

Quantifying the abundance of four large epiphytic fern species in remnant complex notophyll vine forest on the Atherton Tableland, north Queensland, Australia

Jason Cummings, Michelle Martin and Anne Rogers

¹School for Field Studies, PO Box 141, Yungaburra QLD 4884

²Present address GHD Pty Ltd, Belconnen ACT 2617 email:jason.cummings@ghd.com.au

Abstract: Epiphytes are generally considered rare in complex forests on the western edge of the Atherton Tablelands, north Queensland. This assertion is based on comparisons with wetter forests in the Wet Tropics bioregion, but is of limited use in restoration projects where targets need to be quantified. We quantified ‘rarity’ for a subset of the epiphyte community in one of the largest remaining patches of Type 5b rainforest at Wongabel State Forest (17°18' S, 145°28' E). The abundance of large individuals of the epiphytic fern species *Asplenium australasicum*, *Drynaria rigidula*, *Platycerium bifurcatum*, and *Platycerium superbum* were recorded from 100 identified mid-storey or canopy trees. Epiphytes were less rare than the canopy trees sampled, averaging 1.7 individuals per tree. A clumped distribution was suggested with large epiphytes only occurring on 57 of the 100 trees. As tree size increased so did the number of individuals and species of large epiphytes recorded; only trees taller than 20 m yielded more than one epiphyte. Trees from the Meliaceae and Rutaceae hosted the most epiphytes, but host tree specificity patterns were not conclusive. Techniques for including epiphytes in restoration planning and projects are considered, and a quantified restoration target for epiphyte communities in Type 5b plantings is outlined.

Cunninghamia (2006) 9(4): 521–527

Introduction

Historical land clearing associated with timber-getting and agriculture has led to significant fragmentation of the rainforests of tropical North Queensland (Goosem et al. 1999). Since the establishment of the Wet Tropics World Heritage Area in 1988, the economic base for many local communities has gradually changed from forestry to tourism. Given the high biodiversity values of the rainforests in tropical North Queensland, and the creation of an extensive reserve system, conservation efforts for these rainforests have increasingly included restoration of forest linkages across the fragmented landscape (WTMA 2004). Rainforest communities on the Atherton Tablelands of tropical North Queensland are some of the most highly fragmented, and are at further risk from predicted climate changes (Hilbert et al. 2001). Therefore, the imperative to restore these communities, and linkages between them, is paramount (Catterall et al. 2004).

‘Type 5b’ forest, or complex notophyll vine forest, was first mapped by Tracey and Webb (1975) and has the notoriety of recently being scheduled as one of Australia’s first *critically endangered* ecosystems (QLD EPA Regional Ecosystem 7.8.3, DEH 2005). The majority of this forest type occurs on nutrient rich basalt soils across a variety of elevations associated with the Atherton Tablelands in far North Queensland. Land clearing has resulted in the loss of at least 90 % of its original area. The reduction in size

and connectivity between patches has been recognised as a major conservation issue for this forest type (DEH 2005), and stimulated the restoration of patches and corridors on the Atherton Tablelands.

Since the mapping and description of ‘Type 5b’ rainforest (Tracey & Webb 1975, Tracey 1987), significant efforts have been made to save this endangered forest type through reservation and ecological restoration. At the site scale, creation of new patches of rainforest on private and government land have relied primarily on planting and weed control (Goosem & Tucker 1995; Tucker et al. 2004) with many now achieving canopy closure (Kanowski et al. 2003). At this stage of restoration, it is appropriate to consider whether the plantings are on a trajectory towards becoming patches of Type 5b rainforest.

Epiphytes are plants rooting on the surface of tree trunks or branches without harming the host tree (Benzing 2004). Epiphytes contribute to species diversity, primary productivity, biomass, litter fall, water retention, and provide substrate for nitrogen fixing bacteria (Benzing 1998, Munoz et al. 2003). Epiphytes also provide important resources including forage sites and shelter to many canopy animals such as birds (Cruz-Angon & Greenberg 2005), pythons (Freeman et al. 2005), and invertebrates (Ellwood et al. 2002). From a Wet Tropics perspective, epiphytes contribute a substantial component of ‘complexity’ to ‘complex’ forests (Tracey 1987) and

have been used as an indicator of structural complexity in comparing local plantations, ecological restoration plots and mesophyll and notophyll forests (Wardell-Johnson et al. 2005). Ecological restoration projects on the Atherton Tablelands have now been undertaken for over 20 years, focusing on the re-planting of forest communities in land that was previously used for agriculture (Goosem & Tucker 1995; Catterall et al. 2004). With the successful establishment of tree cover (Kanowski et al. 2003), the question of how to re-introduce those elements of rainforest ecosystems that make them 'rainforest' (e.g. lianes, large-leaved herbs, palms, and epiphytes) can be examined. Restoration of forest types that are defined by the presence of epiphytes (amongst other life forms), will ultimately necessarily involve restoration of epiphyte communities. Establishment of epiphyte communities will enhance energy capture, moisture capture and retention, and biotic community diversity in restoration plantings, continuing the process of returning agricultural pasture to a complex forest.

Despite their inherent importance, there has been no systematic survey of epiphyte populations across the Wet Tropics. The comparison of restoration plots with reference forest communities has been recommended to monitor progress and assess success (Kanowski et al. 2003; Catterall et al. 2004; Wardell-Johnson et al. 2005), to do this we need to quantify the various structural elements in complex forests to provide benchmarks for restoration plots. We have initiated a program to begin to determine ways of re-introducing epiphytes to rainforest plantings, but we have no knowledge of appropriate restoration targets (e.g. biomass of epiphytes per m³, number of species per tree etc.) for plantings. If the goal is to restore complex forest communities, restoration success cannot be demonstrated without such targets (Lake 2001).

Several large epiphyte species occur in Type 5b rainforests (Plate 1), including (but not limited to) *Asplenium australasicum* (Bird's Nest Fern), *Drynaria rigidula* (Basket Fern), *Platynerium bifurcatum* (Elkhorn Fern), and

Table 1. Species richness and abundance of epiphytes for tree families in complex notophyll vine forest in Wongabel State Forest, north Queensland. Families below the line had fewer than 5 trees sampled.

Tree family	Number of trees sampled	Number of epiphyte species recorded	Epiphyte species richness per tree (means +/- se)	Epiphyte abundance per tree (means +/- se)
Meliaceae	14	8	1.00 (0.23)	3.71 (1.05)
Rutaceae	13	7	1.08 (0.35)	2.46 (0.81)
Lauraceae	11	7	0.82 (0.23)	1.55 (0.47)
Euphorbiaceae	6	2	1.00 (0.37)	1.50 (0.56)
Monimiaceae	6	3	1.00 (0.45)	1.83 (0.79)
Sapindaceae	6	3	0.50 (0.22)	0.67 (0.33)
Sterculiaceae	5	4	0.80 (0.37)	1.20 (0.49)
Alangiaceae	3	1	0.33 (0.33)	0.33 (0.33)
Boraginaceae	3	2	0.33 (0.33)	0.33 (0.33)
Myrtaceae	3	3	0.00 (0.00)	0.00 (0.00)
Sapotaceae	3	3	0.33 (0.33)	0.67 (0.67)
Verbenaceae	3	2	0.33 (0.33)	0.67 (0.67)
Anacardiaceae	2	2	1.50 (0.50)	3.50 (1.50)
Apocynaceae	2	1	1.00 (0.00)	1.00 (0.00)
Elaeocarpaceae	2	2	0.50 (0.50)	2.00 (2.00)
Fabaceae	2	1	1.00 (0.00)	1.50 (0.50)
Moraceae	2	2	1.50 (1.50)	2.00 (2.00)
Myristicaceae	2	1	0.50 (0.50)	1.50 (1.50)
Nyctaginaceae	2	1	1.00 (0.00)	1.00 (0.00)
Proteaceae	2	1	1.00 (1.00)	1.00 (1.00)
Urticaceae	2	2	1.00 (0.00)	1.00 (0.00)
Araliaceae	1	1	0.00 (NA)	0.00 (NA)
Ebenaceae	1	1	1.00 (NA)	1.00 (NA)
Flacourtiaceae	1	1	0.00 (NA)	0.00 (NA)
Surianaceae	1	1	0.00 (NA)	0.00 (NA)
Thymelaeaceae	1	1	0.00 (NA)	0.00 (NA)
Ulmaceae	1	1	0.00 (NA)	0.00 (NA)

Platyserium superbum (Staghorn Fern). Two of these species (or their congeners) have been noted for their functional significance; *Asplenium nidus* has been implicated in mediating forest climate (Palmer & Stork 2005) and hosting invertebrate communities (Ellwood et al. 2002), whilst *Drynaria rigidula* has been noted as providing a basking habitat for large pythons (Freeman et al. 2005; pers. obs.). Despite differences in shape, the contribution each of these species makes to canopy soil organic matter (*sensu* Nadkarni et al. 2002) via their nest building growth processes (Jones & Clemesha 1976), means each is likely to contribute to maintaining forest humidity. Further, each of these species also contributes in their own right to forest structure and biodiversity. The aim of this study was to survey large epiphytes in a patch of Type 5b forest to to: (1) document their abundance within a mature Type 5b forest stand; (2) highlight potential affinities between epiphyte species and

host taxa; and (3) recommend quantified targets for epiphyte establishment in developing Type 5b restoration plantings on the Atherton Tablelands.

Methods

Wongabel State Forest, located on the western edge of the Atherton Tablelands (17°18' S, 145°28' E) in the wet tropics region of north Queensland, is a reserve of approximately 600 ha containing Type 5b rainforest (complex notophyll vine forest; Webb & Tracey 1975). The Type 5b forest at Wongabel occurs on basalt soil, and has a multi-layered canopy ranging in height from 25 to 45 m, and a distinct shrub layer (Webb & Tracey 1975).

In March 2005 100 trees whose crowns reached the canopy or were in the mid-storey were surveyed. Trees sampled were

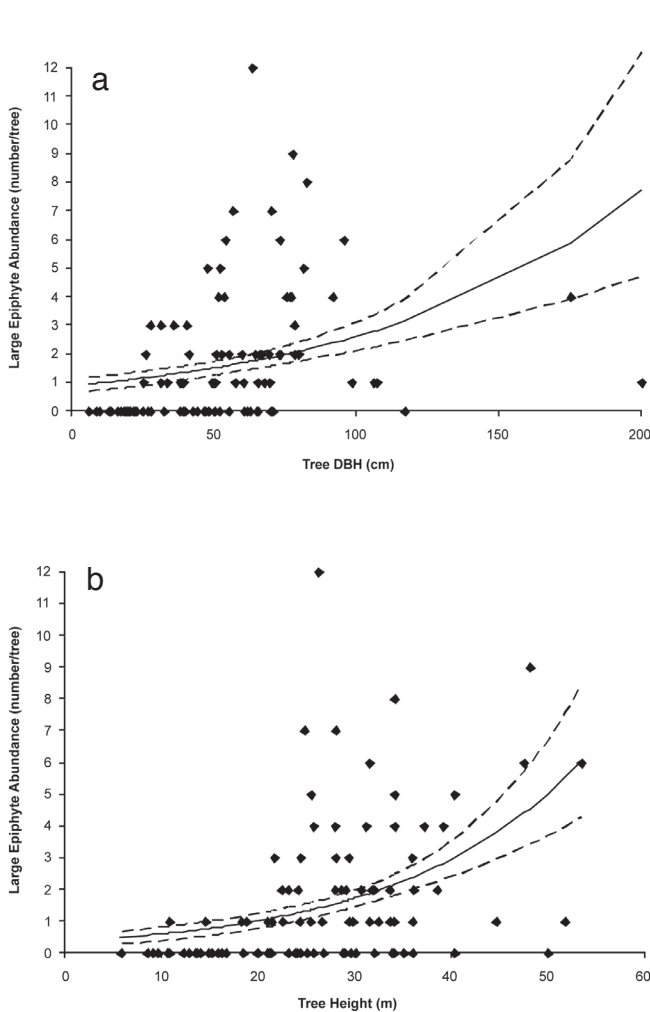


Fig. 1. The relationship between large epiphyte abundance and a) tree dbh, and b) tree height. Diamonds are observed values, the solid line is the predicted mean and dashed lines are lower and upper 95 % confidence limits.

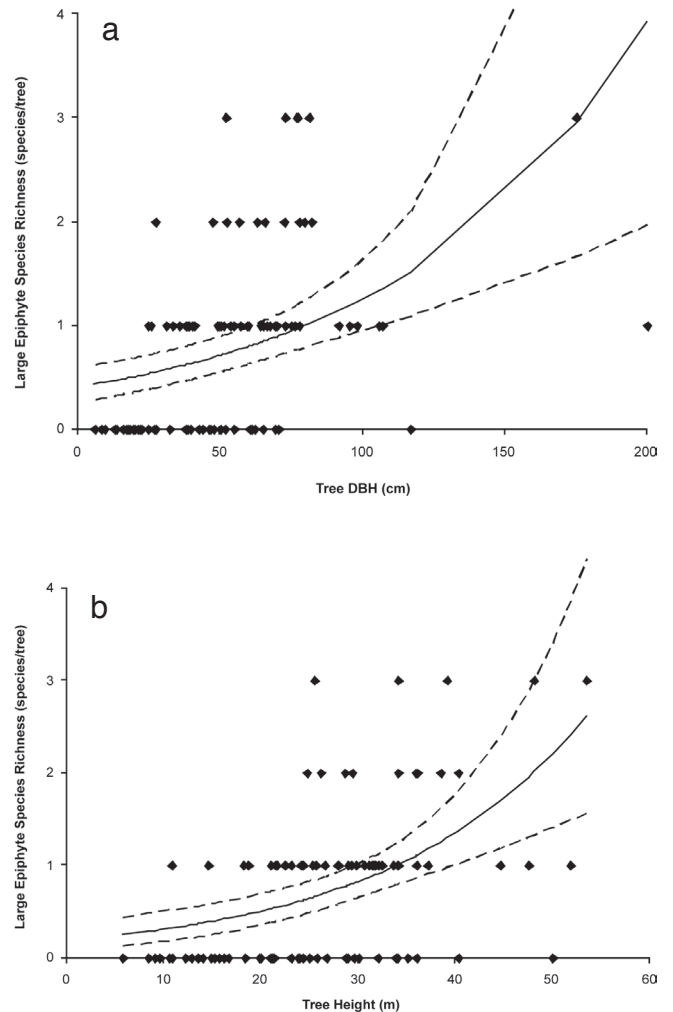


Fig. 2. The relationship between large epiphyte species richness and a) tree dbh, and b) tree height. Diamonds are observed values, the solid line is the predicted mean and dashed lines are lower and upper 95 % confidence limits.

all within 20 m of a trail through the forest and identified using a botanical guide developed specifically for this trail (Queensland Department of Forestry 1987). The presence and abundance of *Asplenium australasicum* (Aspleniaceae, Bird's Nest Fern), *Drynaria rigidula* (Polypodiaceae, Basket Fern), *Platynerium bifurcatum* (Polypodiaceae, Elkhorn Fern), and *Platynerium superbum* (Polypodiaceae, Staghorn Fern) were recorded (Andrews 1990). These species were selected as they can be readily distinguished from the ground once their reproductive fronds have developed, and are large and therefore potentially functionally significant (e.g. for moisture capture and forest humidity retention). To ensure accurate species identification from the ground using binoculars, only epiphytes with a basal diameter (the area of contact between the fern and the host tree) greater than about 10 cm were recorded. Host tree height and diameter at breast height (dbh) were recorded using a clinometer and diameter tape, respectively.

Poisson regressions using a log-link function were used to determine whether host-tree height or dbh influence the abundance and species richness of large epiphytes. Multiple regressions were not used as host tree dbh and height are not independent. The test of significance of the logistic regression models was the Wald statistic, which is tested against the Chi-square distribution (StatSoft 1999). All analyses were performed using the program STATISTICA (StatSoft, Oklahoma, USA).

Results

Large epiphytes occurred on 57 % of trees sampled, at an overall average of 1.7 (+/- 0.3) epiphytes per tree. The average abundance of large epiphytes on the 57 host trees was 2.9 (+/- 0.4). No trees sampled had all four species surveyed, with an overall average species richness of 0.8 (+/- 0.1). For host trees only, epiphyte species richness increased to 1.4 (+/- 0.1) epiphyte species per tree.

Asplenium australasicum was the most frequent large epiphyte, with 113 individuals recorded on 46 of the 100 trees sampled. On host trees, *Asplenium australasicum* abundance averaged 2.5 (+/- 0.3) individuals per tree. Individuals of *Drynaria rigidula* were recorded 35 times on 20 host trees at an overall average abundance of 1.1 (+/- 0.3) individuals per host tree. Only 16 *Platynerium superbum* and 3 *Platynerium bifurcatum* were recorded on the 100 trees sampled.

Both host tree height (Wald statistic = 52.9, df = 1, $p < 0.001$) and dbh (Wald statistic = 37.5, df = 1, $p < 0.001$) contributed to variation in epiphyte abundance. As tree height and dbh increased, the number of large epiphytes also increased (Fig. 1). Total epiphyte abundance ranged from 0–1 in 'small trees' (< 20 m) to 0–12 in relatively 'large trees' (> 20 m). Similarly, host tree height (Wald statistic = 21.2, df = 1, $p < 0.001$) and dbh (Wald statistic = 20.3, df = 1, $p < 0.001$)

contributed to the number of species of large epiphytes recorded. With increasing tree size, epiphyte species richness increased, within the 1–4 species range (Fig. 2).

Representatives of 27 families were sampled for epiphytes, with 7 families having 5 or more individuals sampled (Table 1). Host trees from the Meliaceae and Rutaceae, the most commonly sampled families, exhibited the greatest frequency of epiphyte abundance. The Sapindaceae yielded about 25 % of the epiphyte abundance compared to Meliaceae and Rutaceae with the Lauraceae, Euphorbiaceae and Monimiaceae intermediate. Species richness patterns with respect to host tree family were less evident, each of the aforementioned families, except the Sapindaceae, averaged around 1 species of large epiphyte per tree.

Discussion

Large epiphytes were, on average, as abundant as the trees in Wongabel State Forest at 1.7 individuals per tree and occurring on 57 % of all trees. There has been no estimate of epiphyte abundance in Australian tropical rainforests, although they have been estimated to contribute up to 10 % of native plant species richness in tropical forests and approximately 5 % in sub-tropical forests (Wardell-Johnson et al. 2005). In Brazilian rocky outcrops, an average of 9.5 vascular epiphytes per *Vellozia piresiana* (a small tree) was recorded, but this survey included a larger array of epiphyte species across size ranges (de Souza Werneck & Espirito-Santo 2002). Only 23 % of *Vellozia piresiana* did not host epiphytes. On tree ferns in Tasmanian closed forests, frequency of occurrence of *Asplenium bulbiferum* and *Microsorium pustulatum* (Polypodiaceae) ranged from 18–26 % and 10–18 %, respectively (Roberts et al. 2003). Despite the difficulties in comparisons, it is likely epiphyte abundance in Type 5b rainforest is lower than tropical forests elsewhere in the Tropics but greater than southern Australian forests.

Asplenium australasicum was the most abundant large epiphyte species in this forest, occurring on nearly half of the trees sampled. *Asplenium* species have been noted for their abundance in tropical forests throughout the world (Ellwood & Foster 2004). *Asplenium* species often contain significant invertebrate communities (Ellwood et al. 2002) and their rosette shape captures and retains moisture. The abundance of *Asplenium australasicum* in this Type 5b rainforest patch seems contradictory to the assertion that epiphytes are rare in this forest type (Tracey 1987), and ignoring them in restoration efforts may reduce the functional complexity of restoration plantings. When compared to wetter forest types in this region, *Asplenium australasicum* may be relatively less abundant in Type 5b forest, but until its relative abundance in different forest types is quantified, a degree of caution should be taken when considering management, and especially restoration, of these forests.

Taken together, the other three epiphyte species surveyed, summed to less than half of the number of large epiphytes recorded. Comparisons of the recorded abundances of *Drynaria rigidula*, *Platyserium bifurcatum* and *Platyserium superbum* with other locations are difficult, with no information on abundances available. Interestingly, *Drynaria rigidula* is noted for its occurrence in drier, more open forests in Queensland (Andrews 1990) and was not listed as an epiphyte that occurred in this forest type when it was described (Tracey 1987). Given that *Platyserium bifurcatum* was listed for Type 5b rainforest (Tracey 1987), and that in this survey it occurred 10-times less frequently than *Drynaria rigidula*, a change in epiphyte community composition may have occurred in the last 20 years. Given the potential for epiphyte communities to be used as climate change indicators (Benzing 1998), further work is required to test this hypothesis across remnants of Type 5b rainforest.

Tree size contributed to the number and species richness of large epiphytes in Type 5b rainforest. Larger trees supported more epiphytic bromeliads in Costa Rican tree plantations (Merwin et al. 2003). For three host tree species, *Polypodium polypodioides* (Polypodiaceae) abundance increased with tree dbh in American sub-tropical forest (Callaway et al.

2002). Tree size relates to several factors that contribute to epiphyte establishment and growth. Larger trees are likely, on average, to be older, allowing more time to capture spores. Taller trees provide better access for epiphytes to light, whilst large trees, both in terms of height in canopy and surface area available, likely capture more water than small trees, an essential determinant of epiphyte distribution (Benzing 2004). The increase in abundance of epiphytes with tree size in this Type 5b patch is in accordance with findings elsewhere. For restoration of Type 5b forest to be considered successful, large epiphytes should occur on approximately half of the trees in restoration plots once those trees reach a height greater than 20 m.

The Meliaceae and Rutaceae displayed the greatest abundance of large epiphytes, whilst the species richness was relatively even amongst host-tree families. Host tree specificity explains the distribution of some epiphytic taxa (e.g. Nieder et al. 2000; Callaway et al. 2002; Moran et al. 2003) but not others (e.g. Zimmerman & Olmsted 1992). The evidence for host tree specificity in the case of epiphyte species surveyed here is inconclusive but warrants further investigation. From a pragmatic perspective, introduction of epiphytes into restoration plantings should initially focus on host trees from the Meliaceae and Rutaceae families.



Fig. 3. An example of *Platyserium superbum* and *Asplenium australasicum* occurring in Wongabel State Forest, where epiphytes are considered 'rare' compared to other forest types

Management Implications

For a subset of the epiphyte community, the assertion that epiphytes are rare in Type 5b forests (Tracey 1987; DEH 2005) has now been quantified. On average, large epiphytes are only as rare as the trees that comprise this forest type. We have observed members of the genera *Pyrrosia*, *Belvisia*, *Antrophyum* and *Dendrobium* in this forest patch, undoubtedly if these smaller epiphytes were included in the survey, epiphytes would be more abundant per unit area than host trees. Semantics aside, epiphytes warrant consideration in planning restoration of these complex forest communities and this study allows the development of quantified goals for their establishment.

A goal of establishing large epiphytes on approximately half of the trees in a restoration planting seems reasonable given their observed abundances in this forest. Under ideal circumstances, conditions favourable to epiphyte establishment will be created and dispersal from adjacent remnants should occur (Kanowski et al. 2003; Catterall et al. 2004; Wardell-Johnson et al. 2005). To promote and accelerate restoration of structurally complex forests, epiphytes should be considered for early reintroduction to restoration plantings, particularly given their functional significance. *Asplenium australasicum* and *Drynaria rigidula* should provide an initial focus for restoration efforts once canopy closure has been achieved in Type 5b restoration plantings. Individuals could initially be sourced from local tree falls or land being cleared, but ideally propagation techniques from spores should be considered (e.g. Bourne 1994).

Ecosystem function will likely be enhanced by placement of epiphytes into restoration plantings; habitat complexity will be increased and moisture and energy capture and retention will be enhanced. Further, with epiphytes incorporated into a restoration planting, the elusive claim of 'restoration success', with respect to establishing complex forest communities, will be one step closer.

Although structural complexity has been considered at a broad scale across re-forestation types (Kanowski et al. 2003; Catterall et al. 2004), there has been little consideration of establishing complexity within restoration plantings. In young restoration plantings (6–22 years old), epiphyte frequency has been recorded at approximately 17 % of nearby intact forest (Kanowski et al. 2003) and epiphyte species have been noted to colonise plantations greater than 50 years of age (Keenan et al. 1997). Given the functional benefits that epiphytes may provide to a young restoration planting, their accelerated inclusion into plantings should be considered. Under circumstances where restoration plantings are spatially isolated and thus recruitment may be limited (Tucker & Murphy 1997), epiphytes may need to manually reintroduced to move the planting towards a complex forest community.

Acknowledgements

Tim Curran and an anonymous reviewer provided valuable comments on a draft of this manuscript. The work was fully supported by the School for Field Studies, and represents contribution 05/JC01 to the Centre for Rainforest Studies' 5-year Research Plan.

References

- Andrews, S.B. (1990) *Ferns of Queensland*. (Queensland Dept of Primary Industries: Brisbane).
- Benzing, D.H. (1998) Vulnerabilities of tropical forests to climate change: the significance of resident epiphytes. *Climatic Change* 39: 519–540.
- Benzing, D.H. (2004) Vascular epiphytes. Pp. 175–211 in Lowman, M.D. & Rinker, H.B. (eds.), *Forest Canopies* (Elsevier Academic Press: Sydney).
- Bourne, R.A. (1994) The development of a program of commercial production of staghorns from plant tissue culture. *Combined Proceedings International Plant Propagators' Society* 44: 90–93.
- Callaway, R.M., Reinhart, K.O., Moore, G.W., Moore, D.J. & Pennings, S.C. (2002) Epiphyte host preferences and host traits: mechanisms for species-specific interactions. *Oecologia* 132: 221–230.
- Catterall, C.P., Kanowski, J., Wardell-Johnson, G., Proctor, H., Reis, T., Harrison, D. & Tucker, N.I.J. (2004) Quantifying the biodiversity values of reforestation: perspectives, design issues and outcomes in Australian rainforest landscapes. Pp. 359–393 in Lunney, D. (ed.), *Conservation of Australia's Forest Fauna* (Royal Zoological Society of NSW, Sydney).
- Cruz-Angon, A. & Greenberg, R. (2005) Are epiphytes important for birds in coffee plantations? An experimental assessment. *Journal of Applied Ecology* 42: 150–159.
- de Souza Werneck, M. & do Espirito-Santo, M.M. (2002) Species diversity and abundance of vascular epiphytes on *Vellozia piresiana* in Brazil. *Biotropica* 34: 51–57.
- DEH (2005) Mabi Forest - Advice to the Minister for the Environment and Heritage from the Threatened Species Scientific Committee (TSSC) on Amendments to the List of Ecological Communities under the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) (Dept of Environment and Heritage: Canberra).
- Ellwood, M.D.F. & Foster, W.A. (2004) Doubling the estimate of invertebrate biomass in a rainforest canopy. *Nature* 429: 549–551.
- Ellwood, M.D.F., Jones, D.F. & Foster, W.A. (2002) Canopy ferns in lowland dipterocarp forest support a prolific abundance of ants, termites, and other invertebrates. *Biotropica* 34: 575–583.
- Freeman, A.B., Freeman, A.N.D. & Krockenberger, A. (2005) Predators on the prowl: how does Australia's largest snake survive in a fragmented landscape? Poster presentation. (Joint Meeting of Ichthyologists and Herpetologists, Tampa, Florida).
- Goosem, S., Morgan, G. & Kemp, J.E. (1999) Wet Tropics. Chapter 7 in P.S. Sattler & R.D. Williams (eds), *The Conservation Status of Queensland's Regional Ecosystems*. (Environmental Protection Agency: Brisbane).
- Goosem, S. & Tucker, N.I.J. (1995) *Repairing the rainforest: theory and practice of rainforest re-establishment in north Queensland's Wet Tropics* (Wet Tropics Management Authority: Cairns).
- Hilbert, D.W., Ostendorf, B. & Hopkins, M.S. (2001) Sensitivity of tropical forests to climate change in the humid tropics of north Queensland. *Austral Ecology* 26: 590–603.
- Jones, D.L. & Clemesha, S.C. (1976) *Australian Ferns and Fern Allies*. (A.H. & A.W Reed, Sydney).
- Kanowski, J., Catterall, C.P., Wardell-Johnson, G.W., Proctor, H. & Reis, T. (2003) Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology and Management* 183: 265–280.
- Keenan, R.J., Lamb, D., Woldring, O., Irvine, T. & Jensen, R. (1997) Restoration of plant biodiversity beneath tropical tree plantations in Northern Australia. *Forest Ecology and Management* 99: 117–131.
- Lake, P.S. (2001) On the maturing of restoration: linking ecological research and restoration. *Ecological Management and Restoration* 2: 110–115.
- Merwin, M.C., Rentmeester, S.A. & Nadkarni, N.M. (2003) The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. *Biotropica* 35: 37–47.
- Moran, R.C., Klimas, S. & Carlsen, M. (2003) Low-trunk epiphytic ferns on tree ferns versus angiosperms in Costa Rica. *Biotropica* 35: 48–56.
- Munoz, A.A., Chacon, P., Perez, F., Barnert, E.S., & Armesto, J.J. (2003) Diversity and host tree preferences of vascular epiphytes and vines in a temperate rainforest in Southern Chile. *Australian Journal of Botany* 51: 381–391.
- Nadkarni, N.M., Schaefer, D., Matelson, T.J., & Solano, R. (2002) Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, Monteverde, Costa Rica. *Pedobiologia* 46: 24–33.

- Nieder, J., Engwald, S., Klawun, M. & Barthlott, W. (2000) Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland Amazonian rain forest (Surumoni Crane Plot) of southern Venezuela. *Biotropica* 32: 385–396.
- Palmer, N. & Stork, N. (2005) *The Australian Canopy Crane 1999–2005: supporting world class canopy research*. (Rainforest CRC: Cairns, Australia).
- Queensland Department of Forestry (1987) *Visitor information: Wongabel botanical walk*. (Queensland Dept of Forestry: Atherton District).
- Roberts, N.R., Dalton, P.J., & Jordan, G.J. (2003) A species list for the bryophytes and ferns occurring as epiphytes on Tasmanian tree ferns. *Hikobia* 14: 25–31.
- StatSoft (1999) STATISTICA for Windows. (StatSoft: Oklahoma).
- Tracey, J.G. (1987) *The vegetation of the humid tropical region of north Queensland*. (CSIRO: Melbourne).
- Tracey, J.G. & Webb, L.J. (1975) *Vegetation of the humid tropical region of north Queensland* (CSIRO: Brisbane).
- Tucker, N.I.J. & Murphy, T.M. (1997) The effects of ecological rehabilitation on vegetation recruitment: some observations from the Wet Tropics of north Queensland. *Forest Ecology and Management* 99: 133–152.
- Tucker, N.I.J., Wardell-Johnson, G., Catterall, C.P., & Kanowski, J. (2004) Agroforestry and biodiversity: improving conservation outcomes in tropical northeastern Australia. Pp. 431–452 in Schroth, G., da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, H.L. & Izac, A.N. (eds.), *Agroforestry and Biodiversity Conservation in Tropical Landscapes* (Island Press: Washington DC).
- Wardell-Johnson, G., Kanowski, J., Catterall, C.P., McKenna, S., Piper, S. & Lamb, D. (2005) Rainforest timber plantations and the restoration of plant biodiversity in tropical and subtropical Australia. Pp. 162–182 in Erskine, P.D., Lamb, D. & Bristow, M. (eds.), *Reforestation in the Tropics and Subtropics of Australia* (Rural Industries Research and Development Corporation, Canberra, and the Rainforest CRC: Cairns).
- WTMA (2004) *Wet Tropics Conservation Strategy (2004)* (Wet Tropics Management Authority and Queensland Parks and Wildlife Services: Cairns).
- Zimmerman, J.K. & Olmstead, I.C. (1992) Host tree utilization by vascular epiphytes in a seasonally inundated forest (Tintal) in Mexico. *Biotropica* 24: 402–407.