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Rainforest-restoration success as judged by assemblages of soil- and litter-dwelling mites (Arachnida: Acari)*

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Abstract

Decline in rainforest cover in many areas of Australia is being countered by various methods of forest reestablishment, including ecological restoration plantings, timber plantations, and unmanaged regrowth. We used assemblages of soil- and litter-dwelling mites to determine which style most closely recaptures the assemblage structure of mites associated with intact rainforest at 84 tropical and subtropical sites in eastern Australia. The six habitat types surveyed were pasture (the typical 'pre-restoration' state), unmanaged regrowth, monoculture forestry, multi-species forestry, ecological restoration and intact rainforest (the 'target' state). Forestry and ecological restoration sites were 5–20 years old. Mites were extracted from soil/litter samples and (excluding Oribatida) identified to family or to finer levels. For two diverse but taxonomically difficult superfamilies characteristic of rainforest, Uropodoidea and Trombidioidea, identification was to morphotaxon. Presence/absence data were analyzed in several ways. First, we used our data to create a list of 'indicator taxa' for pasture and rainforest, and determined the abundance of these indicators in each of the four reforestation methods. We also calculated morphotaxon richness for uropodoids and trombidioids and compared these values among habitat types. In both of these analyses, ecological restoration was most similar to rainforest. We used ordination and ANOSIM to compare mite assemblages among habitat-types. Although mite assemblages clearly distinguished between rainforest and pasture sites, they did not identify any of the four reforestation methods as being consistently similar to rainforest. They did, however, indicate that monoculture forestry and multi-species forestry plantations were often not readily distinguishable from pasture. This may have as much to do with silvicultural methods common to these plantations (e.g., pruning, herbicide application, and maintenance of a relatively open canopy) as to the low diversity of trees present in plantations. We conclude with a brief discussion of the utility of mites in rapid bioassessment programs in Australia, and suggest that the most pragmatic approach involves focusing on a few easily recognized indicators rather than on entire assemblages.

Key words: Astigmata, Australia, bioindicators, Endeostigmata, forest, Mesostigmata, pasture, Prostigmata.

Introduction

Over the past century, vast tracts of tropical and subtropical rainforest have been cleared for lumber and to make way for agriculture (Whitmore, 1997; Lamb *et al*., 2005). Remaining areas of rainforest have lost much of their biodiversity due to fragmentation and reduction in habitat area (Terborgh, 1992; Adam, 1994; Turner, 1996; Laurance & Bierregaard, 1997; Brooks *et al*., 1999). Although the conservation of remaining fragments is of primary importance, there is also the hope that revegetation of cleared areas may reverse some damage by buffering remnants from surrounding land uses, increasing the habitat available to rainforest plants and animals, and facilitating dispersal of biota among remnants (Lugo, 1997; Parrotta *et al*., 1997a; Lamb, 1998; Herbohn *et al*., 2000; Tucker, 2000; Bonham *et al*., 2002; Hartley, 2002; Kanowski *et al*., 2003; 2005a, b; Lamb *et al*., 2005; Wright & Muller-Landau, 2006; Edwards *et al*., 2010).

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In Australia, subtropical rainforests were extensively cleared between 1860 and the early part of the 20th century. Today, an estimated 340,000 ha of rainforest remains in subtropical south-east Queensland and north-east New South Wales, less than half that present at European settlement (Floyd, 1990; Hitchcock, 1991; McDonald *et al*., 1998). Clearance of tropical rainforest in Australia is more recent. Much of the upland forest inland of Cairns, Queensland, was cleared between 1900 and 1920, and conversion of forested land to agriculture continued until the 1950s. Now, most of the remaining rainforests in the region are protected as part of the Wet Tropics World Heritage Area, declared in 1988, although many small remnants are in private ownership. About 750,000 ha of rainforests remain in the 'Wet Tropics' region of north-east Queensland (15º30'–19ºS), of an estimated 965,000 ha present at the time of European settlement (Winter *et al*., 1987; Collins, 1994).

Several styles of reforestation have been practiced in former rainforest landscapes in Australia and elsewhere, not all of them aimed solely at restoration (Kanowski *et al*., 2003; Catterall *et al*., 2004). For example, large areas of the tropics and subtropics have been planted with monocultures of fast-growing timber trees (Lamb *et al*., 2001). Mixed-species plantations for high quality cabinet timber have been established in some regions, typically on a small scale (Lamb *et al*., 1997; Harrison & Herbohn, 2001). Other projects have used diverse and densely-planted mixtures of trees and shrubs with the explicit intent of restoring rainforest to cleared land (Kooyman, 1991; Parrotta *et al*., 1997b). Finally, many areas of cleared land have been allowed to revert to secondary forest, sometimes with the active assistance of landholders, but most often through abandonment (Janzen, 1988; Brown & Lugo, 1990). These approaches to reforestation clearly vary in cost and potential economic return, and they are also likely to vary in value to rainforest plants and animals (Lugo, 1997; Lamb, 1998; Harrison *et al*., 2000; Lamb *et al*., 2005).

How does one determine the relative success of different styles of reforestation for the restoration of biota? One approach is to assess whether the organisms that colonize a restored site are similar to those that are *a priori* known to be typical inhabitants of intact rainforest. This method is appropriate for taxa whose habitat preferences are already well established, such as most vascular plants and vertebrates (e.g. Kanowski *et al*., 2006), but not for the majority of life (e.g. fungi, most invertebrates) (Kanowski *et al*., 2005a; Nahmani *et al*., 2006). Another approach is to compare biotic assemblages associated with different reforestation styles to those found in the pre-existing condition (e.g., pasture or clear-cut) and in the intended goal (rainforest) (e.g., Reay & Norton, 1999). The most successful reforestation methods are those that result in assemblages most similar to those observed in the least disturbed local rainforest areas (Catterall *et al*., 2004). These methods do not require pre-existing knowledge of habitat preferences; indeed, one outcome of this approach is the creation of new information about the distributions and habitat associations of organisms.

Although it is important to assess colonization of restored sites by plants (Honnay *et al*., 2002; Jacquemyn *et al*., 2003; Harden *et al*., 2004) and by large and charismatic fauna such as birds (Hansson, 2001), reptiles (Kanowski *et al*., 2006) and butterflies (Meyer & Sisk, 2001), there are other taxa whose presence should also be monitored. Here we focus on one subset of soil- and litter-dwelling invertebrates, the mites (Arachnida: Acari). We do so not because they are charismatic or because they are known to include many species indicative of 'healthy' forest [in contrast to many saproxylic insects, which are associated with the dead wood typical of old-growth forests (Grove, 2002)]; rather, we do so for pragmatic and ecological reasons. First, a great diversity of mites can be collected quickly, allowing researchers to visit many sites over a short period of time in the field. In contrast, detectability of birds, amphibians and reptiles is dependent on weather and overlap with breeding seasons, and mammals typically occur at such low densities that false absences are likely to be recorded. Second, birds, mammals and some flying insects are relatively vagile, and their presence at a restored site—although it indicates use—does not necessarily indicate residence. One can be much more certain that the presence of flightless invertebrates such as mites does indicate residence in the reforested site. Finally, mites and other microarthropods have an important influence on de-

composition and soil nutrient cycles (Seastedt, 1984) and hence may affect development of rainforest-like soil function.

Here we compare mite assemblages associated with four methods of reforestation currently occurring in tropical and subtropical Australia to determine which method most closely recaptures the assemblage structure of mites typical of intact rainforest. We also attempt to determine habitat associations for soil and litter mites with the hope that these assignations will prove useful in constructing multi-taxon tools for monitoring biodiversity (Lawton *et al*., 1998). We do not claim that these associations are definitive, but rather that they are hypotheses to be further tested in different regions.

Materials and Methods

Study areas and habitat-types

Detailed descriptions of study sites and vegetation structure are presented in Kanowski *et al*. (2003). Sites were situated in two regions of eastern Australia: the Atherton Tablelands, an upland plateau in tropical north-east Queensland (17º–17º30'S;, 145º30'–145º45'E), and the lowland subtropics of south-east Queensland and north-east New South Wales, between Gympie and Casino (26º30'–29ºS; 152º30'–153º30'E). Tropical sites were located at mid-elevations (500–850 m a.s.l.) and, with few exceptions, on basaltic soils. Rainfall at these sites ranges from 1,300–3,000 mm per annum. Subtropical sites were located in the lowlands and foothills (10–400 m a.s.l.) on basaltic and metasedimentary soils with rainfall between 1,100–2,000 mm per annum.

Reforestation methods examined in this study are those most commonly practiced in former rainforest landscapes in eastern Australia: monoculture timber plantations, mixed species cabinet-timber plantations, diverse ecological restoration plantings, and unmanaged regrowth (Lamb *et al*., 1997; Kanowski *et al*., 2003; Catterall *et al*., 2004). In both tropics and subtropics, 5–10 replicate sites of each reforestation style were selected, together with five pasture reference sites and ten rainforest reference sites, totaling 40 sites in the tropics and 44 in the subtropics (Table 1). Replicate sites in most treatments were separated by 1–10 km, but this degree of spatial separation was not possible for monoculture plantations, most of which were restricted to a few locations in State Forests.

We restricted the study to reforested sites that were at least five years old, by which time canopy closure could reasonably be expected in the denser plantings. Most sites surveyed in the study covered at least 4 ha, although a few sites as small as 2 ha had to be included to allow sufficient replicates in some treatments. Although we also surveyed mature monoculture plantations (38–70-years -old) (Kanowski *et al*., 2003), in this paper we report only the results for young monoculture plantations (5–15-year-old) in order to better compare monoculture sites to cabinet timber and ecologi-

TABLE 1. Descriptions and sample sizes for the habitat-types examined in eastern Australia.

Habitat-type	Description	Number of sites in tropics	Number of sites in subtropics
Pasture (P)	actively used cattle pasture on formerly rainforested land	5	5
Young monoculture plantation (YP)	forestry monocultures (hoop pine, *Araucaria cunninghamii*)	5	5
Cabinet timber (CT)	multispecies plantings (5–20 spp.) of mixed native rainforest, *Eucalyptus*, and exotic timber trees	5	10
Regrowth (RG)	unmanaged regrowth on abandoned pasture	5	5
Ecological restoration (ER)	diverse (20 to >100 spp.), high-density plantings of native rainforest trees and shrubs	10	9
Rainforest (F)	relatively undisturbed rainforest that had not been logged for ≥20 years	10	10

cal restoration sites, which had median ages of seven and nine years, respectively. In young monoculture plantations and cabinet timber sites, weeds were controlled by slashing, herbicide and grazing, and trees were pruned. At ecological restoration sites, weeds (i.e., invasive non-rainforest plants) were controlled by hand or by herbicide, but trees were generally not thinned or pruned. Unmanaged regrowth sites were primarily abandoned dairy pasture. In the tropics, unmanaged sites were dominated by woody scramblers (e.g. *Lantana camara* L.), whereas in the subtropics they were dominated by trees such as camphor laurel [*Cinnamomum camphora* (L.)] and privet (*Ligustrum lucidum* Ait. f.). Unmanaged regrowth sites were approximately 10–20-years-old in the tropics and 30–40 -years-old in the subtropics, a reflection of the different times since the collapse of the dairy industry in the two regions (Kanowski *et al*., 2003).

In both regions, active beef- or dairy-cattle pasture sites located on previously rainforest-covered land were used as the 'pre-existing condition'. In the tropics, intact rainforest reference sites (representing the 'target') were located in complex notophyll or mesophyll vine forest (Tracey, 1982). Three sites were located near the margin of extensive rainforest (contiguous with rainforest > 100,000 ha in extent) and seven were in remnants 40–400 ha in size. In the subtropics, seven rainforest reference sites were located in complex notophyll vine forest on moist sites on basalt, and three in Araucarian notophyll/microphyll vine forest (Floyd, 1990) on drier sites on metasediments. Three of the sites were located in large remnants 150–250 ha in extent contiguous with extensive rainforest, and the remainder in remnants of 4–50 ha, the largest available remnants within the target ranges of altitude and geology. All rainforest reference sites may have been subjected to selective logging in the past century, but logging did not appear to have occurred on any reference site within the last two decades. At each site a 0.3 ha (30m x 100m) transect was established. Location of these transects relative to the edges of the sites varied depending on size and shape of site, topography, and ease of access. For small sites, the transect was placed as equidistant as possible from edges; in large sites, transects were typically a minimum of 50 m into the interior. All mite collections and measurements of vegetation structure took place in these transects (see Kanowksi *et al*., 2003 for details). Hereafter we refer to the six habitat types as Pasture, Rainforest, Young Monoculture Plantation, Cabinet Timber, Ecological Restoration and Regrowth.

Collection, extraction and identification of mites

From each 0.3 ha transect, a single 2 L sample of the upper decomposing layer of litter and organic soil was collected by hand. Collection was haphazard throughout the transect, with 1 L being gathered during an 'outward' traverse and 1 L gathered during the 'return' traverse, following slightly different paths parallel to the midline of the transect. The collected soil and litter was mixed together and then split into two 1 L allotments, each of which was placed in a Tullgren funnel beneath a 40 W light bulb. Samples were extracted over a period of three days into 80% ethanol. Although Tullgren funnels are not the most exhaustive method for extracting soil mites (André *et al*., 2002; HP *pers. obs*.), our purpose was not to provide a complete inventory but to allow comparison among sites (i.e., the goal was to determine relative rather than absolute composition). Sampling and extraction took place in the tropics in October and November 2000 (end of dry season) and in the subtropics in February and March 2001 (end of wet season). Because of this seasonal difference as well as geographical separation, data from the tropics and subtropics are analyzed separately.

Extracted samples were examined under a dissecting microscope and mites sorted to morphotaxa. Several exemplars of each morphotaxon were mounted on microscope slides in Heinze PVA medium (Evans, 1992). This work was done by a single trained technician to ensure consistency in recognition of morphotaxa. All mites except members of the Oribatida were processed. Oribatids were excluded because of lack of time and taxonomic expertise, and because they make relatively poor slide-mounts, not because they were deemed less likely to be informative. Morphotaxa were not enumerated beyond presence/absence per sample. Mounted mites were cured at 45°C on slide-

warming trays for a minimum of four days before being examined using a phase-contrast compound microscope. Magnification up to 1,000x under oil immersion was sometimes necessary for identification. One of us (HP) identified each mounted specimen to family, and when possible to subfamily or genus, using the keys in Walter & Proctor (2001) and unpublished keys produced by D.E. Walter (then of the Department of Zoology & Entomology, University of Queensland). Juvenile dermanyssine Mesostigmata that could not be identified to family were excluded. Mite systematics is at an early stage for free-living soil mites in Australia, and so identification to species and sometimes genus is not possible for the majority of taxa. Members of three taxa that were particularly diverse but for which there were no keys to Australian genera (the mesostigmatan taxa Laelapidae and Uropodoidea, and the prostigmatan taxon Trombidioidea) were assigned morphotaxon codes. Uropodoids and trombidioids were also of interest because previous collections in the study regions had suggested that they were more abundant and diverse in rainforests than in drier forest types (HP, *pers. obs.*). The process of assigning codes was as follows. Each mounted adult representative of these three groups was digitally imaged using a digital camera attached to a compound microscope equipped with differential-interference contrast (DIC) lighting. Specimens were then assigned to morphotaxa through comparison of the digital images. Species of Uropodoidea and Trombidioidea have strongly heteromorphic juvenile stages (nymphs and larvae, and larvae, respectively). These juvenile stages were placed in their own categories because they could not readily be assigned to particular adult-based morphotaxa. Phoretic deutonymphs of the suborder Astigmata ('hypopodes') were also identified as a single category separate from adults. Because these juveniles as well as those of Erythraeidae, Trombidioidea and Uropodoidea frequently have associations with larger arthropods (via phoresy and parasitism) that may allow them to occupy different habitats than adults, there is ecological justification for their being placed in separate stage-related categories. Subsequent examination of specimens and images of Laelapidae by an expert in mesostigmatan taxonomy (D.E. Walter, *pers. comm.)* revealed that our assignment of morphotaxa had split the laelapids into different genera or species-groups within genera (reported in Appendix). We therefore suggest that our morphotaxon designations for the Uropodoidea and Trombidioidea also likely reflect generic or subgeneric ranks. Specimens of all identified mites are deposited in the Acari subsection of the E. H. Strickland Entomological Museum of the University of Alberta.

Identifying indicators of rainforest and pasture

Unlike for well-studied groups like plants, birds and lizards (Kanowski *et al*., 2005a; Kanowski *et al*., 2006), there is little *a priori* knowledge of what mites are typical for most different habitat types in Australia (see Beaulieu & Weeks, 2007). We therefore used the IndVal approach of Dufrêne & Legendre (1997) within the PCOrd statistics package (McCune & Mefford, 1999) to identify indicator taxa, with significance at $p< 0.05$. A Pasture indicator is one that occurs in many Pasture sites and very few Rainforest sites, and vice versa for Rainforest indicators. We examined only the data from Pasture and Rainforest sites to determine this. For this analysis we considered Trombidioidea and Uropodoidea at superfamilial rather than morphotaxon level, but we maintained separation between adult and juvenile stages.

We used one-way ANOVA followed by LSD tests [SPSS version 11.5 (2002)] to explore whether mite taxon richness, or richness of certain 'indicator' groups identified by the method described above, could be used to estimate success of rainforest restoration. We examined three types of richness: (1) richness at the finest taxonomic resolution we reached (superfamilies, families, subfamilies, genera) but excluding morphotaxa; (2) trombidioid and uropodoid morphotaxon richness; (3) richness of taxa identified as indicators of Pasture or Rainforest using the method described above. Data for trombidioid morphotaxa and forest indicators in the subtropics were heteroscedastic, and so we employed Kruskal-Wallis tests followed by individual Mann-Whitney tests to determine where significant differences lay.

Multivariate analysis

Multivariate analyses were run using PATN for Windows, version 3.11 (Belbin, 1989; software available from http://www.patn.com.au/). Distance matrices for sites were based on the Bray-Curtis distance coefficient; however, since our taxonomic data consisted of only presence-absence of mite taxa, the coefficient was equivalent to Sørensen distance coefficient (= 1- Sørensen similarity coefficient) (Legendre & Legendre, 1998). We analyzed these data in three forms: (1) all taxa at family level (except for Trombidioidea and Uropodoidea, which were included as superfamilies); (2) all at the finest taxonomic resolution (superfamilies, families, a few subfamilies, and many genera, mostly of Mesostigmata), excluding morphotaxa; (3) at the finest resolution including morphotaxa. The rationale for analysis at three levels is that although fine resolution may be more likely to distinguish among habitat types, it also requires a great deal more time, effort and expertise (e.g. Nahmani *et al*., 2006). We hoped to determine whether the less exhausting process of identification to family would provide the same result as that to genus or morphotaxon. Singletons (i.e. taxa collected from only one site) were excluded prior to analysis. No mite taxon occurred at every site, and so there was no need to exclude ubiquitous taxa. Ordination was by semi-strong hybrid multidimensional scaling (SSH, Faith *et al*., 1987) with 1,000 random starts (50 iterations per start). Vectors for taxa that were strongly ($p < 0.01$) associated with patterns in the ordinations were determined using a principal axis correlation (PCC) procedure, with significance determined by Monte Carlo analysis of ordination (MCAO, 1,000 random starts). Restoration success was judged by the proximity in multivariate space of revegetated sites to the cluster of intact Rainforest sites. This was assessed both visually (by examining ordinations) and by the multivariate analogue of ANOVA, analysis of similarity (ANOSIM) (Belbin, 1993) using 1,000 random starts. As an additional method to visually represent variation in success, we used distance values from the Sørensen matrix to calculate the mean Sørensen distance to Rainforest sites for each of the different habitat- types (see also Grimbacher & Catterall, 2007). Number of pairwise distances varied greatly due to differences in sample size for the different habitat-types (e.g., for the five Pasture and ten Cabinet Timber sites in the subtropics, there were 50 and 100 distances from the ten Rainforest sites, respectively); therefore, we perform no additional statistics on these means and use them for graphical purposes only.

We used site-based environmental data as extrinsic variables to determine what characteristics were most closely associated with mite assemblages ($p < 0.01$ according to PCC/MCAO). These extrinsic variables played no role in creating ordinations, but could be queried as to whether they 'agreed' or 'disagreed' with the ordinations defined by mite taxa. These variables included soil characteristics [proportions of sand, silt and clay; bulk density (g/cm^3)] two litter characteristics [tonnes/ha; depth (cm) for subtropics alone], and plant structural features [basal area; total stems; relative cover of grasses, ferns, herbs; vertical complexity; woody debris index; canopy cover (%)], and total number of vascular plant species/quadrat. For measurement details see Kanowski *et al*. (2003). Because some of these variables had small ranges of values and others very large ranges, we range-standardized each variable so that it ranged from 0 to 1 prior to analysis.

Results

Richness

All major groups of mites known to occur in eastern Australia, including Oribatida, were represented in our collections (Appendix 1, oribatids not mentioned). We identified mites from 47 families from tropical sites and 57 families from subtropical sites. These counts exclude the superfamilies Canestrenoidea (a single instance), Uropodoidea and Trombidioidea and the functional group 'hypopodes', the phoretic deutonymphal stage of Astigmata (Appendix). Excluding morphotaxa of Trombidioidea and Uropodoidea and adult/juvenile divisions, we identified 69 taxa from tropical

sites and 82 from subtropical sites (Appendix), with 13 unique tropical and 26 unique subtropical taxa. Many of these unique taxa were collected at only a single site, and thus their absence from one of the two regions likely indicates rarity rather than true geographic restriction. Of the two very diverse groups identified to morphotaxa, the Uropodoidea showed both greater local richness (12 tropical, 16 subtropical morphotaxa) and greater overlap between regions (five shared morphotaxa between tropics and subtropics) than did Trombidioidea (six tropical, 13 subtropical, one shared).

Total taxon richness excluding morphotaxa showed no significant differences among the tropical habitat types (Fig. 1A) (one-way ANOVA, F= 0.912, df= 39, p= 0.49). In the subtropics, habitat types differed in total number of taxa (F= 2.79, df= 43, p= 0.03), with Regrowth and Cabinet Timber plantations having significantly fewer taxa than Pasture and Rainforest. Cabinet Timber sites also had significantly fewer taxa than Young Monoculture Plantations (Fig. 1B). For both regions, Pasture and Rainforest sites had similar total mite richness.

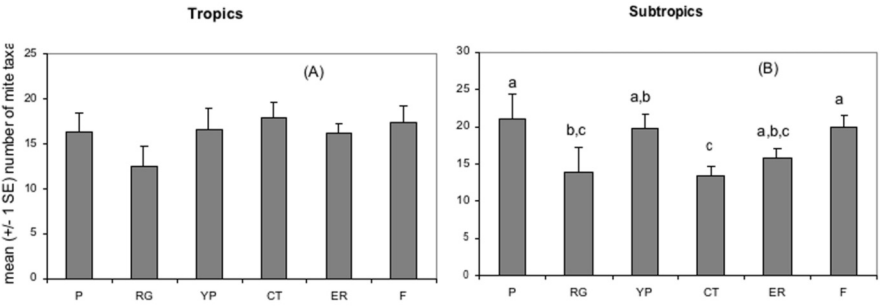

FIGURE 1. Mean number of mite taxa at different habitat-types in (A) tropical and (B) subtropical regions. Counts are at the finest taxonomic level identified for the various groups (see Table 1), excluding morphotaxa within Trombidioidea and Uropodoidea and the divisions of some taxa into adult and pre-adult stages. Bars with different letters are significantly different at p< 0.05 (ANOVA). There were no significant differences among site types in the tropics. P= Pasture, RG= unmanaged Regrowth, YP= Young Monoculture Plantation, CT= Cabinet Timber, ER= Ecological Restoration, F= Rainforest.

Trombidioid and uropodoid morphotaxon richness differed significantly among habitat types in both regions (Fig. 2). Rainforest sites invariably had the highest richness and Pasture sites had among the lowest. In the tropics, no reforestation method was consistently richer than others, but in the subtropics Ecological Restoration was richer in trombidioid morphotaxa than all other reforestation methods, and was richer in uropodoid morphotaxa than Cabinet Timber.

Indicators

Table 2 shows the mite taxa that were identified as 'indicators' of Pasture and Rainforest. Eight indicator taxa were unique to either the tropics or subtropics, but some (three indicator taxa for Pasture, two for Rainforest) were shared across regions. Pasture indicators include several taxa associated with exposed and/or grassy areas (e.g. Cunaxidae, Erythraeidae), dung (e.g. Parasitidae) or other decomposing organic matter (e.g. Acaridae) (Krantz, 1978; Kethley, 1990). For Rainforest indicators (Table 2), it is more difficult to surmise what microhabitats were occupied because there is little ecological knowledge about these taxa; however, the inclusion of both Uropodoidea and Trombidioidea confirmed previous casual observations that these groups are particularly common and diverse in rainforest litter.

The mean number of indicator taxa per habitat-type is shown in Fig. 3. With the exception of Young Monoculture Plantations in the subtropics, Pasture sites had, logically, significantly more Pasture-indicator taxa than any other habitat-type. Similarly, Rainforest sites had significantly more Rainforest-indicator taxa than any other habitat-type in both tropical and subtropical regions. For reforestation methods in the tropics, Pasture indicators occurred relatively frequently in Young Mono-

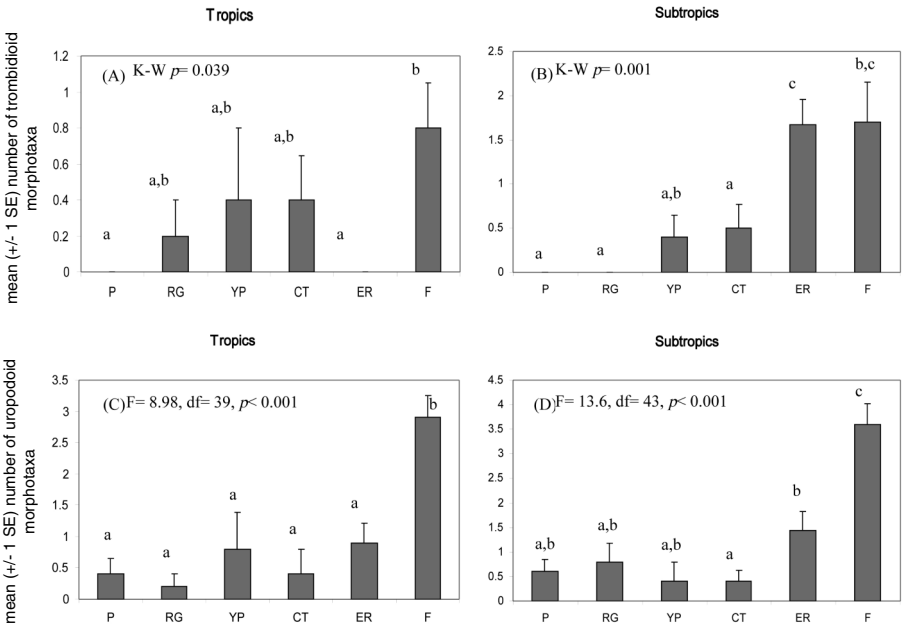

FIGURE 2. Morphotaxon richness per site of different habitat types for adult Trombidioidea in (A) tropical and (B) subtropical regions, and for adult Uropodoidea in (C) tropical and (D) subtropical regions. For (A) and (B) data were heteroscedastic and were analyzed using Kruskal-Wallis tests with Mann-Whitney pairwise tests serving as post-hoc tests. Data in (C) and (D) were analyzed with one-way ANOVAs and LSD tests. Bars with different letters are significantly different at $p < 0.05$. P= Pasture, RG= unmanaged Regrowth, YP= Young Monoculture Plantation, CT= Cabinet Timber, ER= Ecological Restoration, F= Rainforest.

TABLE 2. Mite taxa and life-history stages identified as indicators of Pasture or of Rainforest in eastern Australia.

Indicator of:	Tropical sites alone	Subtropical sites alone	Both tropical and subtropical sites
Pasture	Acaridae, Tarsonemidae	Digamasellidae, Erythraeidae	Cunaxoidinae (Cunaxidae), Parasitidae, Tydeidae
Rainforest	Hypopodes[a]	Alicorhagiidae, Labidostomatidae, Trachytidae	Trombidioidea[b], Uropodoidea[c]

[a]Phoretic deutonymphs of the suborder Astigmata.
[b]Larvae were significant indicators in the tropics, and adults in the subtropics.
[c]Juveniles were significant indicators in the subtropics, and both juveniles and adults in the tropics.

culture Plantation, Cabinet Timber and Ecological Restoration habitat types, whereas Rainforest indicators occurred at similar moderate frequencies in all reforestation types. A similar pattern for Pasture indicators occurred in the subtropics, but Rainforest indicators are clearly higher in subtropical Ecological Restoration than in any other reforestation method. Out of the four comparisons (Fig. 3A–D), Young Monoculture Plantation was the habitat type most frequently similar to pasture, whereas Regrowth and Ecological Restoration were each similar to Rainforest in a single comparison.

Multivariate analysis

In all three datasets differing in taxonomic resolution, ANOSIM found that mite assemblages invariably distinguished between Rainforest and all other habitat types (Fig. 4, p values all < 0.01). Conversely, Regrowth, Young Monoculture Plantation, and Cabinet Timber were not significantly

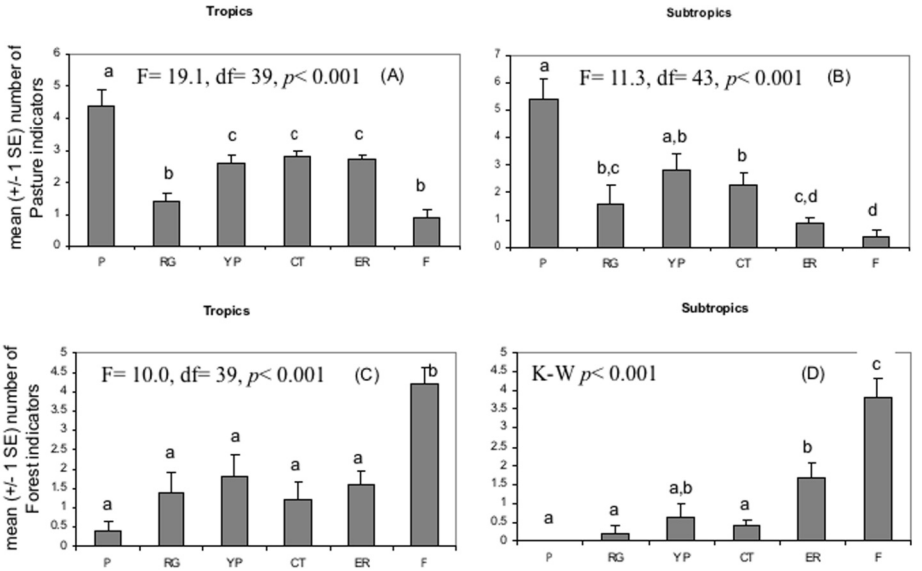

FIGURE 3. Numbers of Pasture (A and B) and Rainforest (C and D) indicator taxa occurring per for different habitat-types in tropical and subtropical regions. P= Pasture, RG= unmanaged Regrowth, YP= Young Monoculture Plantation, CT= Cabinet Timber, ER= Ecological Restoration, F= Rainforest.

different from Pasture ($p > 0.05$) in one, two and five analyses (out of six in total), respectively, whereas Ecological Restoration was always significantly different from Pasture ($p < 0.001$). Significant distinctions among habitat-types did not increase with finer taxonomic resolution (Fig. 4: total of 24, 23, and 24 significant differences observed from lowest to highest resolution, respectively).

Stresses for two-dimensional SSH-MDS were always greater than 0.26, indicating that ordination figures based on two dimensions would poorly reflect the true multivariate distances (Belbin, 1993). Three-dimensional analyses had lower stresses (0.18–0.22); however, we admit that they are still not completely ideal for visual representation. Ordinations for finest-taxon data are shown in Figs. 5–7. In Fig. 5 we hide the symbols for all but the reference sites to show how the separation of Rainforest and Pasture sites is evident. In Figs. 6 and 7, in which all habitat-types are included, patterns are more difficult to interpret. In the tropics (Fig. 6), the reforestation method that appears least similar to rainforest is Regrowth, and the most similar is Ecological Restoration. In the subtropics (Fig. 7), the least similar appears to be Cabinet Timber and the most similar Ecological Restoration. These interpretations are supported by plots of mean Sørenson distances of the different habitat types from Rainforest (Fig. 8).

Fig. 6B shows vectors for tropical mite taxa whose presence/absence is strongly correlated with the ordination (at $p < 0.01$). As would be expected from the indicator taxon list (Table 2), vectors for Uropodoidea point towards Rainforest, and for Tarsonemidae towards Pasture. Fig. 6C shows vectors for the extrinsic environmental variables that were strongly correlated with the ordination ($p < 0.05$). Fig. 7B and c show strongly correlated vectors for mites and environmental variables for subtropical sites. As for the tropics, many of the most strongly correlated mite taxa were also identified as indicators (see Table 2). Correlation of extrinsic variables with the mite-based ordination is suggestive of potential causal influences of the environmental variables on the distribution of mite taxa. Important environmental vectors in both regions appear to differentiate between open, grassy sites and closed-canopy sites with high structural diversity, stem densities and woody debris. Because of this strong and consistent correlation between the ordinations created by mite data and the over-

	TROPICAL						SUBTROPICAL				
						family level					
(A)	P	RG	YP	CT	ER	**(B)**	P	RG	YP	CT	ER
RG	0.051					RG	0.014				
YP	0.182	0.091				YP	0.039	0.010			
CT	0.232	0.010	0.465			CT	0.017	0.020	0.090		
ER	0.000	0.000	0.000	0.172		ER	0.000	0.033	0.011	0.000	
F	0.000	0.000	0.000	0.000	0.000	F	0.000	0.000	0.000	0.000	0.000
						finest-taxon level, no morphotaxa					
(C)	P	RG	YP	CT	ER	**(D)**	P	RG	YP	CT	ER
RG	0.051					RG	0.014				
YP	0.020	0.081				YP	0.093	0.010			
CT	0.172	0.141	0.515			CT	0.306	0.011	0.284		
ER	0.000	0.000	0.010	0.071		ER	0.000	0.011	0.009	0.000	
F	0.000	0.000	0.000	0.000	0.000	F	0.000	0.002	0.000	0.000	0.000
						morphotaxa included					
(E)	P	RG	YP	CT	ER	**(F)**	P	RG	YP	CT	ER
RG	0.031					RG	0.014				
YP	0.007	0.067				YP	0.010	0.018			
CT	0.139	0.144	0.404			CT	0.298	0.011	0.249		
ER	0.000	0.000	0.004	0.268		ER	0.000	0.044	0.014	0.000	
F	0.000	0.000	0.005	0.002	0.000	F	0.000	0.006	0.000	0.000	0.000

FIGURE 4. Matrices of ANOSIM *p*-values for different habitat-types in tropical and subtropical regions based on assemblages of mite taxa identified to three different levels of taxonomic resolution. Low *p*-values indicate little statistical similarity among habitat-types. P= Pasture, RG= unmanaged Regrowth, YP= Young Monoculture Plantation, CT= Cabinet Timber, ER= Ecological Restoration, F= Rainforest.

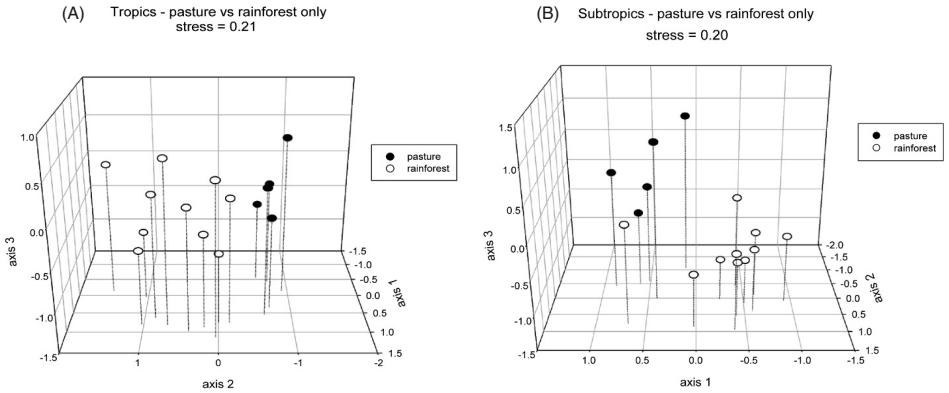

FIGURE 5. Ordinations of habitat-types based on finest-level mite taxa (excluding morphotaxa) showing only the Pasture and Rainforest sites for (A) tropical and (B) subtropical regions. Ordinations showing all habitat-types are presented in Figs. 6 and 7.

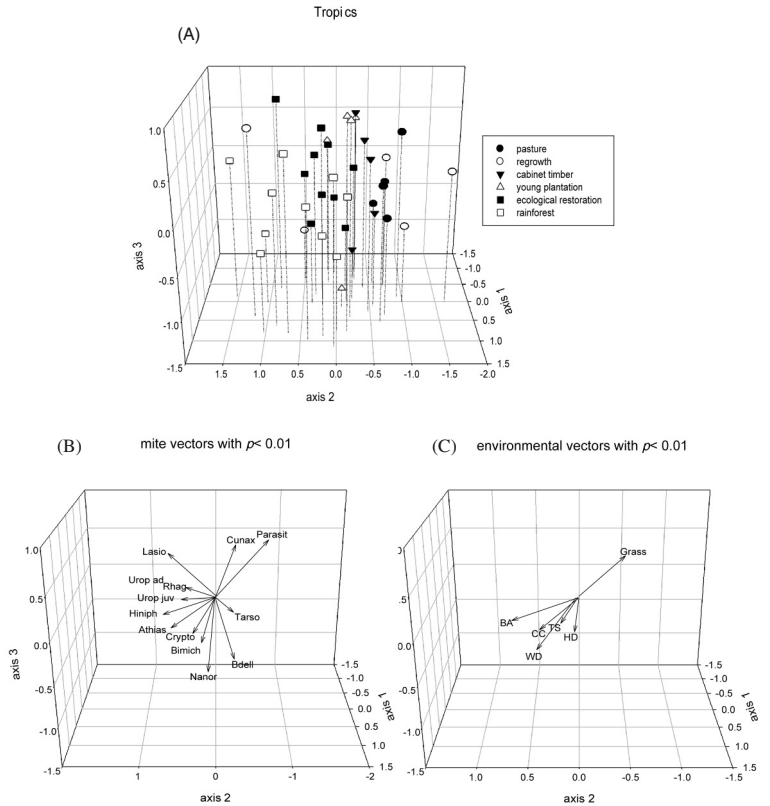

FIGURE 6. Ordination of tropical sites based on finest-level mite taxa (excluding morphotaxa) showing all habitat-types (A). Significant ($p< 0.01$) intrinsic mite vectors are shown in (B) and significant extrinsic environmental vectors in (C). Abbreviations for mites are Athias *Athiasella* (Ologamasidae), Bdell= Bdellidae, Bimich= Bimichaeliidae, Crypto= Cryptognathidae, Cunax= Cunaxinae (Cunaxidae), Hiniph= *Hiniphis* (Ologamasidae), Lasio= *Lasioseius* (Ascidae), Nanor= Nanorchestidae, Parasit= Parasitidae, Rhag= Rhagidiidae, Tarso= Tarsonemidae, Urop ad= Uropodoidea adults, Urop juv= Uropodoidea juveniles. Abbreviations for environmental variables are BA= basal area, CC= canopy cover, Grass= grass cover, HD= height diversity, TS= total stems, WD= woody debris index.

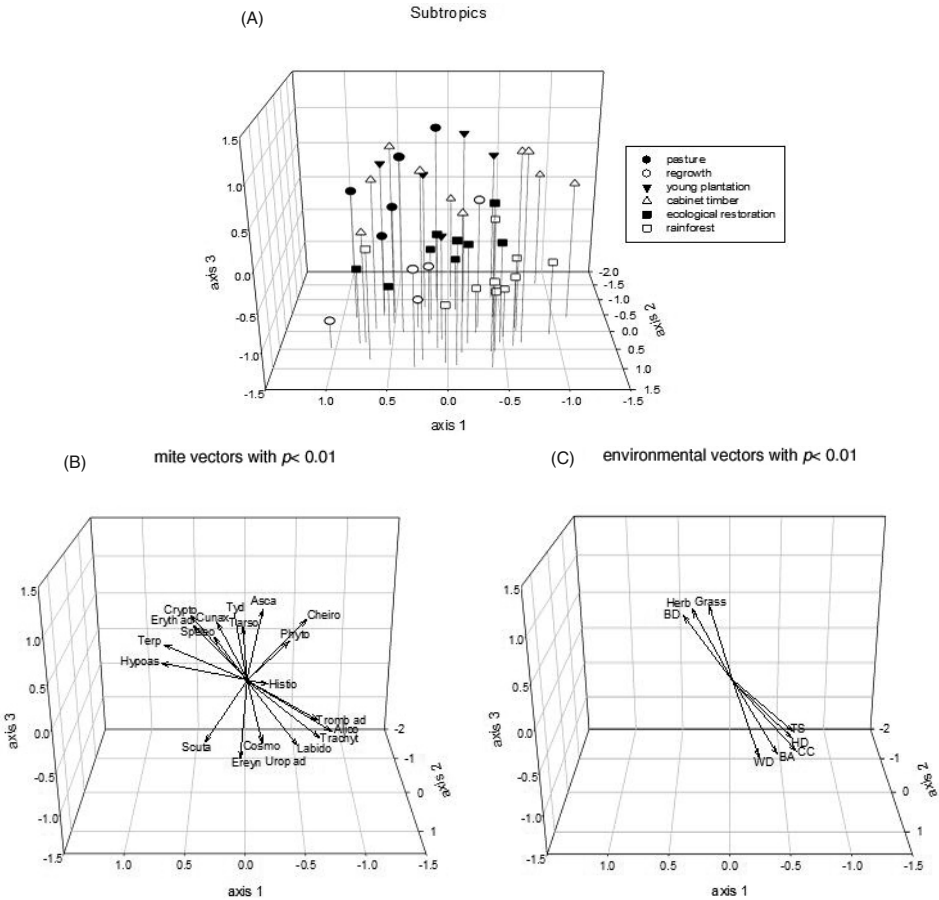

FIGURE 7. Ordination of subtropical sites based on finest-level mite taxa (excluding morphotaxa) showing all habitat-types (A). Significant ($p< 0.01$) intrinsic mite vectors are shown in (B) and significant extrinsic environmental vectors in (C). Abbreviations for mites are: Asca= *Asca* (Ascidae), Alico= Alicorhagiidae, Cheiro= *Cheiroseius* (Ascidae), Cosmo= *Cosmolaelaps* (Laelapidae), Crypto= Cryptognathidae, Cunax= Cunaxinae (Cunaxidae), Ereyn= Ereynetidae, Eryth ad= Erythraeidae adults, Histio= Histiostomatidae, Hypoas= Hypoaspidinae (Laelapidae), Labido= Labidostomatidae, Phyto= Phytoseiidae, Scuta= Scutacaridae, Speleo= Speleorchestidae, Tarso= Tarsonemidae, Terp= Terpnacaridae, Trachyt= Trachytidae, Tromb ad= Trombidioidea adults, Tyd= Tydeidae, Urop ad= Uropodoidea adults. Abbreviations for environmental variables are BA= basal area, BD= bulk density, CC= canopy cover, Grass= grass cover, HD= height diversity, Herb= herbaceous cover, TS= total stems, WD= woody debris index.

lain environmental data, it seems likely that the mite assemblages are primarily distinguishing between 'open grassland' and 'closed forest'.

Discussion

How well do mites discriminate between pasture and rainforest in eastern Australia?

Our study shows that cleared pastures within tropical and subtropical landscapes support mite assemblages that are clearly and consistently different from those inhabiting nearby rainforest sites, regardless of taxonomic resolution. Had they not done so it would have suggested that presence-

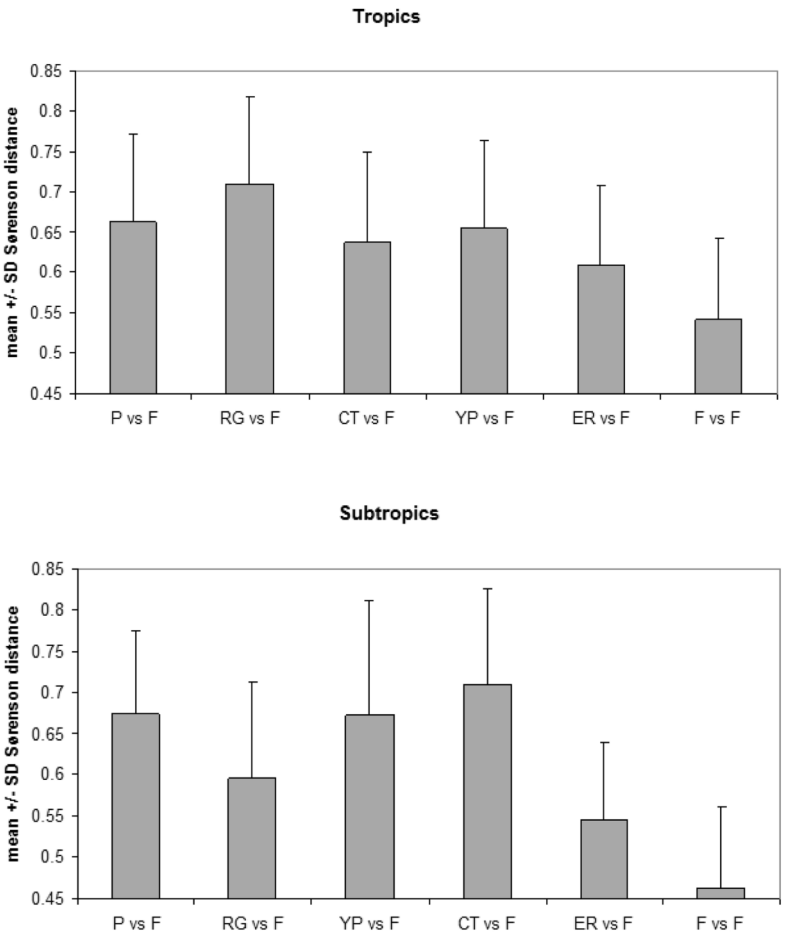

FIGURE 8. Mean Sørenson distances of the different habitat-types from rainforest (F). Means were calculated from the distance matrix produced by PATN for the data set including finest-level mite taxa (excluding morphotaxa). Note that the scale begins at 0.45 to make the differences among habitat-types more prominent. For number of sites within each habitat-type, see Table 1. P= Pasture, RG= unmanaged Regrowth, YP= Young Monoculture Plantation, CT= Cabinet Timber, ER= Ecological Restoration, F= Rainforest.

absence mite data above species level are insufficiently sensitive to judge the relative success of different reforestation methods. Other researchers have also found that soil invertebrate taxa identified to "easily recognizable taxonomic units" are readily able to discriminate between pasture and forest (Schnell *et al*., 2003). Research on the biology of free-living mites in Australian rainforest is in its infancy, with almost all studies (including this one) focused on the distribution and diversity of mite taxa rather than on the ecological roles they play, and often on arboreal taxa rather than those living in soil and litter (e.g. Walter & Proctor, 1998; Proctor *et al*., 2002; Beaulieu *et al*., 2010). This makes it difficult to explain why certain groups of mites were indicators (Table 2). In a few cases we can put forward reasonable hypotheses. For example, members of the pasture-indicator family Parasitidae feed on invertebrates associated with ungulate dung (Krantz, 1978). Members of the Digamasellidae and Rhodacaridae are small and slim, characteristics suited for squeezing through

the narrow pore-spaces in compacted soil associated with trampled pasture (Beaulieu & Weeks, 2007). Rainforest-indicating Trombidioidea and Uropodoidea have dispersal stages associated with larger animals (e.g. insects, spiders, vertebrates), and their diversity and abundance may be a reflection of the availability of hosts that themselves may be dependent on moist forest substrates. In contrast, members of another rainforest-indicator group, the Labidostomatidae, are sit-and-wait predators with no special dispersal stage. Here one might raise the *ad hoc* argument that these relatively large-bodied sedentary mites cannot readily colonize recently established forest. However, for many other groups speculation is difficult. This is particularly true for the Endeostigmata, in which one family was an indicators of rainforest (Alicorhagiidae) and several were important in creating the ordinations (Alicorhagiidae, Bimichaeliidae, Nanorchestidae). Essentially nothing is known about the ecology of endeostigmatans that could help us understand why they are so discriminating.

Do mites discriminate among reforestation methods?

Although mites were consistent in differentiating between the 'starting point' of Pasture and the 'goal' of Rainforest, they were less clear about which method of reforestation was most successful. While some reforestation methods are not statistically distinguishable from Pasture (e.g., Cabinet Timber in the tropics and in two of the three analyses in the subtropics), Rainforest sites are invariably different from all other habitat-types. A very pessimistic interpretation is that no reforestation method can succeed in bringing back the full function and diversity of rainforest mites. On the other hand, one could hypothesize that the differences are due to the young ages of all deliberately replanted sites (< 30 years), and that given enough time, their mite assemblages may converge upon that typical of the rainforest state. Slow recovery of arthropod assemblages after disturbance has been observed for mites associate with mined sites. In Australia, Cuccovia & Kinnear (1999) found that 20 years was insufficient for an 'intact' assemblage of oribatids to recolonize mine pits, and in Canada, St. John *et al*. (2002) showed that 40 years was not enough for full reestablishment of mites on mine tailings. Dunn (2004) found that ant assemblages in secondary neotropical forests might take 40 or more years to approach the structure of those found in mature forests. Similarly, Schnell *et al*. (2003) observed that very young eucalypt plantation sites (4–5 years old) in temperate Australia had ant assemblages no different from those of pasture; six years later, the assemblages had diverged significantly from pasture, though still not approaching the structure of assemblages found in nearby woodland.

As reforested sites age, their canopies gradually close and vegetation structure becomes more complex. But time alone is unlikely to be a cure-all for rainforest biota, as management style and other factors beyond the control of managers can also affect colonization by forest-dwelling animals (du Bus de Warnaffe & Dufrêne, 2004). Most plantation forestry methods (pruning, herbicide application) aim for rapid, straight growth of trees, resulting in a grassier substrate with drier microclimate than less rigorously managed styles (Kanowski *et al*., 2003). Results of the present study suggest that mite assemblages principally distinguish between 'open grassland' and 'closed forest'. Other taxa examined at these sites also responded to canopy closure, with rainforest-dependent reptiles being absent until at least 50% canopy cover was attained (Kanowski *et al*., 2006). Kanowski *et al*. (2003, 2005a) observed that both structure and vertebrate fauna in old (40–70 y) monoculture forestry sites were more similar to those of rainforest in the tropics but not in the subtropics, and attributed this regional difference both to local climatic factors and variation in silvicultural methods.

Ecological Restoration sites had greater canopy closure and less grass than most of the other reforestation styles (Kanowski *et al*., 2003), and so one might expect that it would have the most rainforest-like biota. Based on frequency of indicator taxa only (Fig. 3), Ecological Restoration sites in the subtropics had the most Rainforest indicators and fewest Pasture indicators. In this, mites are in agreement with bird assemblages studied at the same sites (Kanowski *et al*., 2005a). Subtropical Ecological Restoration sites also had the greatest number of trombidioid and uropodoid morphotaxa of all reforestation methods (Fig. 2B, D). For tropical sites, however, there is no reforestation method

that stands out as superior with regard to mite indicator taxa (Fig. 3A, B) or trombidioid and uropodoid morphotaxa (Fig. 2A, B). This is in contrast to avian assemblages, which clearly recognized Ecological Restoration sites as better habitat for rainforest birds than Young Monoculture Plantations and Cabinet Timber in both the tropics and subtropics (Catterall *et al*., 2004, Kanowski *et al*., 2005a). Similarly, rainforest-associated reptiles in the tropics were fairly common in Ecological Restoration sites but were absent from Young Monoculture and Cabinet Timber (Kanowski *et al*., 2006). Interpretation of these differences in use of young reforested sites by rainforest-associated vertebrates and mites is again hampered by our ignorance of tropical mite biology and taxonomy.

Can mites be used in rapid bioassessment of rainforest recovery in Australia?

There is good ecological justification for including mites in rainforest bioassessment programs. Complete restoration of forest also involves restoration of function (Reay & Norton, 1999; Stanturf *et al*., 2001; Ruiz-Jaen & Aide, 2005), including soil function. Mites are important agents of decomposition through their direct consumption of plant debris, predation on other decomposers (e.g. nematodes), and vectoring of fungal and bacterial propagules (Walter & Proctor, 1999). The role of soil mites and other invertebrates in transporting spores of mycorrhizal fungi (Lilleskov & Bruns, 2005) is of particular importance, given evidence that re-establishment of vegetation is often accelerated by mycorrhizal inoculation (Walker, 1999; Allen *et al*., 2003). All of these characteristics are strong arguments in favour of assessment programs that incorporate mites (Ruf & Beck, 2005).

Although theory supports the inclusion of mites, there are some practical difficulties with mite-oriented surveys (for a discussion of taxon-specific methodological problems in biodiversity surveys, see Pawar, 2003). An hour in the field translates to days or weeks in the laboratory preparing and identifying specimens. Because of this, only a relatively small amount of substrate per site can be thoroughly extracted and examined if one's goal is to compare mite assemblages across many sites. Also, while there are guides to species-level identification of flora and terrestrial vertebrate fauna in most regions, including Australia, local knowledge of mite fauna is almost universally incomplete with the exception of some northern European countries, the U.K., and terrestrial Antarctica. It is thus not surprising that the best developed programs using soil mites as indicators are located in Great Britain (Black *et al*., 2003), Germany (Ruf & Beck, 2005) and the Netherlands (Rutgers *et al*., 2009). New biomonitoring programs that include mites will require a long preliminary period of taxonomic effort (see, e.g., Walter, 2009). Finally, although mites are ubiquitous and diverse—two characters vital for any taxon being considered for wide-scale biomonitoring—most families cannot be readily distinguished by the untrained eye, and require moderate to high magnification and sometimes slide-mounting. These activities are beyond the expertise and/or resources of many agencies interested in rapid bioassessment. Simply comparing numbers of morphotaxa among habitat-types is unlikely to be a good alternative to knowing the taxonomic identity of the mites. This is because, unlike some other animal taxa that show very low richness in tropical pastures (Australian beetles, Grimbacher *et al*., 2006; Australian reptiles, Kanowski *et al*., 2006; Neotropical ants and birds, Dunn, 2004), mite richness is similarly high in both pasture and rainforest (Fig. 2; see also Proctor *et al*., 2003). Furthermore, our results indicate that presence-absence data above species level does not clearly reveal changes in mite assemblages associated with reforestation. Identification to species and/or complete enumeration may be required, but this would dramatically increase costs. Gulvik (2007) recommends using the ratio of number of individual Oribatida to Prostigmata as an indicator of habitat stability, with high ratios associated with forests and old meadows, and low ratios with recently disturbed soils. This would be relatively easy for untrained personnel to estimate, provided they could discriminate between juvenile oribatids and other mites. However, this indicator does not appear to be universally applicable, as Nakamura *et al*. (2003) observed that the numerical dominance of oribatids compared to all other mites was much higher in pasture than in nearby remnant rainforest.

Nevertheless, we do consider a few mite taxa to be good candidates as easily recognizable indicators of the rainforest state in Australia. These are members of the heavily-armoured Labidostomatidae and the velvet mite superfamily Trombidioidea. Members of both groups are relatively large-bodied, morphologically distinctive, and usually brightly colored. The Uropodoidea are also strong indicators of Rainforest, and most taxa can be distinguished from other Mesostigmata by having pedofossae (excavations) for their legs and a flattened, circular to oval shape. Use of a medium-quality dissecting microscope, and the ability to differentiate members of the Erythraeidae (long-legged velvet mites, indicators of Pasture in this study) from trombidioids are all that are needed to include these taxa in a more general arthropod-based assessment program. These recommendations are currently geographically limited to eastern Australia, and researchers elsewhere are advised to determine whether the patterns in mite assemblages that we have found also hold true in their areas. Trombidioids, labidostomatids and uropodoids are cosmopolitan in distribution. An assessment protocol in which only these three groups of mites were identified would require relatively little time per sample; from our experience, a 2 L extraction could be scanned and these target taxa picked out in 20 min or less, compared to several hours for the sorting and mounting of all mite morphotaxa. This savings in time would allow many more samples to be taken from research sites, improving the likelihood of detecting target taxa. Should such an approach be followed, exemplars of target taxa plus the residuals containing all other specimens should be deposited at a university, museum or government institution to facilitate future study (this is the process followed by the Alberta Biodiversity Monitoring Institute for its soil extractions: see 'springtails and mites' protocol at http://www.abmi.ca/abmi/reports/reports.jsp?categoryId=0&subcategoryId=63). As a final comment, our use of mites should not be taken as advocacy of their superiority as indicator taxa, but rather as a complement to a multi-factor approach including plant structure and floristics, ecological function, birds, reptiles, mammals, ants, beetles and other invertebrates (Proctor *et al*., 2003; Catterall *et al*., 2004; Ruiz-Jaen & Aide, 2005).

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APPENDIX . Mite taxa identified from study sites. Numbers not in parentheses indicate number of sites of each habitat type in which the taxon was present. For Trombidioidea and Uropodoidea, total number of morphotaxa collected from each habitat type is also given. Immatures that could be identified to the taxa listed are included; for some groups, different life-history stages are presented separately. P= Pasture, YP= Young Monoculture Plantation, CT= Cabinet Timber, RG= unmanaged Regrowth, ER= Ecological Restoration, F= Rainforest.

			Tropical sites						Subtropical sites					
Higher taxa	**Family or superfamily**	**Genus or subfamily (stage)**	**P (5)**	**YP (5)**	**CT (5)**	**RG (5)**	**ER (10)**	**F (10)**	**P (5)**	**YP (5)**	**CT (10)**	**RG (5)**	**ER (9)**	**F (10)**
Astigmata	Acaridae		3	-	-	-	1	-	3	-	—	1	1	4
	Canestrenoidea		-	-	-	-	1	-	-	-	-	-	-	-
	Glycyphagidae		-	-	-	1	-	-	-	-	-	-	-	-
	Histiostomatidae		1	-	1	2	-	1	1	2	4	1	2	2
	Pyroglyphidae		-	-	-	1	-	-	-	-	-	-	-	-
	hypopodes[a, b]		-	3	3	2	5	7	3	4	4	4	8	10
Endeostigmata	Alicorhagiidae		-	-	-	-	-	3	-	-	-	-	1	8
	Bimichaeliidae		-	2	-	2	4	6	2	3	5	4	8	7
	Grandjeanicidae		-	-	-	-	-	-	-	-	-	-	1	1
	Lordalychidae		-	-	-	-	-	-	-	-	-	-	-	1
	Nanorchestidae	*Nanorchestes*	-	1	2	1	3	3	-	1	3	-	1	3
		Speleorchestes	1	2	1	1	1	-	3	4	2	-	-	1
	Terpnacaridae		-	-	-	-	-	-	1	1	1	-	-	-
Prostigmata	Acarophenacidae		-	-	-	-	-	-	-	1	-	-	-	-
	Anystidae		-	1	1	2	5	1	1	1	2	-	2	1
	Barbutiidae		-	-	-	-	-	-	-	-	-	1	-	-
	Bdellidae		2	1	3	3	5	2	-	4	3	-	1	3
	Caligonellidae		1	-	-	-	-	-	1	1	-	-	-	-
	Cheyletidae		-	-	-	-	1	-	-	-	-	-	1	-
	Cryptognathidae		2	1	2	1	-	1	1	4	1	-	-	1
	Cunaxidae	Bonziinae	-	-	-	-	-	-	-	-	-	-	1	1
	Cunaxinae		-	2	2	-	6	3	1	4	2	2	3	-
	Cunaxoidinae		5	4	4	2	3	2	5	5	6	-	2	2
	Dasythyreidae	*Xanthodasythyreus*	-	-	-	-	-	-	-	1	-	-	-	-
	Ereynetidae		-	1	-	1	1	4	2	-	-	4	3	7
	Erythraeidae[b]	(adults)	2	-	1	1	-	2	4	3	2	-	-	-
		(larvae)	1	-	-	2	2	1	1	1	-	-	-	-
	Eupodidae		4	5	5	4	10	9	5	5	9	3	9	8
	Labidostomatidae		-	-	-	-	-	2	-	-	-	1	-	8
	Microdispidae		1	2	2	2	2	3	3	3	2	-	2	1
	Paratydeidae		-	-	-	-	-	-	1	-	-	-	-	-
	Penthaleidae		-	1	-	-	-	-	-	-	-	-	-	-
	Penthalodidae		-	-	-	-	-	2	-	-	-	-	-	1
	Pseudocheylidae		-	1	-	-	-	-	-	-	-	-	-	-
	Pygmephoridae		3	1	1	1	3	2	3	-	1	-	-	2
	Raphignathidae		-	1	-	2	-	-	2	2	1	-	-	1
	Rhagidiidae		-	1	-	1	1	4	-	1	1	-	4	5
	Scutacaridae		2	4	3	1	2	1	3	1	1	4	3	6
	Smaridiidae		-	-	-	-	-	2	-	-	-	-	-	1
	Sphaerolichidae		-	-	-	-	-	-	-	-	-	-	-	1
	Stigmaeidae		2	3	2	2	5	2	1	4	4	1	3	1
	Tarsonemidae		5	3	5	3	9	4	3	3	2	1	-	2
	Tenuipalpidae		-	-	1	-	1	-	1	-	-	-	-	-
	Tetranychidae		1	-	-	-	-	-	1	1	-	-	-	-
	Trombidioidea[b]	(adults) /total # morphotaxa	-	1/2	2/2	1/1	-	6/5	-	2/2	3/4	-	8/10	8/8
		(larvae) /total # morphotaxa	-	1	-	1	1	7	1	3	1	1	4	6
	Tydeidae		5	5	5	-	10	4	5	3	5	2	-	2
Mesostigmata	Ameroseiidae		-	-	1	-	2	2	-	-	-	-	-	-
	Ascidae[c]	*Arrhenoseius*	-	-	-	-	-	-	-	-	-	1	1	1
		Asca	5	5	5	3	9	6	2	3	5	1	4	2
		Blattisocius	-	-	-	-	-	1	-	-	-	-	-	-
		Cheiroseius	-	3	2	-	1	2	-	1	5	-	-	-
		Gamasellodes	2	-	1	-	1	2	1	2	1	-	2	1
		Iphidozercon	-	-	-	-	-	-	1	1	1	2	-	2

			Tropical sites						Subtropical sites					
Higher taxa	**Family or superfamily**	**Genus or subfamily (stage)**	**P (5)**	**YP (5)**	**CT (5)**	**RG (5)**	**ER (10)**	**F (10)**	**P (5)**	**YP (5)**	**CT (10)**	**RG (5)**	**ER (9)**	**F (10)**
		Lasioseius	1	3	1	-	1	7	-	-	-	-	1	2
		Proctolaelaps	3	-	1	1	2	2	1	2	1	1	-	3
		Protogamasellus	1	1	-	1	2	-	-	-	2	-	-	-
		Zerconopsis	-	-	-	-	-	1	-	-	-	-	-	-
	Asternoseiidae	*Asternoseius*	-	-	-	-	-	-	-	-	-	-	-	1
	Digamasellidae		-	-	-	-	-	1	4	-	-	-	-	-
	Diplogyniidae		-	-	-	-	-	-	-	-	-	-	-	1
	Eviphididae		-	1	2	-	2	2	-	-	-	1	2	2
	Laelapidae	*Cosmolaelaps*	1	1	1	-	3	4	1	1	2	2	7	6
		Geolaelaps	-	1	1	-	-	3	1	-	1	1	-	-
		Hypoaspidinae	-	-	-	-	-	-	3	1	2	-	2	1
		nr *Laelaptoseius*	-	-	-	-	-	1	-	-	-	-	-	3
		Pseudoparasitus	2	-	2	-	4	-	2	-	2	-	3	-
	Macrochelidae		2	2	4	-	2	1	3	-	1	1	1	4
	Ologamasidae	*Antennolaelaps*	-	-	1	2	2	1	-	-	1	1	1	2
		Athiasella	5	-	2	2	1	7	4	3	8	3	9	8
		Euepicrius	-	-	-	-	-	-	-	-	1	-	-	3
		Gamasellus	-	-	-	-	-	-	-	-	-	-	-	4
		Gamasiphis/ *Gamasiphisoides*/ *Caliphis*	5	3	4	3	9	9	4	2	8	4	6	8
		Geogamasus	-	-	-	-	-	-	-	-	-	1	-	-
		Hydrogamasus?	-	-	-	-	-	-	3	2	5	3	8	3
		Hiniphis	-	-	-	-	1	4	-	-	-	-	-	-
		nr. *Queenslandolaelaps*	-	1	-	-	-	-	-	-	-	-	-	-
		nr. *Euepicrius*	-	-	-	-	-	1	-	-	-	-	-	-
		unknown genus	-	-	-	-	-	2	-	-	-	-	-	-
		Laelaptiella	-	-	-	-	-	-	-	1	1	-	-	1
		Onchogamasus?	-	-	-	-	-	-	-	-	-	-	-	2
		Pyriphis?	-	-	-	-	-	-	-	-	-	-	-	1
		Queenslandolaelaps	-	-	-	-	-	-	1	-	2	-	1	-
	Paramegistidae	*Derrickia*	-	-	-	-	-	-	-	-	-	-	-	1
	Parasitidae		5	4	4	4	7	1	3	-	3	3	3	-
	Pachylaelapidae		-	-	-	-	-	-	1	-	-	-	-	-
	Parholaspididae		-	1	2	-	5	2	-	-	-	1	3	-
	Phytoseiidae		2	-	4	3	8	2	1	2	1	-	-	1
	Podocinidae		2	2	4	2	6	3	-	1	4	-	1	2
	Polyaspididae		-	3	-	-	-	2	1	1	-	4	3	3
	Rhodacaridae		1	-	-	-	-	-	2	-	5	1	-	-
	Trachytidae		-	-	-	-	-	-	-	-	-	-	2	7
	Triplogyniidae		-	-	1	-	-	-	-	-	-	-	-	-
	Uropodoidea[b]	(adults)/ total # morphotaxa)	2(1)	2(4)	1(2)	1(1)	6(5)	10(12)	3(2)	1(2)	3(4)	3(2)	7(8)	10(15)
		(juveniles) /total # morphotaxa	-	-	-	-	5	9	1	3	1	3	2	9
	Veigaiidae		-	2	-	-	3	2	1	2	1	2	4	0
Ixodida	Ixodidae		1	1	-	-	-	-	2	1	-	-	-	-
Holothyrida	Allothyridae		-	-	-	-	-	-	-	-	1	-	1	-

[a]hypopodes = phoretic deutonymphs of Astigmata.
[b]these taxa split into adult and juvenile (phoretic/parasitic) stages because of the possibility of their having different habitat associations.
[c]Ascidae *sensu* Lindquist & Evans (1965).