

Original article

Fungal communities as an experimental approach to Darwin's naturalization hypothesis

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Abstract

Darwin's naturalization hypothesis suggests that the success of an invasive species will be lower when colonizing communities are formed by phylogenetically related rather than unrelated species due to increased competition. Although microbial invasions are involved in both natural and anthropogenic processes, factors affecting the success of microbial invaders are unknown.

A biological invasion assay was designed using *Trichoderma cf. harzianum* as the invader and two types of recipient communities assembled in microcosm assays: communities phylogenetically related to the invader, and communities phylogenetically unrelated to it. Both types of communities were invaded by *T. cf. harzianum*, and the success of colonization was monitored by qPCR; its effect on the genetic structure of recipient fungal communities was then assessed by DGGE profiles. *T. cf. harzianum* established itself in both communities, reaching 1000–10,000 times higher copy numbers in the non-related communities. However, invader establishment does not affect the structure of the invaded communities. These results suggest that the composition of recipient communities and their phylogenetic relationship to the invader affect the success of colonization by *T. cf. harzianum*. While this approach represents a very simplified assay, these microcosms enable an experimental test of Darwin's hypothesis in order to understand the biological invasion process in microbial communities.

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Keywords: Microbial invasion; *Trichoderma cf. harzianum*; Phylogenetic relationship

1. Introduction

Invasive species are organisms that have been transported beyond their natural range and have successfully been established in this new geographical region, generating a negative impact on the local ecosystem [1]. This process represents a global concern and is considered to be one of the most serious threats to local biodiversity and ecosystem functioning [2,3]. For this reason, several studies have focused on biological invasion in an attempt to understand the ecological mechanisms underlying this process and to elucidate reasons for the success or failure of a potential invasive species [4].

A classical hypothesis originally proposed by Charles Darwin (1859), and known as *Darwin's naturalization hypothesis*, has provided the basis for many of these invasion hypotheses and suggests that introduced species are more successful in communities in which their close relatives are missing. Therefore, if an invader arrives at sites with congeneric native species, the resident community will impose stronger competition on the invader species, reducing its invasiveness, since closely related species tend to have similar niches [5].

Traditionally, most studies on biological invasion were derived from research on plant and animal invasions. Although extensive evidence exists concerning the major role of microorganisms in the functioning of ecosystems [6], few studies have examined microbial invasion [7–10]. A possible explanation for the rareness of studies on microbial invasion and the scientific predilection for carrying out research on macroorganisms

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is, in part, due to their microscopic nature, but also to the fact that information on their biogeography and distribution is scarce [11], which makes microorganisms difficult to recognize and label as invasive. Hence, microbial invasions remain practically unexplored until today and information about them comes from the study of microorganisms outside the invasion context, i.e. pathogenesis, biocontrol, mycorrhization, bioremediation and industrial fermentation, among others, as all of these are processes involving inoculation (invasion) of microorganisms into a microbial resident community.

On the other hand, the establishment of an experimental model permitting the maintenance of a small scale system with controlled variables is fundamental for the study of microbial invasion. In addition, microorganisms could be very useful for testing Darwin's hypothesis due to the possibility of manipulating the relatedness between the invader and members of experimental communities. In this context, fungi are among the most ecologically and evolutionarily diverse eukaryotic organisms, having ecological significance as symbionts and decomposers and playing an important role in biogeochemical cycles and nutrient turnover [7,12]. Although recent works have focused on fungi as invaders, most articles about invasive species do not mention fungi in this context, or else only briefly consider them [7].

In particular, *Trichoderma* species, belonging to the *Ascomycota* phylum and *Hypocreales* order are ubiquitous in the soil, where they may represent the majority of the fungal biomass, and play important environmental roles such as degradation of complex organic compounds, for example. There are many mechanisms whereby *Trichoderma* species establish interactions with other organisms, highlighting competence and mycoparasitism and making them excellent biological control agents because of their antagonistic properties towards fungal pathogens [13–15] and their ability to colonize different habitat types and successfully establish themselves in recipient communities into which they have been introduced. These characteristics permit us to consider

Trichoderma spp. as potential invasive species and to recognize their utility in the study of biological invasions [16].

This work seeks to assess whether the composition of recipient communities and their phylogenetic relationship with the fungal invader *Trichoderma* cf. *harzianum* (BpT10a) can affect its success in colonization. This fungus was chosen as an invasive species for both its ability to colonize different microbial communities and the possibility of monitoring its colonization success through a specific SCAR molecular marker [16]. Thus, the main aim of this work was to validate the use of fungal communities as an experimental approach to Darwin's naturalization hypothesis in order to gain a better understanding of microbial invasion processes.

2. Material and methods

2.1. Fungal isolates

Eleven fungal isolates were used in this study for assembling the experimental communities; all of them are available at the fungal collection of the Microbial Ecology Lab., Faculty of Sciences, Universidad de Chile (Table 1). The fungal isolates were selected according to their phylogenetic relatedness with *T. cf. harzianum* BpT10a. The first community was composed of fungi closely related to *T. cf. harzianum*, hereafter referred to as a related community (RC). All fungal members constituting the RC microcosms belong to the order *Hypocreales*: *Trichoderma citrinoviride* (BpTP), *Trichoderma novaezelandiae* (BpT1a), *Trichoderma atroviride* (BpT10), *Beauveria bassiana* (MR-22), and *Fusarium redolens* (HR3). The second community was composed of fungi belonging to orders different from *Hypocreales*, hereafter referred to as an unrelated community (uRC). The fungal members that constituted the uRC microcosms belong to the order *Eurotiales*: *Penicillium canescens* (MR-13), *Aspergillus wentii* (MR-3), *Paecilomyces variotii* (MR-9), *Talaromyces amestolkiae* (MR-25); and to the order *Capnodiales*: *Cladosporium*

Table 1
Fungal isolates used in this study.

Species	Isolate	Origin/provenance	Role	Accession number
<i>Trichoderma citrinoviride</i>	BpTP	Port Consuelo, Chile ^a	RC member ^c	KC812351
<i>Trichoderma novaezelandiae</i>	BpT1a	Neltume, Chile ^a	RC member	KC812353
<i>Trichoderma atroviride</i>	BpT10	Port Fuy, Chile ^a	RC member	KC812348
<i>Beauveria bassiana</i>	MR-22	El Romeral, Chile ^b	RC member	KP963594
<i>Fusarium redolens</i>	HR3	El Romeral, Chile ^b	RC member	NA ^c
<i>Penicillium canescens</i>	MR-13	El Romeral, Chile ^b	uRC member ^d	KP963586
<i>Aspergillus wentii</i>	MR-3	El Romeral, Chile ^b	uRC member	KP963580
<i>Paecilomyces variotii</i>	MR-9	El Romeral, Chile ^b	uRC member	KP963583
<i>Talaromyces amestolkiae</i>	MR-25	El Romeral, Chile ^b	uRC member	KP963597
<i>Cladosporium cladosporioides</i>	MR-12	El Romeral, Chile ^b	uRC member	KP963585
<i>Trichoderma cf. harzianum</i>	BpT10a	Port Fuy, Chile ^a	Invader	KC812341

^a Isolates from the work by Castillo, Isolation and identification of strains of *Trichoderma* sp. natives of Chile. Evaluation of in vitro antagonism against *Botrytis* sp. Biologist Thesis, Universidad Católica de Valparaíso, Chile, 2009.

^b Isolates from the work by Rojas, Isolation and identification of semiarid soil fungi to construct experimental fungal communities, Molecular Biotechnologist Thesis, Universidad de Chile, Chile, 2013.

^c Related community member.

^d Unrelated community member.

^e NA: not available.

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