Oecologia (2009) 160:335–342
DOI 10.1007/s00442-009-1295-z

COMMUNITY ECOLOGY - ORIGINAL PAPER

Relative importance of tree genetics and microhabitat on macrofungal biodiversity on coarse woody debris

Robert Charles Barbour · Michelle J. Storer · Bradley M. Potts

Received: 14 July 2008 / Accepted: 20 January 2009 / Published online: 17 February 2009

Abstract Understanding the contribution of genetic variation within foundation species to community-level pattern and diversity represents the cornerstone of the developing field of community genetics. We assessed the relative importance of intraspecific genetic variation, spatial variation within a forest and microhabitat variation on a macrofungal decay community developing on logs of the Australian forest tree, *Eucalyptus globulus*. Uniform logs were harvested from trees from eight geographic races of *E. globulus* growing in a 15-year-old genetic trial. Logs were placed as designed grids within a native *E. globulus* forest and after 3 years of natural colonisation the presence of 62 macrofungal taxa were recorded from eight microhabitats on each log. The key factor found to drive macrofungal distribution and biodiversity on structurally uniform coarse woody debris was log-microhabitat, explaining 42% of the total variation in richness. Differences between log-microhabitats appeared to be due to variation in aspect, substrate (bark vs wood) and area/time of exposure to colonisation. This findings demonstrates the importance of considering fine-scale (within substrate) variation in the conservation and management of macrofungal biodiversity, an area that has received little previous attention. While a number of recent studies have demonstrated that the genetics of foundation tree species can influence dependent communities, this was not found to be the case for the early log decay community associated with *E. globulus*. Despite genetic variation in wood and bark properties existing within this species, there was no significant effect of tree genetics on macrofungal community richness or composition. This finding highlights the variation that may exist among guilds of organisms in their response to genetic variation within foundation species, an important consideration in a promising new area of research.

Keywords Community genetics · Distal community phenotype · Microhabitat · Macrofungi · Coarse woody debris (CWD)

Communicated by Jeremy Burdon.

R. C. Barbour (✉) · M. J. Storer · B. M. Potts
School of Plant Science and Cooperative Research Centre for Forestry, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia
e-mail: rbarbour@utas.edu.au; Robert.Barbour@utas.edu.au

Introduction

The developing field of community genetics promises new insights into the genetic basis of species interactions and the evolutionary consequences of interactions at the community level (Johnson and Stinchcombe 2007; Wade 2007; Whitham et al. 2006, 2008). Studies in this field have demonstrated that the genetics of foundation species, such as forest trees, can act to structure associated communities of micro-organisms, fungi, arthropods and vertebrates (reviewed in Whitham et al. 2006). This work has typically been focused on the responses to genetic variation within hybrid systems or selected genotypes of individual species, in genera such as *Eucalyptus*, *Populus*, *Oenothera, Quercus, Salix* and *Solidago* (Whitham et al. 2006). Such heritable community phenotypes have been readily detected in communities that are directly associated with the living tree, i.e. herbivores, pathogens and commensalates of living foliage. Increasingly, however, there is evidence that these genetic effects may extend to more distal communities (LeRoy et al. 2006; Schweitzer et al. 2008), and even

ecosystem processes (Madritch et al. 2006; Schweitzer et al. 2004; Silfver et al. 2007).

Despite these findings, little work has assessed the community level consequences of natural patterns of intraspecific genetic variation, typical of foundation species with broad distributions. In forest trees, for example, decades of research have demonstrated that substantial variation in molecular and quantitative genetic traits is common at the landscape levels of provenance or race (Eldridge et al. 1993; White et al. 2007). The division of the natural distribution of species into geographic races provides a genetic framework from which to assess the role of natural patterns of intra-specific genetic variation in structuring dependent communities. Understanding the relative importance of such genetic variation is a key step in placing community genetics into an ecologically and evolutionarily significant context (Johnson and Stinchcombe 2007; Thompson 2005).

Macrofungal decay communities represent a keystone guild within forest ecosystems. As the primary decomposers of plant material, including coarse woody debris, fungi are implicit in nutrient cycling (Dighton et al. 2005; Dix and Webster 1995), and play vital roles in the diversity of invertebrate and microbial communities (Wheeler and Blackwell 1984). In addition, some of the strongest coevolutionary interactions found to exist (i.e. at the individual gene level) have involved fungal pathogens and mutualists with their host plants (Ellis et al. 2008; Martin et al. 2008). Indeed, fungal endophyte (Bailey et al. 2005) and mycorrhizal (Gehring et al. 2006) communities have both been found to be strongly driven by genetic (hybrid cross-type) variation within common environment field trials, as have specific foliage pathogens in response to intraspecific genetic variation (in *E. globulus* for example; see Milgate et al. 2005). However, no studies have used common environment field trials to assess the relative importance of intraspecific genetic variation on macrofungi at the community level, or attempted to disentangle the autocorrelated biotic and abiotic environmental factors that drive their distributions (i.e. Heilmann-Clausen and Christensen 2003, 2005; Jonsell et al. 1998; Rubino and McCarthy 2003).

Eucalyptus globulus is a widely distributed foundation tree species that dominates many native forest communities across south-eastern Australia (Fig. 1). A large amount of quantitative genetic variation exists within the species in nature (Jordan et al. 1993). This variation is spatially structured and has been summarised by partitioning the species into 13 geographic races (Dutkowski and Potts 1999). A number of traits that vary amongst these races have the potential to influence macrofungal wood decay communities (Dighton et al. 2005; Dix and Webster 1995; Schmit 2005; Yu et al. 2003). These include wood chemistry (Poke et al. 2006), wood density (Dutkowski and Potts 1999; Hamilton et al. 2007; McDonald et al. 1997) and bark thickness (Hamilton et al. 2007). Rather than displaying consistent geographic trends in their distribution, these traits tend to be idiosyncratic to each race (Dutkowski and Potts 1999; Hamilton et al. 2007), suggesting strong selection in response to the local environments (Steane et al. 2006). While limited assessment of their role in driving fungal community assemblages has been conducted in *E. globulus*, substantial racial variation has been identified in the amount of heart-wood fungal decay within living trees, ranging from 7 to 26% of the trunk cross-sectional area (same trees used in current study; Hamilton et al. 2007).

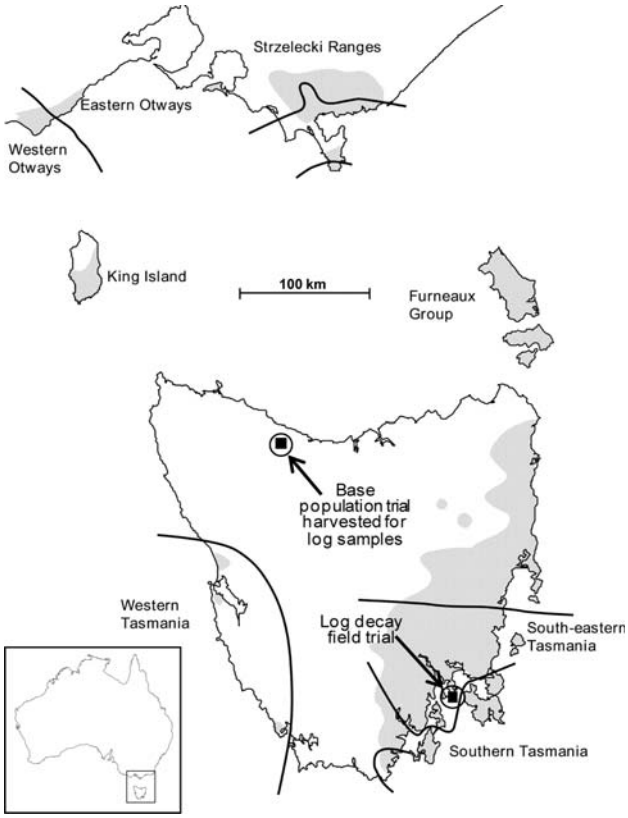

Fig. 1 The natural distribution of *Eucalyptus globulus* across south-east Australia (*grey shading* G.J. Jordan) and the delineated racial classifications of the species (*black lines* based on Dutkowski and Potts 1999). Only races assessed in the current work have been labelled. *Black squares* indicate the locations of *E. globulus* field trials used in the study

Based on these previous findings, the current study aimed to address two hypotheses, firstly, that an influence of tree-genetic variation in wood properties would be detectable at the macrofungal community level, and, secondly, that these tree-genetic effects would be greater in magnitude than local environmental effects. These hypotheses were tested by assessing the diversity and composition of a macrofungal decay community that had developed

following colonisation of logs in a native *E. globulus* forest. These even-aged logs were cut from trees of known pedigree grown in a common environment field trial, and their translocation into the native forest allowed the importance of tree genetics to be assessed relative to spatial variation within the forest and microhabitat (aspect and substrate) variation across each decaying log.

Materials and methods

Genetic material and sampling

The wood-decay field experiment was established from logs sourced from a 15-year-old *E. globulus* base population progeny trial at West Ridgley, northern Tasmania (Fig. 1; see Dutkowski and Potts 1999 for details). This base population trial was established using open-pollinated seed collections (families) from 451 trees sampled across the known natural distribution of *E. globulus* (Fig. 1). These families were arranged in a randomised incomplete block design comprising five replicates and 23 incomplete blocks (see Dutkowski and Potts 1999). Twenty trees from eight races of *E. globulus* were sampled as part of a larger study (Hamilton et al. 2007). The eight races encompassed the broad geographic range of *E. globulus* (Fig. 1) and documented diversity in wood traits that were expected to influence decay fungi (Hamilton et al. 2007; McDonald et al. 1997; Poke et al. 2006). Trees were selected for felling based on their good health and relative growth rates, as well as providing an even distribution across replicates and incomplete blocks of the trial. The logs were harvested from the main stem, just below the major canopy branches at approximately three-quarters of the tree height (i.e. ≈20 m). This sampling high up the tree trunk was conducted to minimise the racial genetic effects of heart wood decay (Hamilton et al. 2007). All logs were cut to 40 cm in length, and were between 7 and 21 cm in diameter over bark.

Wood-decay experiment

We established a wood-decay experiment in September 2004 on a 25° south-facing slope in a dry sclerophyll, native eucalypt forest dominated by *E. globulus* in southern Tasmania (Fig. 1). The experiment was established across two areas within the forest, with each area receiving 80 logs arranged as ten rows and eight columns, with 4 m of separation between each log. Logs were arranged in a randomised block design with rows as blocks, so that each race was represented once in each row. All logs were randomly orientated with their cut ends facing north and south, following the gradient of the slope.

Community assessment

For the purposes of the study, macrofungi were defined as any fungus with a fruit body or spore-bearing surface greater than 1 mm in breadth. All fungal phyla including slime moulds were included in the study. Fungi were identified to species or genus where possible, or assigned to morphotype groups where identification was not possible. If fungi could not be classified in the field, small samples were taken for later microscopic analysis. A specimen collection has been maintained at the School of Plant Science, University of Tasmania. Morphotype groups were based on macro-morphological features such as colour (e.g. Salmon corticioid), and where possible on spore morphology. Basidiomycetes were identified to the genus level using a key developed by Ratkowsky and Gates (2002), and Ascomycetes using keys developed by Breitenbach and Kränzlin (1984). Species identifications, where possible, were achieved with the aid of Fuhrer (2005). For simplification, all fungal species, and genus and morphotype groupings and the single lichen species differentiated, are hereafter referred to as taxa.

The decay community on each log was assessed based on the presence/absence of 62 taxa within each of eight predefined microhabitats on each of the 160 logs. The microhabitats were a visual division of the log into five sections consisting of the two cut ends, the top and the two sides. The top and sides of the log were then divided into microhabitats that consisted of bark and that where the bark had peeled off to expose the underlying wood. Presence/absence data was accumulated from assessments undertaken in autumn (April), winter (June) and spring (November) of 2007. At this time, the logs fell into decay class 2 (wood rather hard, a knife penetrating <1 cm into wood, and bark starting to break up), as defined by Heilmann-Clausen and Christensen (2003), and had been in the forest and available for colonisation for ca. 3 years.

Statistical analysis

We calculated the richness and compositional variation within the macrofungal community for each microhabitat. The compositional variation was summarised by scores on axes derived from a two dimensional (stress = 0.28), non-metric multidimensional scaling (nMDS) ordination of the Bray–Curtis dissimilarity matrix amongst the 1,280 samples (representing 160 logs). This analysis was undertaken with PRIMER (version 6.1.9; Roborough, Plymouth, UK). Once the richness and compositional summaries had been calculated, a two-strata (between logs and within logs), linear mixed model was fitted with REML estimators to microhabitat level data on decay community richness and composition with PROC MIXED of SAS (version 9.1;

Cary, NC, USA). At the log-level, we tested the fixed effects of race of origin, area in the forest, the random effects of row and column within areas and tree within race, and the covariate of log diameter; at the within log level, we tested the fixed effects of microhabitat and the race by microhabitat interaction. To visualise the relative magnitude of these effects, we then fitted a model with all effects treated as random and estimated the proportion of variation attributed to each factor. The partition of the compositional variation was achieved by summing variance components across both nMDS axes for each factor. Finally, non-parametric Kruskal–Wallis tests were conducted using Proc NPAR1WAY of SAS to test the effect of race and microhabitat on individual taxa. The non-parametric analyses for race were conducted on log-level presence/absence data.

Results

Community richness

In total, 62 fungal taxa were identified across the three sampling periods of the study. The richness of this community was not found to be significantly affected by tree race ($F_{7,118} = 1.5$, $P = 0.17$ NS), area ($F_{1,14} = 0.5$, $P = 0.51$ NS), row within area ($Z = 1.0$, $P = 0.16$ NS), column within area ($Z = 1.3$, $P = 0.09$ NS), the covariate of log diameter ($F_{1,971} = 2.8$, $P = 0.09$ NS) nor the race by microhabitat interaction ($F_{49,971} = 0.8$, $P = 0.86$ NS). Tree within race (i.e. variation between logs of the same race; $Z = 4.5$, $P < 0.001$) was found to be significant, representing the general log-to-log variation that includes both tree genetic and environmental effects, and explained 10% of the total variation in richness. The effect of microhabitat, however, was found to be substantial ($F_{7,971} = 127.4$, $P < 0.001$), explaining 42% of the total variation in taxa richness. This effect was mainly due to the low richness on the more recently exposed wood surfaces compared to the bark surfaces, as well as the greater richness on the south-facing cut end of the logs compared to the north-facing end (Fig. 2).

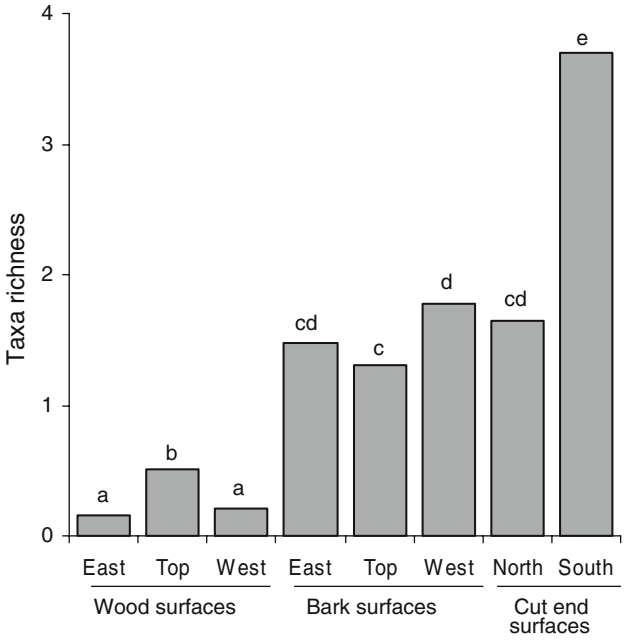

Fig. 2 The effect of log-microhabitat on the richness of a macrofungal community within a common environment wood-decay trial of *Eucalyptus globulus*

Community composition

The partitioning of the compositional variation along the two nMDS axes demonstrated the same patterns of variation to those for richness. The effects of race (axis 1, $F_{7,118} = 0.8$, $P = 0.62$ NS; axis 2, $F_{7,118} = 1.7$, $P = 0.13$ NS), area (axis 1, $F_{1,14} = 0.3$, $P = 0.60$ NS; axis 2, $F_{1,14} = 0.3$, $P = 0.61$ NS), row within area (axis 1, $Z = 0.2$, $P = 0.42$ NS; axis 2, $Z = 0.0$ NS), column within area (axis 1, $Z = 1.0$, $P = 0.16$ NS; axis 2, $Z = 0.0$ NS), the covariate of log diameter (axis 1, $F_{1,971} = 1.9$, $P = 0.17$ NS; axis 2, $F_{1,971} = 1.9$, $P = 0.17$ NS) and the race by microhabitat interaction (axis 1, $F_{49,971} = 0.9$, $P = 0.58$ NS; axis 2, $F_{49,971} = 0.8$, $P = 0.84$ NS) were all non-significant. Tree within race (axis 1, $Z = 4.4$, $P < 0.001$; axis 2, $Z = 3.8$, $P < 0.001$) and microhabitat (axis 1, $F_{7,971} = 45.5$, $P < 0.001$; axis 2, $F_{7,971} = 46.8$, $P < 0.001$) were again significant. Tree within race explained 11% and microhabitat explained 21% of the total compositional variation. Plotting of the microhabitat least-square means in the nMDS ordination space (Fig. 3) summarised the significant compositional differences which occurred between the decay communities on the various microhabitats. The first axis effectively separated the community on the more recently exposed, de-pauperate wood surface microhabitats from that on the bark and cut end substrates, while the second axis describes the composition differences associated with the decay communities on the log cut ends and bark microhabitats.

Responses of individual taxa

Following Bonferroni adjustment for multiple comparisons (adjusted significance threshold, $P < 0.00081$; Snedecor and Cochrane 1980), the non-parametric Kruskal–Wallis tests found the presence of no individual taxa to be significantly affected by race. In contrast, at this adjusted significance level, 21 taxa displayed a significant response to microhabitat variation within logs. Thirteen of these taxa were clearly more common on the south cut end of the logs

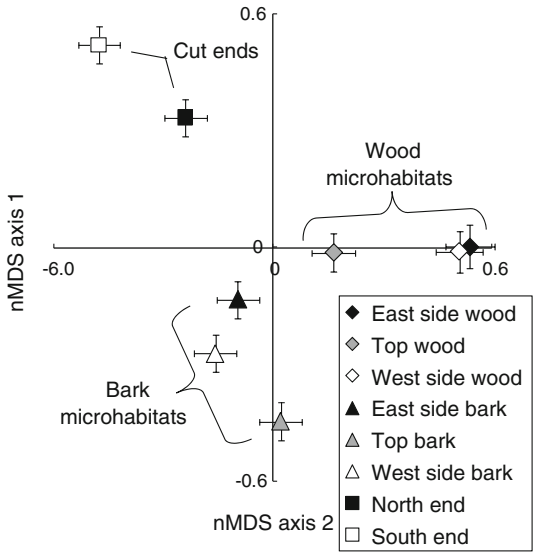

Fig. 3 Two dimensional nMDS ordination summarising the effects of log-microhabitat on the composition of a macrofungal community within a common environment wood-decay trial of *Eucalyptus globulus*. The mean values (±SE) for each microhabitat are shown

(e.g. Fig. 4e, *Peniophora incarnata* (Pers.) P. Karst.), while three showed preference to the bark (e.g. Fig. 4c, *Melanotus horizontalis* (Bull.) P. D. Orton), two for the top side of the bark surfaces (e.g. Fig. 4g, *Mycena piringa* Grgur.), two for both log ends (e.g. Fig. 4b, Ascomycete sp. 'black cups'), and one that was less frequent on the newly exposed surface wood (Fig. 4d, *Annulohypoxylon bovei* var. *microsporum* (J. H. Mill.) Y. M. Ju, J. D. Rogers and H. M. Hsieh).

Discussion

Despite significant genetically-based differences among the *E. globulus* races studied, for wood and bark traits (Dutkowski and Potts 1999; Hamilton et al. 2007; McDonald et al. 1997; Poke et al. 2006), susceptibility of living trees to heart-wood decay (Hamilton et al. 2007) and variation in canopy (Barbour et al. 2009), bark (Barbour et al., submitted) and leaf litter (Barbour et al., submitted) communities in common environment field trials, we were unable to detect a statistically significant tree genetic (race) effect on macrofungal community richness or composition.

In other plant genera, variation associated with different hybrid cross-types and different genotypes of individual species has also been found to affect communities associated with living foliage (i.e. Dungey et al. 2000; Johnson and Agrawal 2005; Wimp et al. 2005), decaying foliage in streams (LeRoy et al. 2006), soil (Schweitzer et al. 2008) and internal plant tissue (Bailey et al. 2005). These findings demonstrate that heritable community phenotypes of foundation species can exist across a diverse range of guilds, regardless of whether they are proximal or distal to the living tree. However, given the lack of statistical evidence for tree genetic effects in the current work, the broad range in environmental variation that exists across the natural distribution of *E. globulus* (Jordan et al. 2000), and the sensitivity of this guild to environmental rather than genetic factors, it appears unlikely that the macrofungal guild will contribute to the heritable community phenotype of *E. globulus*.

Nevertheless, while significant decomposition of the logs had occurred in the current work, 3 years for such coarse woody debris represents an early stage in the entire decomposition process, particularly in the dryer conditions of the site assessed (Dighton et al. 2005; Lindhe et al. 2004). Consequently, we cannot exclude the possibility that the influence of tree genetics may become stronger as the decay process progresses (unpublished data associated with LeRoy et al. 2006), nor that tree genetics may affect decaying log communities in other ways. Tree genetics may affect the type, size or temporal availability of coarse woody debris in the forest. In *E. globulus*, for example, genetic variation in tree architecture, such as the form and extent of forking in the main stem (Lopez et al. 2002), would be expected to affect the senescence of lower limbs during stand development and the availability of coarse woody debris for fungal colonisation. In addition, size and shape variables such as the number of forks within a log have been shown to have significant affects on fungal community richness (Heilmann-Clausen and Christensen 2003). Genetic variation for tree mortality in response to stand development has also been documented for this species (Chambers et al. 1996), providing another example of potential genetic affects on the availability of coarse woody debris.

While there was significant variation between logs in our experiment (i.e. the tree within race effect), which may be due to tree genetic or environmental causes, the main factor found to be affecting the macrofungal community was expressed at the within-log level (i.e. the microhabitat effect). Significant variation in community richness and composition was seen between the bark and the habitat created where the bark had peeled off to expose the underlying wood. The low richness of the community on the more recently exposed wood is likely to reflect the smaller surface area of these microhabitats and/or differences in the time that these microhabitats had been available for colonisation (Dighton et al. 2005; Heilmann-Clausen and Christensen 2003, 2005). The difference seen between the north and south cut ends of the logs, however, directly reflects a marked aspect effect, with the richer community seen on the wetter more shaded south end (Dix and Webster 1995; Jonsell et al. 1998). Whether this degree of community

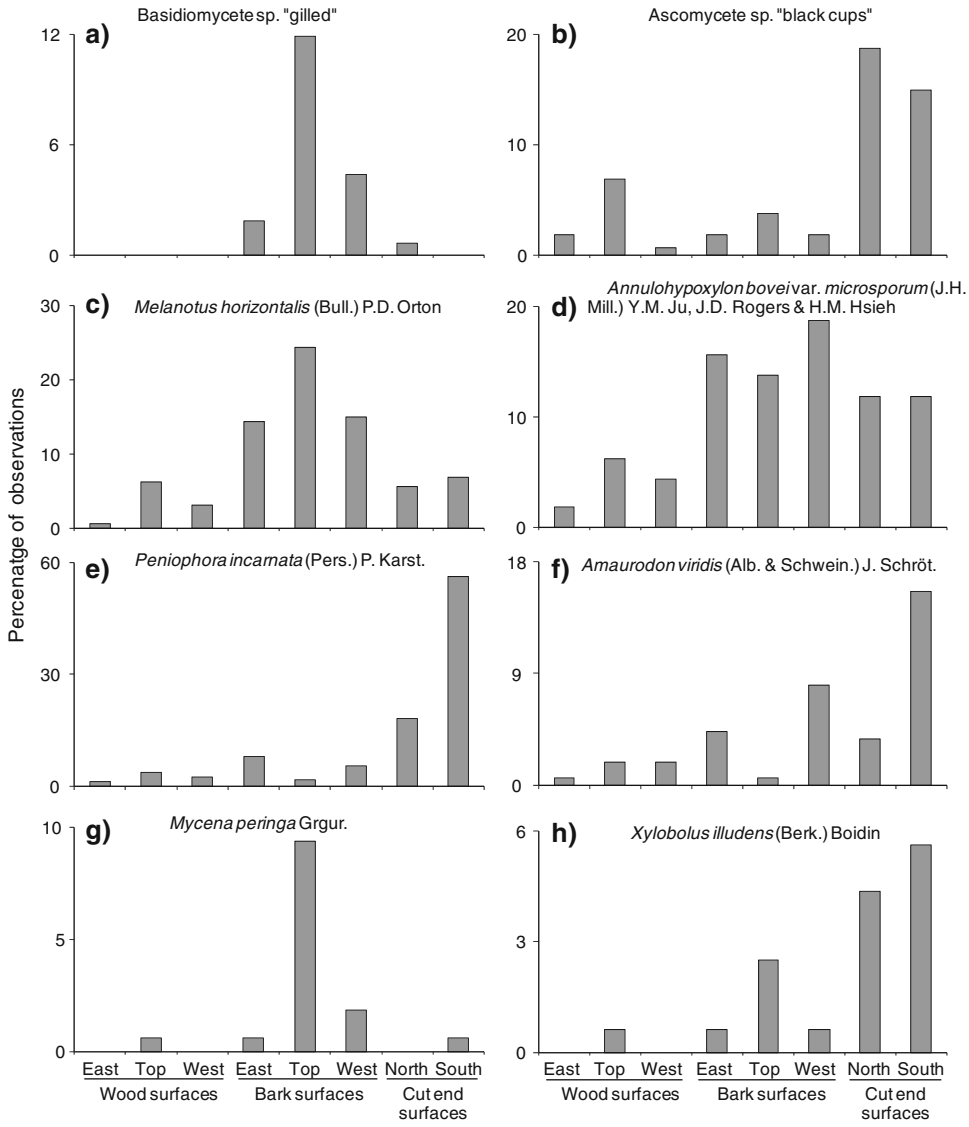

Fig. 4 Responses of individual macrofungal taxa to variation in log-microhabitat within a common environment wood-decay trial containing logs of *Eucalyptus globulus*. The eight taxa presented were all found to display significant variation across microhabitats, as tested with non-parametric Kruskal–Wallis tests. The data show the percentage of times ($n = 160$) the taxa was recorded in the microhabitat

partitioning would be seen in a wet eucalypt forest, where moister availability is less limiting, is still to be determined. In a similar study to the current work, assessing plant genetic (hybrid cross-type) and environmental (moisture and site-to-site) influences on ectomycorrhizal and arbuscular mycorrhizal associations in *Populus*, Gehring et al. (2006) also found that abiotic factors played a much stronger role than genetic factors in determining community organisation; however, in this case they did find a significant genetic effect. While a number of studies have also demonstrated the importance of log diameter in affecting richness or composition of macrofungal communities (Heilmann-Clausen and Christensen 2004; Lindhe et al. 2004; Lindner et al. 2006), this factor was not found to be significant over the scale assessed in the current work, using standardised coarse woody debris.

The use of a standardised substrate, i.e. logs of the same age, species and site of origin, which were placed within a randomised field trial has identified that the vast majority of assignable fungal community variation within a site can be held at the within-substrate (microhabitat) level due to variation in aspect, surface area and temporal availability to colonisation. While considerable research has highlighted the importance of substrate type (i.e. logs, stumps, litter and mineral soil) to fungal community structure and diversity (Dighton et al. 2005; Goodman and Trofymow 1998; Tedersoo et al. 2003), no studies appear to have experimentally quantified the effects of microhabitat within these broader substrate types, especially in relation to other environmental influences within a forest. The findings of the current work, therefore, highlight the importance of considering such effects in understanding fungal community ecology and the need to consider finer-scale habitat variation in conservation strategies aimed at this guild (Heilmann-Clausen and Christensen 2003, 2005; Lonsdale et al. 2008).

Acknowledgments This research was supported under the Australian Research Council's Discovery Projects funding scheme (project numbers DP0451533 and DP0773686). The authors wish to thank Gunns Ltd for providing access to the base population trial as well as S. Grove for specialist advices regarding establishment and assessment of the trial, S. Nichols for technical assistance and G. Gates for assistance with fungal taxonomy. Experiments and procedures reported in this work comply with the current laws of Australia.

References

Bailey JK, Deckert R, Schweitzer JA, Rehill BJ, Lindroth RL, Gehring C, Whitham TG (2005) Host plant genetics affect hidden ecological players: links among *Populus*, condensed tannins, and fungal endophyte infection. Can J Bot 83:356–361

Barbour RC, deLittle DW, O'Reilly-Wapstra JM, Jordan GJ, Steane DA, Humphreys JR, Bailey JK, Whitham TG, Potts BM (2009) A geographic mosaic of genetic variation within a foundation tree species and its community-level consequences. Ecology (in press)

Breitenbach J, Kränzlin F (1984) Fungi of Switzerland: a contribution to the knowledge of the fungal flora of Switzerland, vol 1. Ascomycetes. Mykologia, Lucerne

Chambers PGS, Borralho NMG, Potts BM (1996) Genetic analysis of survival in *Eucalyptus globulus* ssp. *globulus*. Silvae Genet 45:107–112

Dighton J, White JF, Oudemans P (2005) The fungal community: its organization and role in the ecosystem, 3rd edn. Taylor & Francis, Boca Raton

Dix NJ, Webster J (1995) Fungal ecology. Chapman & Hall, Melbourne

Dungey HS, Potts BM, Whitham TG, Li H (2000) Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. Evolution 54:1939–1946

Dutkowski GW, Potts BM (1999) Geographic patterns of genetic variation in *Eucalyptus globulus* ssp. *globulus* and a revised racial classification. Aust J Bot 47:237–263

Eldridge K, Davidson J, Harwood C, van Wyk G (1993) Eucalypt domestication and breeding. Clarendon Press, Oxford

Ellis JG, Dodds PN, Lawrence GJ (2008) Flax rust resistance gene specificity is based on direct resistance–avirulence protein interactions. Annu Rev Phytopathol 45:289–306

Fuhrer B (2005) A field guide to Australian fungi. Bloomings Books, Melbourne

Gehring CA, Mueller RC, Whitham TG (2006) Environmental and genetic effects on the formation of ectomycorrhizal and arbuscular mycorrhizal associations in cottonwoods. Oecologia 149:158–164

Goodman DM, Trofymow JA (1998) Distribution of ectomycorrhizas in microhabitats in mature and old-growth stands of Douglas-fir on southeastern Vancouver Island. Soil Biol Biochem 30:2127–2138

Hamilton MG, Greaves BL, Potts BM, Dutkowski GW (2007) Patterns of longitudinal within-tree variation in pulpwood and solidwood traits differ among *Eucalyptus globulus* genotypes. Ann For Sci 64:831–837

Heilmann-Clausen J, Christensen M (2003) Fungal diversity on decaying beech logs—implications for sustainable forestry. Biodivers Conserv 12:953–973

Heilmann-Clausen J, Christensen M (2004) Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. For Ecol Manage 201:105–117

Heilmann-Clausen J, Christensen M (2005) Wood-inhabiting macrofungi in Danish beech-forests—conflicting diversity patterns and their implications in a conservation perspective. Biol Conserv 122:633–642

Johnson MTJ, Agrawal AA (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). Ecology 86:874–885

Johnson MTJ, Stinchcombe JR (2007) An emerging synthesis between community ecology and evolutionary biology. Trends Ecol Evol 22:250–257

Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodivers Conserv 7:749–764

Jordan GJ, Potts BM, Kirkpatrick JB, Gardiner C (1993) Variation in the *Eucalyptus globulus* complex revisited. Aust J Bot 41:763–785

Jordan GJ, Potts BM, Chalmers P, Wiltshire RJE (2000) Quantitative genetic evidence that the timing of vegetative phase change in *Eucalyptus globulus* ssp. *globulus* is an adaptive trait. Aust J Bot 48:561–567

LeRoy CJ, Whitham TG, Keim P, Marks JC (2006) Plant genes link forests and streams. Ecology 87:255–261

Lindhe A, Åsenblad N, Toresson H (2004) Cut logs and high stumps of spruce, birch, aspen and oak—nine years of saproxylic fungi succession. Biol Conserv 119:443–454

Lindner DL, Burdsall HH Jr, Stanosz GR (2006) Species diversity of polyporoid and corticioid fungi in northern hardwood forests with differing management histories. Mycologia 98:195–217

Lonsdale D, Pautasso M, Holdenrieder O (2008) Wood-decaying fungi in the forest: conservation needs and management options. Eur J For Res 127:1–22

Lopez GA, Potts BM, Dutkowski GW, Apiolaza LA, Gelid PE (2002) Genetic variation and inter-trait correlations in *Eucalyptus globulus* base population trials in Argentina. For Genet 9:217–231

Madritch M, Donaldson JR, Lindroth RL (2006) Genetic identity of *Populus tremuloides* litter influences decomposition and nutrient release in a mixed forest stand. Ecosystems 9:528–537

Martin F, Aerts A, Ahrén D, Brun A, Danchin EGJ, Duchaussoy F, Gibon J, Kohler A, Lindquist E, Pereda V, Salamov A, Shapiro HJ, Wuyts J, Blaudez D, Buée M, Brokstein P, Canbäck B, Cohen D, Courty PE, Coutinho PM, Delaruelle C, Detter JC, Deveau A, DiFazio S, Duplessis S, Fraissinet-Tachet L, Lucic E, Frey-Klett P, Fourrey C, Feussner I, Gay G, Grimwood J, Hoegger PJ, Jain P, Kilaru S, Labbé J, Lin YC, Legué V, Le Tacon F, Marmeisse R, Melayah D, Montanini B, Muratet M, Nehls U, Niculita-Hirzel H, Secq MPO-L, Peter M, Quesneville H, Rajashekar B, Reich M, Rouhier N, Schmutz J, Yin T, Chalot M, Henrissat B, Kües U, Lucas S, Van De Peer Y, Podila GK, Polle A, Pukkila PJ, Richardson PM, Rouzé P, Sanders IR, Stajich JE, Tunlid A, Tuskan G, Grigoriev IV (2008) The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis. Nature 452:88–92

McDonald A, Borralho N, Potts BM (1997) Genetic variation for growth and wood density in *Eucalyptus globulus* ssp. *globulus* in Tasmania. Silvae Genet 46:236–241

Milgate AW, Potts BM, Joyce K, Mohammed CL, Vaillancourt RE (2005) Genetic variation in *Eucalyptus globulus* for susceptibility to *Mycosphaerella nubilosa* and its association with tree growth. Australas Plant Pathol 34:11–18

Poke FS, Potts BM, Vaillancourt RE, Raymond CA (2006) Genetic parameters for lignin, extractives and decay in *Eucalyptus globulus*. Ann For Sci 63:812–821

Ratkowsky D, Gates G (2002) Keys to the Tasmanian families and genera of gilled fungi. Tasmanian Nat 124:2–24

Rubino DL, McCarthy BC (2003) Composition and ecology of macrofungal and myxomycete communities on oak woody debris in a mixed-oak forest of Ohio. Can J For Res 33:2151–2163

Schmit JP (2005) Species richness of tropical wood-inhabiting macrofungi provides support for species-energy theory. Mycologia 97:751–761

Schweitzer JA, Bailey JK, Rehill BJ, Martinsen GD, Hart SC, Lindroth RL, Keim P, Whitham TG (2004) Genetically based trait in a dominant tree affects ecosystem processes. Ecol Lett 7:127–134

Schweitzer JA, Bailey JK, Fischer DG, LeRoy CJ, Lonsdorf EV, Whitham TG, Hart SC (2008) Plant–soil–microorganism interactions: heritable relationships between plant genotype and associated soil microorganisms. Ecology 89:773–781

Silfver T, Mikola J, Rousi M, Roininen H, Oksanen E (2007) Leaf litter decomposition differs among genotypes in a local *Betula pendula* population. Oecologia 152:707–714

Snedecor GW, Cochrane WG (1980) Statistical methods, 7th edn. The Iowa State University Press, Ames

Steane DA, Conod N, Jones RC, Vaillancourt RE, Potts BM (2006) A comparative analysis of population structure of a forest tree, *Eucalyptus globulus* (Myrtaceae), using microsatellite markers and quantitative traits. Tree Genet Genomes 2:30–38

Tedersoo L, Kõljalg U, Hallenberg N, Larsson K (2003) Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. New Phytol 159:153–165

Thompson JN (2005) The geographic mosaic of coevolution. The University of Chicago Press, Chicago

Wade MJ (2007) The co-evolutionary genetics of ecological communities. Nat Rev Genet 8:185–195

Wheeler Q, Blackwell M (eds) (1984) Fungus–insect relationships, perspectives in ecology and evolution. Columbia University Press, New York

White TL, Adams WT, Neale DB (2007) Forest genetics. CAB International, London

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, Leroy CJ, Lonsdorf EV, Allan GJ, DiFazio SP, Potts BM, Fischer DG, Gehring CA, Lindroth RL, Marks JC, Hart SC, Wimp GM, Wooley SC (2006) A framework for community and ecosystem genetics: from genes to ecosystems. Nat Rev Genet 7:510–523

Whitham TG, DiFazio SP, Schweitzer JA, Shuster SM, Allan GJ, Bailey JK, Woolbright SA (2008) Extending genomics to natural communities and ecosystems. Science 320:492–495

Wimp GM, Martinsen GD, Floate KD, Bangert RK, Whitham TG (2005) Plant genetic determinants of arthropod community structure and diversity. Evolution 59:61–69

Yu Q, Yang DQ, Zhang SY, Beaulieu J, Duchesne I (2003) Genetic variation in decay resistance and its correlation to wood density and growth in white spruce. Can J For Res 33:2177–2183