First record of North American fungus *Rhizopogon pseudoroseolus* in Australia and prediction of its occurrence based on climatic niche and symbiotic partner preferences

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Abstract

In 2017 a North American fungus, *Rhizopogon pseudoroseolus* (Boletales, Basidiomycota), formerly known in Oceania as only occurring in New Zealand, was found for the first time in South Australia. The morphological identification of collected specimens was confirmed using an internal transcribed spacer barcoding approach. In this study, the biogeography of *R. pseudoroseolus* is also presented, based on sporocarp and ectomycorrhiza records. Species distribution modeling implemented in MaxEnt was used to estimate the distribution of the potential range of *R. pseudoroseolus* in Australia and New Zealand. The obtained model illustrates, in the background of climatic variables and distribution of a symbiotic partner, its wide range of suitable habitats in New Zealand, South-East Australia, and Tasmania. Precipitation of the coldest quarters and annual mean temperature are important factors influencing the potential distribution of the fungus. The occurrence of *Pinus radiata*, the ectomycorrhizal partner of *R. pseudoroseolus*, is also an important factor limiting expansion of the fungus' invasion range.

Keywords *Rhizopogon pseudoroseolus* · Suilloid fungi · Foreign fungus · Fungal biogeography · Ecological niche modeling · *Pinus radiata*

Introduction

Suilloid fungi are crucial during *Pinaceae* invasions into new areas. They are therefore regarded as main biological drivers of global pine invasions (Policelli et al., 2019). Co-invasion of trees with their symbiotic fungi is the most geographically widespread phenomenon in plant-fungus interactions outside their natural range (Dickie et al. 2010). The most important group of ectomycorrhizal (ECM) fungi moved from their native range is the suilloid fungi, specifically the genera *Suillus* and *Rhizopogon* (Vellinga et al. 2009). However, a large body

of literature has been published regarding ECM fungi being introduced with *Pinaceae* outside their native range. In the Northern Hemisphere, where several non-native pine species have been naturalized with their assembled symbionts (Vellinga et al. 2009; Tedersoo 2017; Pietras et al. 2018; Pietras and Kolanowska 2019), the role of ECM fungi in the co-invasion has been less observed (Kohout et al. 2011). The introduction of ECM fungi in the Southern Hemisphere, where the invasion of various pine species has been intensively studied, a co-invasion-dominated process has been clearly determined (Dickie et al. 2010; Salgado Salomón et al. 2011).

The genus *Rhizopogon* (Boletales, Basidiomycota) constitutes the largest ectomycorrhizal group forming truffle-like sporocarps. Out of approximately 160 described taxa, numerous species are multi-host cosmopolitan fungi, which are recorded commonly in the Northern Hemisphere. However, the highest diversity of *Rhizopogon* genera occurs in North America, where these fungi form ectomycorrhizal assemblages with several *Pinaceae* species (Massicotte et al. 1999). Almost 20 species belonging to the *Rhizopogon* genus have been transported to new areas as a result of co-introduction with North American conifers (Vellinga et al.

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2009). *Rhizopogon* species, similar to the closely related *Suillus* genera, belongs to early successional colonizers (Leski et al. 2009, Hankin et al. 2015, Policelli et al., 2019). *Rhizopogon pseudoroseolus* is associated with the *Rhizopogon* subgenus *Roseoli* (Martín and García 2009, Visnovsky et al. 2010). This rare but widely distributed fungus is typically associated with pines in North America (Trappe et al. 2009). Outside its native range, the fungus was reported in the Southern Hemisphere, in New Zealand and Argentina, probably as a result of co-introduction with American pine species (Walbert et al. 2010, Urcelay et al. 2017). Until now, *R. pseudoroseolus* has not been found in other parts of the Southern Hemisphere. Therefore, the aim of this study was to present the first record of this North American false truffle in Australia. Additionally, species distribution modeling was used to predict the occurrence of *R. pseudoroseolus* in Australia and New Zealand based on climatic niche preferences and the distribution of its ectomycorrhizal tree partner.

Materials and methods

Field survey

Sporocarps of *Rhizopogon pseudoroseolus* were found during a field survey in Belgrove South (Victoria, Australia; 37° 55' 50" S, 145° 21' 20" E) in May 2017. Three mature sporocarps (Fig. 1A) grew partly belowground near approximately 10-year-old *Pinus radiata* pines in Belgrove St. Recreation Reserve. Sporocarps collected were examined using macro- and micro-morphological observations (using a ZEISS Axio Imager 1A with Nomarski differential interference-contrast; photographs were taken using a ZEISS Axio Cam MRc5 digital camera), dried, and deposited in the University of Gdansk (UGDA) (herbarium fungal collection with voucher number UGDA-F102). Morphological identification was confirmed

Fig. 1 (A) Sporocarps of *Rhizopogon pseudoroseolus* recorded for the first time in Australia, and (B) view of its spores (ZEISS Axio Imager 1A with Nomarski differential interference-contrast; photographs were taken using a ZEISS Axio Cam MRc5 digital camera, bar = 20 μ m)

using a molecular method based on Sanger sequencing. DNA extraction and PCR conditions followed Pietras et al. (2018). The PCR products were sequenced in both directions, using ITS5 forward and ITS4 reverse primers (Pietras et al. 2016), at the Laboratory of Molecular Biology of Adam Mickiewicz University (Poznań). The obtained sequences were verified visually on chromatograms using BIOEDIT. The nuclear internal transcribed spacer (ITS) consensus sequence of *R. pseudoroseolus* obtained in this study was deposited in GenBank with its accession number MK415052. The analysis of phylogenetic relations between *R. pseudoroseolus* and closely related taxa was conducted in MEGA X (Kumar et al. 2018).

Data collection and potential distribution of *R. pseudoroseolus*

The dataset of records for *R. pseudoroseolus* was created using Mycology Collections Portal (mycoportal.org), Global Biodiversity Information Facility website (GBIF.org (08 February 2018b)), UNITE (unite.ut.ee), and Atlas of Living Australia (NZVH 2019) databases, searching among preserved specimens and ectomycorrhiza observations. In the created model, data concerning the distribution of *Pinus radiata*, a symbiotic partner of *R. pseudoroseolus* in Australia and New Zealand, were also taken into account. Thus, the occurrence data of *P. radiata* accessible in GBIF (GBIF.org (08 May 2018a)) were also downloaded (212 records for native and 235 for invasive range, respectively). Models of suitable niche distribution for *R. pseudoroseolus* and *P. radiata* were created using the MaxEnt 3.3.2 software (Phillips et al. 2006). This approach provides an opportunity to determine the climatic niche preference of the fungus in North America and project its range to Australia and New Zealand based on areas where those variables are most similar with respect to symbiotic partner occurrence as well. Therefore, additionally, *P. radiata* occurrence data were added to the model to assess the potential distribution of *R. pseudoroseolus*. In total, 24 different locations of *R. pseudoroseolus* (20 from sporocarps and 4 from ectomycorrhizal observations; Appendix 1) and 447 records of *P. radiata* (Appendix 2) were included in the MaxEnt analysis (Fig. 1A). The predicted distribution of suitable niches was assessed using 12 climatic variables in 2.5 arc minutes (± 21.62 km² at the equator, Hijmans et al. 2005, see Supplementary Material S1), selected based on the previously published papers (Pietras et al. 2018, and citations therein). All parameters of the model (number of bootstrap replications, maximum iterations of the optimization algorithm, and convergence threshold) followed Pietras et al. (2018). The model was estimated using the AUC (Area Under the Curve) metric, where values between 0.9 and 1 indicate high performance of the model.

Results and discussion

Sporocarps were found for the first time in Australia growing near young radiata pines. Examined specimens were globose, flattened and tapering at the end, and 3–4 cm in diameter (Fig. 1A). The peridium was pinkish when young and darkened when dried, thin, and tightly attached to gleba. Reaction to KOH was not distinctive, but sporocarp showed a very strong reaction with FeSO₄, coloring peridium to dark olive, or even dark blue. The rhizomorphs appressed at the base. Gleba was white until dry, when it turned olive, with small chambers that were empty. Spores cylindrical were noted with rounded ends (Fig. 1B), 8–11.24 µm long (mean 9.61 µm, SD = 0.84; based on the measurement of 100 randomly selected spores). *Rhizopogon pseudoroseolus* was described originally in 1966. However, Martín (1996) proposed a taxonomical revision within the *Rhizopogon* genera, and, based on macro-morphological features, mainly peridium and gleba color, synonymized 36 taxa including *R. pseudoroseolus*, to *R. roseolus*. Based on ITS analysis, Martín and García (2009) distinguished *R. pseudoroseolus* from the *R. roseolus* group. Both differ in terms of spore size, and only *R. pseudoroseolus* shows a very strong reaction with FeSO₄. Those two well-distinguished features were observed in the case of specimens collected by the author in Australia. In contrast to *R. roseolus*, a strong reaction with FeSO₄ and spores longer than 3 µm clearly classify the collected specimens to *R. pseudoroseolus*. The morphological identification was confirmed using an ITS barcoding approach. The obtained consensus sequence revealed 100% similarity with the sequences of *R. pseudoroseolus* sporocarps originated from North America (see Supplementary Material S2A), including the paratypes of this taxon collected in the 1960s and deposited in the University of Michigan Herbarium (sequences: AJ810040, AJ810042). Additionally, Australian voucher was genetically very similar (more than 99% similarity) to the sequences of *R. pseudoroseolus* obtained from the ectomycorrhizas of *P. radiata* and *P. ponderosa* sampled in New Zealand plantations (sequences: GQ267486, KM596880, Walbert et al. 2010; Wood et al. 2015). In comparison with the sequences of *R. roseolus* deposited in GenBank, the sequence obtained in this study differed by 4–5%. Such a level of genetic diversity is standard interspecific variability within ITS. Therefore, with no doubt, specimens collected in Australia can be classified to *R. pseudoroseolus* and constitute the first record of the fungus in the continent (Supplementary Material S2).

The obtained model of *R. pseudoroseolus* distribution presents high performance, indicated by high AUC scores (AUC = 0.974; SD = 0.011). The most important climatic factors limiting the occurrence of *R. pseudoroseolus* are the precipitation in the coldest quarter and annual mean temperature (33.5 and 13.9% of the contribution, respectively). Both climatic variables confirm the recent description of the climatic niche of suilloid fungi outside their native range (Pietras et al. 2018, Pietras and

Kolanowska 2019). The precipitation in the coldest quarter indicates the seasonality of sporocarp production in relation to total precipitation of the coldest 3 months of the year (June–August in Australia and New Zealand). Based on the results obtained, *R. pseudoroseolus* can be regarded as a species with relatively high-temperature requirements (annual mean temperature) but preferring a wet, but mild climate (high precipitation in the coldest quarter). At the global scale, climatic factors are regarded as one of the best predictors, followed by edaphic and spatial patterning, of fungal richness and diversity (Tedersoo et al. 2014). Results obtained in this study emphasized the role of climatic conditions in the expansion of alien fungi.

In North America, *Rhizopogon pseudoroseolus* is known as an ECM symbiont of different pine species, such as *P. contorta* (Molina & Trappe 1994), *P. banksiana* (Hankin et al. 2015), and *P. resinosa* (Martín and García 2009). The fungus occurs rarely but is widely distributed in both Western and Eastern parts of the continent (Supplementary Material S3A). The species distribution model created based on both *Pinus radiata* occurrence data and climatic variables shows wider prediction for *R. pseudoroseolus* occurrence in the native environment (Supplementary Material S3B). The obtained result is expected and suggests that the geographical range of the fungus in its native environment is underestimated. This is confirmed by the results of environmental sequencing studies recording the presence of *R. pseudoroseolus* mycelium in the soil (Rasmussen et al. 2018) and in pot experiments (Scott et al. 2019, Zwiazek et al. 2019, Hankin et al. 2015). Outside the native range, *R. pseudoroseolus* was found in the Southern Hemisphere with *P. elliottii* in Argentina (Urcelay et al. 2017) and in New Zealand in plantations of *P. contorta* and *P. radiata* (Wood et al. 2015; Walbert et al. 2010). The observation in Argentina constitutes a single record in this region, and thus could not be used for modeling in this study. The Australian record was added in this work to the New Zealand observations (Fig. 2a). The number of records gathered is more than the minimum number of localities required by MaxEnt to obtain reliable predictions (Pearson et al. 2006). The obtained model shows strong prediction for numerous suitable habitats located in most areas of New Zealand. Similarly, suitable habitats were detected in the region where *R. pseudoroseolus* was found for the first time in Australia and in areas where it has never been recorded in this continent (other regions of south Victoria, south-east parts of New South Wales and the entirety of Tasmania, Fig. 2b). The distribution of suitable niches of *Pinus radiata*, an ectomycorrhizal partner of *R. pseudoroseolus*, shows overlap with the current range of this tree in New Zealand and Australia (Fig. 1A, B). Radiata pine was chosen for modeling because it is currently the most important plantation species in New Zealand, constituting almost 90% of New Zealand's short-rotation forest crop plantations (approximately 1,600,000 ha). This tree also occurs frequently in south-east Australia and Tasmania (GBIF.org (08 May 2018a)). Recent papers show that the most important factor limiting the spread of

Fig. 2 **a** Records of *Rhizopogon pseudoroseolus* (red star, first record in Australia; red dots, known records in New Zealand) and its host partner *Pinus radiata* in Australia and New Zealand (yellow dots). **b** Present distribution of the suitable habitats of *R. pseudoroseolus* in Australia and New Zealand (based on climatic variables and ECM partner occurrence). **c** Present distribution of suitable habitats of *P. radiata*; habitat suitability legend for **b** and **c**

symbiotic fungi is the distribution of their ECM partners (Pietras et al. 2018, Pietras and Kolanowska 2019). In this study, the obtained model illustrated that one of the most important factors (reaching 29.8% contribution) crucial for *R. pseudoroseolus* expansion is the occurrence of *P. radiata*. Thus, areas where *P. radiata* occurs should also be considered as regions of high risk of *R. pseudoroseolus* expansion. This assumption was confirmed by strong prediction for the fungus occurrence in regions, where until now it had not been found. The second possibility is that the current range of *R. pseudoroseolus* in Australia and New Zealand is underestimated and this fungus occurs in many more areas, but due to production of small, ephemeral sporocarps, its presence is hidden. The belowground surveys connected with molecular analysis demonstrated that mycorrhizas of *R. pseudoroseolus* dominate assemblages of mycorrhizal fungi of *P. radiata* in

New Zealand, reaching 69% abundance (Walbert 2008). Wood et al. (2015) recorded ectomycorrhizas of *R. pseudoroseolus* in New Zealand's plantations of *P. contorta*. What is more interesting is that the authors evidenced a 3-way interaction between non-native brushtail possums (*Trichosurus vulpecula*) dispersing spores of non-native fungi (including *R. pseudoroseolus*) and facilitating the invasion of North American *P. contorta* in New Zealand. In Australia, where possums are native and share the same habitats as *P. radiata* and *R. pseudoroseolus*, a similar interaction seems to be evident. Moreover, in Australia, mycophagy by small mammals is a key dispersal process of truffle-like fungi, including *Rhizopogon*. The dispersal of spores of hypogeous fungi on the fecal pellets of Australian mammals has been detected at relatively long distances from the source of inoculum (Nuske et al. 2019).

The introduction and spread of foreign symbiotic fungi can be a relevant problem in nature conservation, especially in regions where several ECM tree species have been introduced (Dickie et al. 2016). This study shows that climatic conditions, symbiotic partner, and animal vector occurrence should be considered as three factors crucial for the expansion of *R. pseudoroseolus* in future. These factors should be also taken into account to plan appropriate management strategies preventing the spread of this fungus in Australia and New Zealand. Invasions of ECM fungi seem to be unstoppable and are considered as potentially threatening native mycobiota (Banasiak et al. 2019). In case of co-invasion of *R. pseudoroseolus* and radiata pine, some management strategies proposed by Dickie et al. (2016), like blocking animal and human vectors or elimination of tree host, can be used to slow down the expansion of the fungus and to impede the invasion of the tree.

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Appendix 1

Rhizopogon pseudoroseolus occurrence data

Appendix 2

Pinus radiata occurrence data

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