2004]; gills whitish and then salmon- to apricot-coloured,

^{1.} Studies in the Amanitaceae (Tulloss R.), USA: http://www.amanitaceae.org/?Amanita%20inopinata

^{2.} Nederlandse Mycologische Vereniging (NMV) – Verspreidingsatlas Paddenstoelen online: http://www.verspreidingsatlas.nl/003250.



Fig. 1. Amanita inopinata, Edegem, Belgium (Photo Guido Van Boeckel).



Fig. 2. Amanita inopinata, forest of Guines, France (Photo Abel Flahaut).

annulus grey with narrow black edge; stem rooting, lacking an obvious volva, its lower portion being covered by fine black recurved hair-like fibrils on a dirty salmon-coloured or bright tawny background. Microscopically, the spores are amyloid and clamps are abundant at the base of basidia and on general veil hyphae. The spores of the specimen from Mont-sur-Marchienne (Belgium) are amyloid and their size is $7.5-\underline{8.57}-9.5$ (-11.0) $\times 5.3-\underline{6.12}-7.0$ µm, Q = $1.31-\underline{1.40}-1.58$, which corresponds well with literature data. The spores with a length above 9.5 µm are probably produced by 2-spored basidia (Reid, 1987).

Classification: The species clearly belongs to the sect. *Lepidella* because of its amyloid spores, the appendiculate pileus margin and its friable volva. However, as observed by Dr. Bas (Reid, 1987; Bas, 2001), the species is quite isolated in this section. It is a member of the rather aberrant subsect. *Vittadiniae* (Bas, 1969: 346), together with a.o. *A. vittadinii* (Moretti) Vittad. and *A. nauseosa* (Wakef.) D.A. Reid. These species share the presence of volval remnants that consist mainly of chains of large, inflated, cylindrical to elongate or fusiform cells, and a cylindrical to fusiform stipe without a true basal bulb. Tulloss (see his website) suggests to place *A. inopinata* in a new monospecific stirps *Inopinata*.

Very recently, Vizzini *et al.* (2012) showed by molecular analysis that the species of the subsect. *Vittadiniae* Bas (1969) were gathered in a monophyletic clade, clearly isolated from the rest of the genus *Amanita*, of which they constitute a primitive group. They consequently decided to treat these species in a separate genus. Another option would have been to place them in a separate subgenus inserted on the base of the *Amanita* phylogenetic tree.

Vizzini *et al.* (2012) chose to restore, with emendation, the genus *Aspidella* E.-J. Gilbert, to accommodate these species. We believe it is not the best choice. Among the 24 taxa cited by Gilbert (1940: 79) in genus *Aspidella*, *A. vittadinii* is the only one to belong to *Aspidella* ss. Vizzini *et al.* (2012). Almost all the other *Aspidella* ss. Gilbert belong to subsect. *Solitariae* Bas and not to subsect. *Vittadiniae*.

Ecology: Besides the morphological peculiarities indicated above, the subsect. *Vittadiniae* is very original within the genus *Amanita*, because it contains non-ectomycorrhizal species (Bas, 2001; Wolfe *et al.*, 2012a, 2012b; Vizzini *et al.*, 2012). Wolfe *et al.* (2012a) failed to find evidence of symbiotic root structures when searching for them in a natural population of *A. inopinata.* The same authors report that inoculation of uncolonized *Pinus* seedlings with *A. inopinata*, in the laboratory, did not result in any sign of a mutualistic or pathogenic interaction with plants, while an ectomycorrhizal control species (*A. muscaria* (L.) Lam.) in the same experiment formed obvious EM root tips.

We compiled a list with the frequency of the various tree species under which A. inopinata has been collected in Europe, and this fungus appears to have been essentially collected under conifers: eight times under Taxus baccata, five times under Chamaecyparis lawsoniana, three times under x Cupressocyparis leylandii, twice under Cupressus sp. and Cedrus sp., and only once under Cupressus macrocarpa, Pinus nigra subsp. nigra, Pinus sylvestris, Picea sitchensis, Picea + Pseudotsuga + Abies, Sequoia sempervirens, Taxodium distichum, Thuja sp. and an unspecified " conifer plantation ". The list of collections contains also some broadleaved trees: three collections under Fraxinus excelsior, two under Aesculus hippocastanum, and a single collection from Acer campestre, Acer pseudoplatanus + Ilex aquifolium, Crataegus monogyna, Celtis occidentalis, Quercus sp. and Prunus serrulata.

Many of these trees are not known to develop ectomycorrhizae (fide Harley & Harley, 1987): *Chamaecyparis*, x *Cupressocyparis*, *Cupressus*, *Sequoia*, *Taxodium*, *Taxus*, *Thuja*, *Aesculus* and *Acer*. *Prunus serrulata* is probably not ectomycorrhizal either. The other tree genera in the list, representing 30% of the collections, are known ectomycorrhizal hosts: *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Celtis, Crataegus, Fraxinus, Ilex* and *Quercus*), but this does not imply that a symbiotic relationship actually existed between *A. inopinata* and these trees (Courtecuisse & Moreau, 2004).

In New Zealand too (Ridley, 2000 and pers. comm.), *A. inopinata* is mostly found under trees that are not ectomycorrhizal (*Chamaecyparis, Cupressus macrocarpa, Evonymus japonicus, Sophora* sp.), but it occasionally fruits under typical ectomycorrhizal hosts (*Leptospermum* sp. and *Pinus* sp.) (Weijtmans *et al.*, 2007). It deserves to be noted that only *Leptospermum* sp. and *Sophora* sp. are native to the country and that most of the biotopes are artificial.

When listing the collection habitats in Europe, it clearly appears that the biotopes are almost always artificial and often more or less ruderalized: ten collections come from parks (castles, ...), six from gardens (in one case, under a trampoline), another six from churchyards, three are cemeteries, two are from college nurseries and another two from woods, whereas the species was collected once in a school ground, a hedgerow at the edge of a pasture, a conifer plantation and a *Fraxinus* plantation.

The impression that *A. inopinata* favors artificial biotopes is confirmed by the list of the trees under which the species has been observed in Europe (see above). The vast majority of these trees are not native in the places where *A. inopinata* was collected, e. g. all cited conifers (except *Taxus* but, in all the growth places cited here, the trees were planted). For the few European collections under broadleaved trees, these trees were indigenous, except for *Aesculus, Celtis occidentalis* and *Prunus serrulata*.

Phenology: This *Amanita* produces sporocarps between 7 March and 19 July (mean: 22 May) in New Zealand, but fruits between (30 July-) 15 September and 15 November (-December) (mean: 18 October) in Europe (Fig. 3). The difference is a consequence of the fact that New Zealand is situated in the southern hemisphere, where the seasons are inverted compared with Europe.

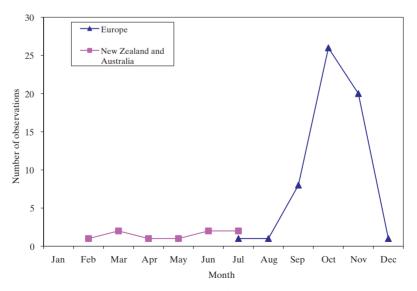


Fig. 3. Phenology of Amanita inopinata in Europe and in New Zealand.

DISCUSSION

Distribution and expansion

The first collections of the species were made in **New Zealand**, more precisely in Auckland City (North Auckland, 1964 and 1972) and Lincoln (Mid Canterbury, 1971) (Ridley, 1991, 2000 and *NatureWatch NZ*³ and *NZFungi*⁴). The specimens are in bad state, mouldy or badly insect damaged, which is probably the reason why Ridley (2000) described them as "*Amanita* sp. 1" instead of creating a new species. Watercolour paintings made after those collections show blackish basidiocarps with pale salmon or apricot gills (Ridley, 2000 ; Taylor, 1981). Further collections of the species have been made in Bulls (Wanganui, in 1992 ; see Ridley, 2000) and at Aorangi Road (Mid Canterbury, in 2010 ; see *NatureWatch NZ*). In the meantime, the species was collected in Lincoln again (2006 and 2008 ; see *NatureWatch NZ*), two km away from the first observation in that region. It seems that no other observation of the species has been made in New Zealand since 2010 (Ridley, pers. comm.), except a collection in Christchurch (Mid Canterbury, in 2011 ; see *iNaturalist.org*⁵). The total number of observations for the country is eight, for a total number of growth places of six. Distribution maps for New Zealand have been published by Ridley (2000) and Uljé (2001, after Ridley's map) and on the web-sites of *NatureWatch NZ* and *NZFungi*.

The first European specimen of *Amanita inopinata* has probably been collected in **Great Britain**. It was growing in Littlehampton (UK, West Sussex, in 1976), in the Glasshouse Crops Research Institute (Weir, 2000). The species has however been described after other British specimens (Reid, 1987), collected in West Kent (Lullingstone Park, in 1981), in Surrey (Tandridge, in 1983, and Kingston Cemetery, in 1986) and in South Essex (Chigwell, in 1984).

Later on, the species has been rather frequently observed in the southeast of England:

- West Kent again (Chelsfield, in 1986, 1993, 1996 and 1998, see Kibby, 2000;
 Mereworth, in 1991; Hadlow, in 1991-1995; Scotney Castle, in 1999, see Kibby, 2000; Tunbridge Wells, in 2004-2008, see Kibby, 2006),
- South Essex again (Chigwell, in 1987 ; Southend-on-Sea, in 2006, see Boniface, 2012 ; Old Harlow, in 2011, see Boniface, 2012),
- Berkshire (Windsor, in 1988; Holyport, in 1988),
- West Sussex again (Bracklesham Bay, in 1990; Petworth, in 1995-1996),
- Surrey again (Tandridge, in 1992-1993, see Palmer, 2003; Ruskin Park, London, in 2006; Croyden, in 2011, see Boniface, 2011; Kew Gardens, in 2012),
- East Kent (Ashford, in 2002; Civiley Wood Turnham, in 2006),
- East Sussex (Battle, in 2004),
- East Suffolk (Flatford, in 2004, 2005 and 2009, see Kibby, 2005 and 2006),
- South Hampshire (Eastleigh, in 2006),
- Middlesex (Bushy Park, in 2009, see Overall, 2011).

Up to now, *A. inopinata* has been observed 49 times in Great Britain, on 27 different sites. Distribution maps for UK have been published by Kibby (2000) and Uljé (2001); see also the *Checklist of Fungi of the British Isles*⁶.

^{3.} NatureWatch NZ, New Zealand: http://naturewatch.org.nz/taxa/3276-Amanita-inopinata

^{4.} NZFungi, New Zealand Fungi (and bacteria), Landcare Research: http://nzfungi.landcareresearch.co.nz/ html/mycology.asp

^{5.} iNaturalist.org: http://www.inaturalist.org/observations/19046

^{6.} Checklist of Fungi of the British Isles, website of the British Mycological Society (BMS): http://www.field-mycology.net/GBCHKLST/gbsyns.asp?intGBNum=12954

At the very beginning of the 21st century, "the inexpected one" jumped over the North Sea and appeared in **the Netherlands**, in Alphen aan den Rijn (Zuid-Holland, in 2000, see Bas, 2001 and Uljé, 2001) and then in the polderpark Cronesteijn, in Leiden (Zuid-Holland, in 2002, see Adema, 2003). More recently, the species has been collected near Hattem (Gelderland, in 2007 and 2008) and near Vlaardingen (Zuid-Holland, in 2009). To date, six observations of the species have been made in the country, on four different sites. A distribution map for the country is available on the web-site of the *Nederlandse Mycologische Vereniging*.

Soon after it's appearance in the Netherlands, *A. inopinata* was observed in northern **France**, at Baincthun (Pas de Calais, in 2003, see Courtecuisse & Moreau, 2004). Two other localities have been discovered more recently, in the same department of Pas de Calais: Moulle (near St-Omer) in 2008 and forêt domaniale de Guines in 2009. The species appeared four times in the country, on three different growth places.

In 2008, a first collection has been made in **Belgium**, at the castle of Drietorens in Londerzeel (Vlaams-Brabant, see Steeman *et al.*, 2011 and *Observations.be*⁷), filling the gap between France and the Netherlands. The species has not been observed again in the country during the three following years but in august-november 2012, it was collected in four different places (Steeman, 2012 and Observation.be): in Londerzeel again (other site), in Mont-sur-Marchienne (Hainaut), in Edegem (Antwerpen) and in Kessel-Lo (Vlaams-Brabant). In total, seven observations of the species have been registered in the country, on five different sites.

Finally, the species has been observed very recently in Australia, in Melbourne (Victoria, in 2013, see the web-site of *Project Noah*⁸).

An addition of the aforementioned figures shows that *Amanita inopinata* has been observed 66 times in Europe (Fig. 4), on 38 different sites, and that England remains by far the region with the highest number of observations.

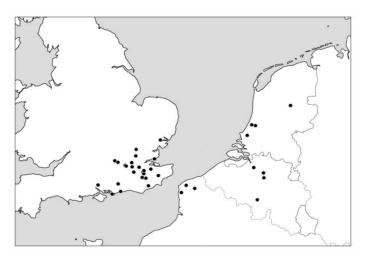


Fig. 4. Distribution map of Amanita inopinata in Europe.

^{7.} Observations.be, website of Aves-Natagora and the Stichting Natuurinformatie, Belgium: http://observations.be/soort/view/20688

^{8.} Project Noah: https://www.projectnoah.org/spottings/22641029

The progressive expansion of the species range in Europe (Fig. 5) confirms the prediction made by Bas (2001) that the species would slowly spread in Western Europe. It also shows that two different processes are involved in the progression of the species: local expansion (30 km and less) and big jumps (50-300 km). When looking in detail at the distributional data, this progressive local expansion, over rather short distances, appears clearly and the three following examples can be given:

1) A progression towards west, from Littlehampton to Bracklesham Bay and Petworth (all West Sussex, resp. in 1976, 1990 and 1991), and then to Eastleight (South Hampshire, 2006).

2) Another progression towards west, starts from Lullingstone park (near Shoreham, West Kent, in 1981) and reaches successively Tandridge and Kingston (both in Surrey, resp. in 1983 and 1986) and then the Windsor Great Park and Maidenhead (both in Berkshire, in 1988).

3) A progression towards south-east, starting from Lullingstone park again (West Kent, in 1981) and reaching Hadlow, then Scotney Castle (both West Kent, resp. in 1991 and 1999) and Battle (East Sussex, in 2004).

A look at the map indicates that the general distribution of the species mainly expands eastward or, more precisely, toward the east-north-east. Given it is also the direction of prevailing wind in this region of the European continent, it leads to the conclusion that wind is most probably the main factor in the dispersion of the species, at least for the "big jumps". The role of the wind in the dispersion of fungi, sometimes even from one continent to another, has already been stressed by several authors (see a.o. Brown & Hovmøller, 2002). As a consequence, it can be easily predicted that the species will continue its progression towards east and that it is going to reach the German territory (esp. Niedersachsen and Nordrhein) in the next ten years. The number of growth places will also continue to grow in the regions where the fungus is already established.

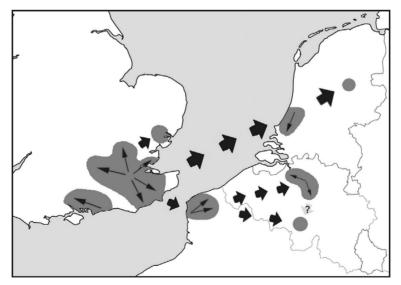


Fig. 5. Progressive expansion of *Amanita inopinata* in Europe, with indication of the itinerary probably followed in the case of long distance dispersal.

It is also interesting to study the speed at which the expansion occurs. Figure 6 shows the annual evolution of the cumulated number of different growth places in Europe. Figure 7 presents the evolution of the annual number of different growth places in which the species has been observed. These graphs clearly show, not only that the expansion of the species continues, but also that it accelerates.

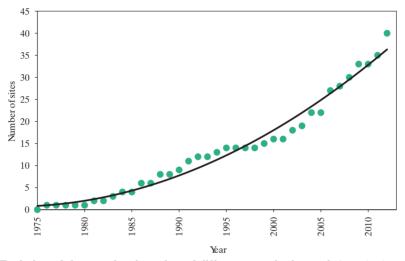


Fig. 6. Evolution of the cumulated number of different growth places of *Amanita inopinata* in Europe.

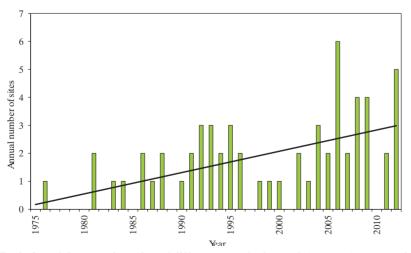


Fig. 7. Evolution of the annual number of different growth places of *Amanita inopinata* observed in Europe.

Amanita inopinata, an invasive species?

As indicated above (and see figs 5, 6 and 7), the distribution area of *Amanita inopinata* gradually widens and this progression accelerates. The species therefore probably deserves to be considered as invasive, even if it has not been included in the "List of Species Alien in Europe and to Europe" published by Hulme *et al.* (2009). This list contains only two *Amanita* species: *Amanita asteropus* Sabo and *Amanita singeri* Bas. It confirms the under-representation of fungi in the databases devoted to invasive or alien species, already stressed by Desprez-Loustau *et al.* (2007).

IUCN describes invasive species as "organisms introduced by man into places out of their natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species". Yet, the consequences of the introduction of exotic mushrooms on the native mycoflora were hardly studied (Desprez-Loustau *et al.*, 2007). In addition, such impact is difficult to measure when the invasive species is a saprotroph.

Among the invasive species, pathogens and, to a lesser extent, mycorrhizal species were especially studied. Studies about saprotrophic invaders remain rare. An exception is probably *Clathrus archeri* (Berk.) Dring, the progression of which was studied in detail (Parent & Thoen, 1986; Parent *et al.*, 2000).

On the occasion of the first discovery of *A. inopinata* in France, Courtecuisse & Moreau (2004) presented an interesting discussion about the concept of "invasive species". They sort the species into three categories: (1) species which are bound to very particular ecological conditions from which they can not escape (e.g. species living in greenhouses or in flowerpots), (2) species introduced with a host and remaining bound to this host (e.g. *Geopora sumneriana* (Cooke) M. Torre and *Cedrus*) and (3) species able to adapt to new hosts and substrates. *Amanita inopinata* (and *A. singeri*, the origin of which remains also unknown) belongs to this last category.

Pringle & Vellinga (2006) used literature data to study the case of *Amanita phalloides* (Vaill. ex Fr.) Link as an example to explore the biogeography and invasion biology of an ectomycorrhizal species. They notice that the geographic distribution, including native ranges, of most fungi are poorly documented and that the lack of natural history data causes confusion over what is native or introduced (this fact is also stressed by Desprez-Loustau *et al.*, 2007 and Hierro *et al.*, 2005). So, when a new locality of a species is discovered in a poorly explored territory, it is difficult to know if it is an introduction or if it is just the first record of the fungus from a region within its native range.

The same authors also stress the fact that confusion on the introduced status and biogeography is the direct result of shifting species concepts. However, for a few especially charismatic fungi, a careful reading of the literature may provide needed data. We believe it is the case of *Amanita inopinata*, which is a very striking and easy to identify species. In addition, the portion of the European territory in which it has been observed, up to now, is very well explored from a mycological point of view.

In a study about global patterns of ectomycorrhizal introductions, Vellinga *et al.* (2009), using the framework provided by Lockwood *et al.* (2007), group fungal examples from the literature into five different outcomes: (1) EM fungi may be introduced but fail to establish, (2) introduced EM fungi may establish but be replaced by local fungi, (3) EM fungi may persist with introduced trees but fail to grow with local hosts, (4) EM fungi may persist with introduced

trees and spread to local hosts, or (5) EM fungi may fail to persist with introduced trees but nonetheless spread to local hosts. Even if *Amanita inopinata* is not an ectomycorrhizal species, the categories of Vellinga *et al.* could be used in some way, after replacement of "host" by "substrate" and of "with introduced trees" by "on the original substrate". In that case, *A. inopinata* could belong to the fourth or to the fifth of these categories.

Origin of the species

Since its discovery, *A. inopinata* has always been considered as an introduced species, not native in Europe. The main arguments are that it is a very striking species, growing in mycologically well-investigated zones in Europe, which make it seem impossible that it could have been present previously while remaining unnoticed.

Bas (2001) considers as probable that the species originally came from New Zealand. He finds "significant that, in New Zealand, from a mycological point of view still rather under-explored, its most northern and most southern locality lie about 750 km apart." Also Taylor (1981) presents the species (under "Amanita sp.") as a species native to New Zealand (see also Kibby 2001). Ridley (2000 and in e-litt. 2013) does not agree with that opinion on the New Zealand origin of A. inopinata, as all of the collection sites in that country are urban or peri-urban and largely consist of "exotic" vegetation not native to New Zealand (Chamaecyparis sp., Cupressus macrocarpa, Pinus sp., Euonymus japonica). He considers it more likely that the species entered New Zealand in the same way that it got to Britain.

However, in Europe, *A. inopinata* almost always appears in disturbed zones such as gardens, parks, cemeteries, churchyards, edges of pastures, etc. After the "disturbance hypothesis" (Hierro *et al.*, 2005), this fact could indicate that *Amanita inopinata* is a ruderal species in its natural range as well, which could be an argument to support the hypothesis that it is native to New Zealand.

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