Colonizing success of saprotrophic and ectomycorrhizal basidiomycetes on islands

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Abstract: The biodiversity of saprotrophic and ectomycorrhizal basidiomycetous macrofungi growing on seven islands in central Japan were compared to examine colonizing success within the context of island biogeography theory. Two hypotheses were tested: that the number of the fungal species depends on island area and that the slope of the species-area curve for saprotrophic and ectomycorrhizal macrofungi differ in response to differences in their nutritional requirements. Data for the number of species that were identified based on sporocarps closely fit the conventional species-area curve. The slopes of the species-area curve for saprotrophic fungi (0.316) and ectomycorrhizal fungi (0.469) were similar to those reported for insects and birds, and plants on other archipelagos, respectively. In addition species-area curve data showed that ectomycorrhizal fungi colonized only islands > 630 m². While the species composition of saprotrophic fungi found on any pair of islands was positively correlated to the ratio of the areas of the island pair being compared (smaller/larger), no such relationship was observed for ectomycorrhizal fungi. Conversely similar ectomycorrhizal fungi, mostly those belonging to the genera Amanita, Inocybe, Boletellus and Russula, were found on pairs of islands with similar vegetation in the same geographic region. These results suggested that the colonizing success by ectomycorrhizal fungi is limited by host plant diversity, which is lower on smaller islands, instead of restricted immigration resulting from limited spore dispersal ability.

Key words: biodiversity, establishment, immigration, minimum area, species-area

Introduction
Basidiomycetous fungi include important saprotrophic decomposers of organic materials and ectomycorrhizal symbionts associated with plants (Leake et al. 2002). Biodiversity is an important criterion for evaluating ecosystems, and fungal species richness and composition in a given community is expected to increase with niche diversity (Dighton and Mason 1985, Frankland 1992). Fungal biodiversity is also likely to be affected by the immigration ability of fungi from adjacent communities and the differential colonizing success of different fungal species. Fungi may disperse by hyphal spreading or spores and propagation is affected by fecundity, while colonizing success is affected by niche availability and intra- and interspecific competition (Baker and Stebbins 1965).

In practice it is not always feasible to discriminate the influence of each factor affecting colonizing success. Mainland fungal communities frequently are surrounded by or close to other communities, further complicating clarification of the factors affecting colonization. However island communities are better suited for examining the factors affecting biodiversity for two reasons. First, islands support discrete communities that are geographically isolated from adjacent communities. These differences in area and topology are likely to affect biotic and abiotic conditions on the islands (MacArthur and Wilson 1967). Second, fungal immigration to islands is largely limited to spore dispersal because hyphal spreading is unlikely unless soil particles with hyphae attached are dispersed by violent storms. These two factors can be used to assess the relative contribution of immigration mode and establishment on the colonizing success of fungi on islands.

For any classification group the number of species inhabiting an island and the island area can be defined by the relationship: \[ \log S = z \log A + \log c, \]
where \( S \) is the number of species, \( A \) is the area, \( z \) and \( c \) are constants; this relationship also is referred to as the species-area curve (Arrhenius 1921, Connor and McCoy 1979). The equilibrium model of the island biogeography theory states that the number of species on any island can be represented as an equilibrium between a decrease in the rate of immigration of mainland species and an increase in the rate of extinction of resident species (MacArthur and Wilson 1967). It is expected that the number of resident species in classification groups showing high immigration rates and/or low extinction rates on any of the islands would change only slightly if a state of equilibrium existed between small and large islands. Therefore such situations would have the effect of reducing the influence of island area on the number of resident species and would be reflected by a decrease in the gradient of the \( z \) slope of the
species-area curve (MacArthur and Wilson 1967, Johnson and Simberloff 1974). However determining actual immigration and extinction rates and distinguishing between the two often is difficult because it requires assessments of species turnover (immigration and extinction) in the laboratory (Wildman 1987, 1992; Andrews et al. 1987) or in the field (Simberloff and Wilson 1969). Net immigration rate should reflect propagule mobility and dispersal ability (Terborgh 1973, Strong and Levin 1975, Peay et al. 2007), and net extinction rate should reflect establishment success or failure depending on niche availability and competition (Terborgh 1973, Blackburn and Duncan 2001, Brook et al. 2003).

Given these considerations, the species-area relationship curves of saprotrophic and ectomycorrhizal fungi could be used to infer their colonization success. Specifically, given the marked differences in the nutritional requirements of the two fungal groups, the establishment success of each group is expected to be different. As a consequence the slopes of the species-area curves for each group also will be different.

Although Andrews et al. (1987) and Wildman (1987, 1992) examined fungal colonization and species turnover in the laboratory, relatively few studies have applied island biogeography theory to studies of fungal colonization in the field, either in habitat islands (Strong and Levin 1975, Peay et al. 2007) or on oceanic islands (Tanesaka and Yoshida 2005). Studies have examined the biodiversity of basidiomycetous macrofungi of seven islands in central Japan (Tanesaka 2000, 2006). These preliminary studies showed that the number of species per island based on sporocarp identification data was better explained by the species-area curve than by the distance from the mainland community (Tanesaka and Yoshida 2005).

The present study aimed to elucidate differences in colonizing success of saprotrophic and ectomycorrhizal basidiomycetes by comparing species diversity on seven islands from an island biogeography perspective. Two hypotheses were tested: (i) the number of saprotrophic and ectomycorrhizal fungi species is positively related to island area and can be explained by conventional species-area curves; and (ii) the nutritional constraints of the two fungal groups will differentially affect establishment success, which will be reflected by different slopes (z) of species-area curves.

**MATERIALS AND METHODS**

*Study sites.*—Basidiomycetous macrofungi were surveyed on seven islands along the southwestern coast of the Kii Peninsula, central Japan.

Peninsula in central Japan (Fig. 1). Four islands, Komarujima, Hatakejima, Maruyama and Motoshima, are located in Tanabe Bay, and the other three islands, Myogajima, Tsuyajima and Kii-osihima, are located in the Kumano-nada region. The smallest island (Komarujima) had an area of 550 m² and the largest island (Kii-osihima) had an area of 9680 000 m² (Table I). The distance between a mainland community and each island was 250–2000 m, and the distance and log-transformed area of each island were not significantly correlated (r = 0.457, P = 0.303). The distribution of the islands and independence of island area and distance to the mainland meant that the species-area relationship could be tested against island area (m²) (MacArthur and Wilson 1967). The mean annual temperature in both regions is approximately 17 C, and the mean annual precipitation is approximately 1800 mm in Tanabe Bay and 2600 mm in Kumano-nada. In both regions the mainland vegetation is dominated by warm-temperate, evergreen broadleaf trees, such as Castanopsis cuspidata var. sieboldii, Quercus phillyraeoides, Myrica rubra and Daphniphyllum macropodum, with the tree cover and species composition on each island depending on island area. Dense Castanopsis stands are present on all islands in the Kumano-nada region (Enomoto and Kariyama 2000) but are less common on Motoshima and are absent from the three smallest islands in the Tanabe Bay region, which are dominated by Q. phillyraeoides, Eurya emarginata or D. tejsmannii; this vegetation is typical of the coastal wind-swept stands in this area (Yamashiro 2002, Yamato et al. 2007).

*Survey and data analysis.*—Sporocarps of macrofungi were recorded during field surveys of suitable habitat; marginal cliffs and dense bush on Kii-osihima and Tsuyajima were not surveyed. Surveys were conducted on foot, after precipitation, mainly in Jun, Jul, Sep and Oct over a 5 y period (1998–2002) on Kii-osihima and for 3 y (2001–2003) on the other six islands (Tanesaka 2006). A total of 189 basidiomycete species belonging to 37 families consisting of 119 saprotrophic and 70 ectomycorrhizal fungi were recorded (Table I). Most of the specimens were deposited at the herbarium of the Kii-osihima Experimental Station, Field Science Education and Research Center, Kyoto University.
It is possible that anthropogenic activities might have resulted in the introduction of some fungal species to the islands, particularly on the largest of Kii-Oshima, which has approximately 2000 inhabitants, the island of Tsuyajima, which was used for palm tree (Arecaceae) cultivation (1950s–1960s), and Hatakejima, which was used for mulberry (Morus bombycis) cultivation until the 19th century. However, it is not likely that the extent of such activities would have been sufficient to affect the overall diversity of the fungal species observed in this study, even if any introduced species could be distinguished from the species that reached the islands through natural means. Consequently, all observed species were included in the present study.

Statistics were calculated with Statistica 6 software (StatSoft Inc.), and a species-area curve for each island was fitted to the following linear regression:

\[
\log S = az + bx + c
\]

where \(S\) is the number of observed species, \(A\) is the area of the island in \(m^2\), \(z\) and \(c\) are derived constants describing slope (\(z\)) and \(y\) intercept of the regression (\(c\)) (Arrhenius 1921). To avoid obtaining a null regression (i.e. when no species could be found) the number of species of mycorrhizal fungi (\(S + 1\)) was regressed against island area.

The similarity of the species composition between pairs of islands was calculated with Ochiai’s similarity index (So):

\[
So = c/√(a/b)
\]

where \(a\) and \(b\) are the numbers of observed species on the two islands and \(c\) is the number of species they have in common (Ochiai 1957). This index gives values ranging from 0 (no similarity) and 1 (complete similarity). So and the ratio of the area between island pairs (smaller/larger) were arcsine-transformed (\(\sin^{-1}(x)\)) to correct for heteroscedasticity before correlation and non-parametric analysis (Sokal and Rohlf 1981).

**RESULTS**

*Species-area relationship.*—For both saprotrophic and ectomycorrhizal fungi the number of species was correlated with island area but the slopes (\(z\)) of the species-area curves for the two groups were different (Fig. 2: saprotrophic, \(z = 0.316, F = 26.8, P = 0.0035\); ectomycorrhizal, \(z = 0.469, F = 51.4, P = 0.00082\)). The regression for saprotrophic fungi implies that at least one species would occur on even the smallest island. Conversely, few ectomycorrhizal fungi had colonized small islands and no mycorrhizal fungi were found on the two smallest islands, Komarujima and Maruyama. Furthermore, regression analysis revealed that a minimum area of 630 \(m^2\) (at \(x\) intercept of 2.78) would be required for successful colonization by an ectomycorrhizal species. No significant relationship was observed between log regressions of the number of species and the approximate direct distance from a mainland community for either saprotrophic (\(F = 0.108, P = 0.75\)) or ectomycorrhizal (\(F = 0.669, P = 0.45\)) fungi.

*Similarities in species composition.*—Ochiai’s similarity index between islands ranged from 0.122 (Komarujima/Kii-Oshima) to 0.460 (Myogajima/Tsuyajima) for saprotrophic fungi and from 0.120 (Hatakejima/Tsuyajima) to 0.538 (Tsuyajima/Kii-Oshima) for ectomycorrhizal fungi (Table II); Komarujima and Maruyama were excluded from the ectomycorrhizal analysis because no ectomycorrhizal fungi were observed on these islands. The overall So for saprotrophic fungi was greater than the So for ectomycorrhizal fungi when respective island pairs were compared (Wilcoxon rank sum; \(N = 10, T = 4, P = 0.0166\)). Furthermore, compared to ectomycorrhizal fungi, higher So values were obtained for saprotrophic fungi between island pairs from different regions (\(N = 6, T = 0, P = 0.028\)) but not between island pairs in the same region (\(N = 4, T = 4, P = 0.715\)). Four saprotrophic species (*Marasmiellus candidus*, *Crepidotus mollis*, *Microporus affinis* and *Phellinus gilvus*) grew on six of the seven islands, and
Polyporus arcularius grew on all seven islands. These common species are responsible for the relatively high So and the shallow z slope for saprotrophic fungi. Conversely most ectomycorrhizal fungi were found on three or fewer islands and only Russula castanopsidis grew on five islands.

A positive correlation was observed between So and the ratio of the area of the respective island pairs (smaller/larger) for saprotrophic fungi ($r = 0.714, P = 0.00028$) but not for the ectomycorrhizal fungi (Fig. 3). So for ectomycorrhizal fungi was higher between island pairs in the same region than between island pairs in different regions (Mann-Whitney test; $U = 0, P = 0.010$), but no such grouping was observed for saprotrophic fungi ($U = 34, P = 0.155$). The relatively high So obtained for ectomycorrhizal fungi within regions was attributed to the occurrence of common species, such as Amanita ceciliae, Inocybe nodulosospora, Boletellus emodensis, R. castanopsidis, R. cyanoxantha, R. liliacea and R. sanguinea, which grow throughout the Kumano-nada region. In the Tanabe Bay region R. castanopsidis and A. pantherina grew only on Motoshima and Hatakejima.

**DISCUSSION**

Sporocarp formation in saprotrophic and ectomycorrhizal basidiomycetes usually fluctuates both annually and seasonally, depending on precipitation. In ectomycorrhizal communities molecular identification techniques have revealed that sporocarps and belowground ectomycorrhizal communities often are poorly correlated and many belowground species do not form sporocarps (Dahlberg et al. 1997, Zhou and Hogetsu 2002, Dickie et al. 2009). Consequently this non-formation of sporocarps may result in an underestimation of saprotrophic and ectomycorrhizal biodiversity based on sporocarp observation data alone. Nevertheless, assuming fruiting patterns are similar across saprotrophic and mycorrhizal fungi present on the islands, the relative

<table>
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<th>Islands</th>
<th>Fungi</th>
<th>Maruyama</th>
<th>Hatakejima</th>
<th>Motoshima</th>
<th>Myogajima</th>
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<tr>
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*a Similarity of the species composition was represented by Ochiai’s index, So. See text.*

*b Numerals in parentheses indicate the number of species found in common on island pairs.*

**Fig. 2.** Species-area curves for (a) saprotrophic and (b) ectomycorrhizal basidiomycetes growing on seven islands along the southwestern coast of the Kii Peninsula. Species number and area were log transformed and plotted. Symbols represent islands in the Tanabe Bay (open circles) and Kumano-nada regions (solid circles).
diversity of the two groups should permit comparisons of general aspects of relative colonizing success on island ecosystems.

Species-area relationship.—The first hypothesis, that the number of saprotrophic and ectomycorrhizal fungal species can be explained by a conventional species-area curve, and that this relationship is independent of the distance from mainland communities, was supported by the findings of this study. Indeed the diversity of both fungal groups closely fitted a typical species-area curve, although the z slope obtained for saprotrophic fungi was shallower than that obtained for ectomycorrhizal fungi. Equilibrium theory predicts that high immigration rates and/or low extinction rates would have the effect of decreasing the gradient of a species-area curve (MacArthur and Wilson 1967, Johnson and Simberloff 1974). Studies on island archipelagos (e.g. California Channel Islands or West Indies) found that there is a tendency for the slope (z) of the species-area curve to be relatively shallow (usually 0.2–0.3) in mobile taxonomic groups, such as insects and birds, compared to less mobile taxa, such as plants (usually > 0.4) (Connor and McCoy 1979). The observations reported here suggested that the difference in the slopes of the species-area curves for saprotrophic and ectomycorrhizal fungi might be attributable to differences in spore-dispersal ability. Basidiomycetes produce lightweight spores in great numbers. Such spores have been found at high altitudes over land and ocean masses (Stackman et al. 1923, Pady and Kapica 1955, James et al. 1999) and may be dispersed over long distances (Burnett 1976). Peay et al. (2007) found that spore dispersal by ectomycorrhizal fungi in habitat islands was more than 1 km. Their suggestion was based on species richness observations and the species-area curves determined for patchy “tree islands” where niche diversity was expected to be low (Peay et al. 2007). The present study also found that species richness of saprotrophic and ectomycorrhizal fungi, particularly communities on large islands located more than 1 km from the mainland community, was not related to the distance from the mainland (250–2000 m).

Most of the existing data on long distance spore dispersal in basidiomycetes has been inferred from studies on genetic variation in natural populations of saprotrophic fungi (Boisselier-Dubayle et al. 1966, Huss 1966, Saville et al. 1996, Xu et al. 1977, James et al. 1999). However there is no evidence to suggest that saprotrophic and ectomycorrhizal fungi spores differ with respect to dispersal ability. Taken together the evidence suggests that the marked difference in the slope (z) of species-area curves observed between the two trophic groups cannot be attributed to differences in spore-dispersal ability.

The second hypothesis, that differences in the nutritional constraints encountered by the two fungal groups will affect their establishment success differently and that this will be reflected in the slopes (z) of their respective species-area curves, also was supported. We note that the slope (z) of the species-area curve obtained for ectomycorrhizal fungi (0.469) was similar to that obtained for plants from other archipelagos as well as the slope calculated for seed-producing plants (0.437) on Kii-oshima (Enomoto and Kariyama 2000), Motoshima (Yamashiro 2002), and Hatakejima and Komarujima (Yamato et al. 2007) (S = 0.437A − 0.083; F = 88.1, P = 0.011: the species-area curve was calculated in this study). This finding is consistent with studies that reported that ectomycorrhizal fungal species richness is correlated with ectomycorrhizal plant species richness (Erland and Taylor 2002, Dickie 2007, Ishida et al. 2007).

Species composition.—Because saprotrophic and ectomycorrhizal fungi have different nutritional requirements the available habitat and species composition...
of vegetation on islands is likely to affect establishment success. Several of the saprotrophic fungi were found commonly on the smaller islands, whereas few ectomycorrhizal species were widespread. The most common saprotrophic species were wood-decomposing fungi that formed numerous small sporocarps on wood surfaces rather than on leaf litter (Tanesaka 2006), suggesting that they produce large numbers of spores on a given amount of substrate. High ligninolytic activity, which is a characteristic of primary colonizers (Reynier 1977, 1978, Shortle and Cowling 1978; Mercer 1982; Tanesaka et al. 1993), also may be an important characteristic affecting the ability of fungi to successfully colonize small islands. Ectomycorrhizal fungi belonging to the genera Amanita, Inocybe, Boletellus and Russula were common on islands with well established plant communities, especially in the Kumano-nada region. Higher So values were obtained for ectomycorrhizal fungi from pairs of islands with similar plant communities, within regions, compared to pairs of islands with different plant communities in different regions. Conversely the So for saprotrophic fungi was related to the ratio of the area between paired islands but not to the island region. These results also support the proposition that different nutritional requirements constrain establishment success; that is that ectomycorrhizal fungi require the presence of specific symbionts to occupy a niche whereas saprotrophic fungi may be less demanding with regards to plant substrates (e.g. wood- and litter-decomposers or white- and brown-rot fungi).

Taken together these results suggest that the colonizing success of ectomycorrhizal fungi is more strongly influenced and restricted by host plant diversity on a given island (Dickie 2007, Ishida et al. 2007) than by spore production, dispersal or germination. Ectomycorrhizal fungi also may be more sensitive to other abiotic and biotic factors (Erland and Taylor 2002), including interactions between ectomycorrhizal and saprotrophic fungi (Leake et al. 2002). Conversely the colonizing success of saprotrophic fungi appears to depend solely on island area, which physically restricts the colonizing success of fungi through offering a smaller target for spores being transported by wind or having less available substrate that is suitable for growth should the spores land.

Significance of island communities.—The present study compared the biodiversity of saprotrophic and ectomycorrhizal fungi and provided evidence of their differential colonizing success and ability to form isolated communities. Additional evidence from molecular identification of sporocarps, belowground biomass or biomass within substrate would further clarify the characteristics of fungal colonization on islands. Such island biogeography studies also would provide information that could be applied to practical ecosystem conservation (Simberloff and Abele 1976, Blackburn and Duncan 2001, Brook et al. 2003, Wardle and Zackrisson 2005). Few ectomycorrhizal fungi were observed to colonize small islands, and the species-area curves derived in this study imply that a minimum area of suitable habitat is required for successful colonization by ectomycorrhizal fungi. Heatwole (1975) proposed that the x intercept of a species-area curve could be used to infer the minimum area necessary to support a breeding population of a particular taxon.

Conversely Dickie et al. (2009) reported that habitat islands of oak (oak savanna) that had been fragmented by frequent fire supported a unique ectomycorrhizal fungi community that included savanna-specific species that were distinct from those associated with a distant forest community. Their findings suggested that the oak savanna may play a role in conserving both fungal species and the forest community (Dickie et al. 2009). These comparative studies of island communities support those of Simberloff and Abele (1976) and Connor and McCoy (1979) who proposed that conservation areas should be designated with specific goals in mind and that such areas should satisfy the particular habitat requirements for the species to be conserved.

Acknowledgments

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Figure 1: A strong species-area relationship for basidiomycetous macrofungi observed on seven islands along southwestern coast of Kii Peninsula. Nankiscibutsu 48:115–121. (in Japanese).


