

13. Kurtz, R. D., DeLaurier, J. M. & Gupta, J. C. The electrical conductivity distribution beneath Vancouver Island: A region of active plate subduction. *J. Geophys. Res.* **95**, 10929–10946 (1990).
 14. Jones, T. D. & Nur, A. The nature of seismic reflections from deep crustal fault zones. *J. Geophys. Res.* **89**, 3153–3171 (1984).
 15. Higgins, M. W. Cataclastic rocks. *Prof. Pap. US Geol. Surv.* **687** (1971).
 16. Cassidy, J. F. & Ellis, R. M. Shear wave constraints on a deep crustal reflective zone beneath Vancouver Island. *J. Geophys. Res.* **96**, 19843–19851 (1991).
 17. Spence, G. D., Clowes, R. M. & Ellis, R. M. Seismic structure across the active subduction zone of western Canada. *J. Geophys. Res.* **90**, 6754–6772 (1985).
 18. Bostock, M. G. *et al.* An inverted continental Moho and serpentinization of the forearc mantle. *Nature* **417**, 536–538 (2002).
 19. Brocher, T. M. *et al.* Seismic evidence for widespread serpentinized forearc upper mantle along the Cascadia margin. *Geology* **31**, 267–270 (2003).
 20. Peacock, S. M. & Hyndman, R. D. Hydrous minerals in the mantle wedge and the maximum depth of subduction thrust earthquakes. *Earth Planet. Sci. Lett.* **26**, 2517–2520 (1999).
 21. Buske, S. *et al.* Broad depth range seismic imaging of the subducted Nazca slab, North Chile. *Tectonophysics* **350**, 273–282 (2002).
 22. Oncken, O. *et al.* Seismic reflection image revealing offset of Andean subduction-zone earthquake locations into oceanic mantle. *Nature* **397**, 341–344 (1999).
 23. Hyndman, R. D., Yorath, C. J., Clowes, R. M. & Davis, E. E. The northern Cascadia subduction zone at Vancouver Island: seismic structure and tectonic history. *Can. J. Earth Sci.* **27**, 313–329 (1990).
 24. Ramachandran, K. *Velocity Structure of SW British Columbia and NW Washington from 3-D Non-linear Seismic Tomography*. PhD thesis, Univ. Victoria, 1–198 (2001).
 25. Graindorge, D. *et al.* Crustal structure beneath Strait of Juan de Fuca and southern Vancouver Island from seismic and gravity analysis. *J. Geophys. Res.* (in the press).
 26. Fisher, M. A., Brocher, T. M., Nokleberg, W. J., Plafker, G. & Smith, G. L. Seismic reflection images of the crust of the northern part of the Chugach Terrane, Alaska: Results of a survey for the Trans-Alaska Crustal Transect (TACT). *J. Geophys. Res.* **94**, 4424–4440 (1989).
 27. Kodaira, S. *et al.* Structural factors controlling the rupture process of a megathrust earthquake at the Nankai trough seismogenic zone. *Geophys. J. Int.* **149**, 815–835 (2002).
 28. Langston, S. *The Seismic Structure of Tofino Basin and Underlying Accreted Terrains*. MSc thesis, Univ. Victoria (1995).
 29. Clowes, R. M. *Crustal Structure of the Northern Juan de Fuca Plate and Cascadia Subduction Zone—New Results, Old Data 55–58* (US Geol. Surv. Open-File Report 02-328 and Geol. Surv. Can. Open File 4350, 2002).
 30. Wang, K. *et al.* A revised dislocation model of the interseismic deformation of the Cascadia subduction zone. *J. Geophys. Res.* **108**(B1), 101029/2001JB001703 (2003).

Acknowledgements We thank M. Fisher, T. Brocher, and many other participants for their part in organizing and carrying out the 1998 SHIPS experiment. The land seismic reflection data were collected as part of the Lithoprobe project. M.R.N. is grateful to S. Carbotte for allowing him to complete this work while he was a Post Doctoral Research Scientist at the Lamont-Doherty Earth Observatory of Columbia University. We thank T. Brocher for a series of critical reviews, A. Calvert and S. Mazzotti for discussions, and the Lamont-Doherty Earth Observatory of Columbia University for financially supporting the publication of this paper.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to M.R.N. (mladen@ldeo.columbia.edu.).

Catastrophic extinctions follow deforestation in Singapore

Barry W. Brook^{*†}, Navjot S. Sodhi[‡] & Peter K. L. Ng[‡]

^{*} Center for Ecological Research, Kyoto University, Otsu 520-2113, Japan

[†] Key Centre for Tropical Wildlife Management, Northern Territory University, Darwin 0909, Northern Territory, Australia

[‡] Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore, 117543, Republic of Singapore

The looming mass extinction of biodiversity in the humid tropics is a major concern for the future¹, yet most reports of extinctions in these regions are anecdotal or conjectural, with a scarcity of robust, broad-based empirical data^{2–4}. Here we report on local extinctions among a wide range of terrestrial and freshwater taxa from Singapore (540 km²) in relation to habitat loss exceeding 95% over 183 years^{5,6}. Substantial rates of documented and inferred extinctions were found, especially for forest specialists, with the greatest proportion of extinct taxa (34–87%) in

butterflies, fish, birds and mammals. Observed extinctions were generally fewer, but inferred losses often higher, in vascular plants, phasmids, decapods, amphibians and reptiles (5–80%). Forest reserves comprising only 0.25% of Singapore's area now harbour over 50% of the residual native biodiversity. Extrapolations of the observed and inferred local extinction data, using a calibrated species–area model^{7–9}, imply that the current unprecedented rate of habitat destruction in Southeast Asia¹⁰ will result in the loss of 13–42% of regional populations over the next century, at least half of which will represent global species extinctions.

Tropical forests represent the Earth's major reservoir of terrestrial biodiversity^{4,11}, yet these biomes are now gravely imperilled by anthropogenic change, including deforestation and habitat degradation^{12,13}, overexploitation of plant and animal populations¹⁴, and the introduction of invasive species¹. If we are to avert or at least mitigate catastrophic loss of species in these areas, it is vital to

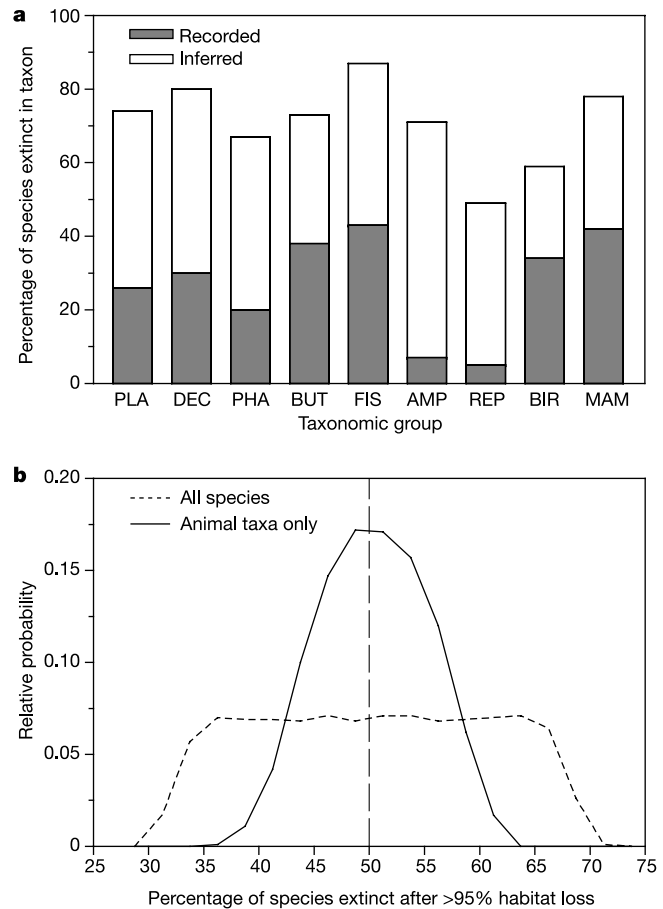


Figure 1 Observed and projected biodiversity loss in Singapore, 1819–2002.

a, Observed (recorded) and inferred extinction rates for vascular plants (PLA; number of modern, historically recorded and inferred species is 1,683, 2,277 and 6,549, respectively), freshwater decapod crustaceans (DEC; 16, 23, 82), phasmids (PHA; 33, 41, 100), butterflies (BUT; 236, 381, 863), freshwater fish (FIS; 35, 61, 269), amphibians (AMP; 25, 27, 87), reptiles (REP; 117, 123, 228), birds (BIR; 144, 218, 347) and mammals (MAM; 26, 45, 117). **b**, Combining the data from **a** provides a probability distribution of potential total species extinctions for all taxa (dashed line) and animal taxa only (continuous line), given a habitat loss exceeding 95% over a 183-year period. This was derived via computer re-sampling of the extinction data by assuming that the true extinction rate was equally and independently likely to lie anywhere between the observed and inferred proportions for each taxa. The vertical line indicates the mean of the animal taxa distribution.

understand the taxonomic and ecological selectivity¹⁵, rate⁸ and extent¹⁶ of local extinctions in already heavily deforested regions. However, until now a lack of appropriate knowledge and infrastructure in mostly developing tropical countries^{3,4,17} has forced an inevitable reliance on indirect measures and theoretical projections of extinctions^{2,7,9}.

We used both historical and modern checklists of species occurrences¹⁸ from tropical Singapore (103° 50' E, 1° 20' N) to estimate local extinctions¹⁹ in a wide range of taxa over a 183-year period in relation to large-scale habitat loss (Supplementary Information provides a complete catalogue of checklists). Since the British first established a presence in Singapore in 1819, more than 95% of the estimated 540 km² of original vegetation cover has been entirely cleared^{6,13}, and less than 10% of the 24 km² of remaining forest is primary (the majority being secondary re-growth)⁵. We focused on relatively well-studied taxonomic groups; that is, vascular plants, freshwater decapod crustaceans, phasmids, butterflies, freshwater fish, amphibians, reptiles, birds and mammals (excluding bats). However, given that a large fraction of the island's forest had already been cleared before the first reliable species records in the 1870s, the extinction of many species most sensitive to disturbance probably went unrecorded^{5,6,13,16}. To account for this gap, we also used checklists from nearby Peninsular Malaysia (assuming an equivalent species composition in corresponding habitats) to infer the possible pristine species composition of Singapore in 1819 (see Methods). The loss of local populations is highly relevant to global extinctions, because species disappear after all local populations have become extinct^{4,19}. Our analyses provide an empirical complement to the use of species distribution maps that infer less directly the extinction of populations from documented range reductions²⁰.

The observed local extinction rates in Singapore (Fig. 1a, shaded bars) were variable across taxonomic groups ($G = 67.4$, degrees of freedom (d.f.) = 8, $P < 0.001$). The overall loss of biodiversity was at least 28% (881 of 3,196 recorded species). Extinctions of butterflies, freshwater fish, birds and mammals (the most visible and well-studied animal taxa) were high (34–43%) and quite consistent ($G = 1.45$, d.f. = 3, $P = 0.694$) in the face of large-scale deforestation and habitat modification. Similarly, roughly a quarter of all vascular plant, freshwater decapod crustacean and phasmid species have disappeared. Conversely, amphibians and reptiles have apparently suffered comparatively fewer extinctions (5–7%). Our estimates of the possible (inferred) biodiversity loss in Singapore (Fig. 1a, white bars) suggest that the total local extinction of species (recorded and unrecorded) may be as high as 73%. The differences between observed and inferred extinctions are relatively small for some taxa (for example, 34–59% in birds), but substantial in others (7–71% in amphibians). A simple combinatorial simu-

lation of the observed–inferred proportional extinction bounds data (see Methods) produces a probability distribution of total biodiversity loss (Fig. 1b) peaking at 50.4% (95% confidence interval = 41.2–59.6%).

Most evidence indicates that the true biodiversity loss in Singapore is closer to our inferred than observed estimates. Although extinctions are notoriously difficult to document with certainty²¹, the small and intensively sampled area of remaining forest means that our extinction data probably include few 'false negatives'. Our extant species lists also include long-lived species with populations too small to be viable in the long term (for example, white-bellied woodpecker *Dryocopus javensis* (<5 individuals present), banded leaf monkey *Presbytis femoralis* (<15) and cream-coloured giant squirrel *Ratula affinis* (<10))²². These 'living dead' taxa will almost certainly become extinct in the coming decades^{4,8}. Some buffering of Singapore's local populations through re-colonization from neighbouring Malaysia has probably occurred (thereby increasing their resilience to extinction), but is believed to have been relatively low because of the poor dispersal abilities of most of the taxa treated, as well as ethological and habitat barriers (water, extensive mangroves and urban and agricultural development along the adjacent coastlines) impeding even mobile species such as birds²³. Peninsular Malaysia itself has already lost about 60% of its pristine habitat in historical times (so past unrecorded extinctions are also expected there)⁴, and its biota has not been as exhaustively studied as Singapore's. This suggests that Peninsular Malaysia has almost certainly experienced some extinctions in the past 200 years, and that it is unlikely the current biodiversity of this region substantially exceeds the past diversity in Singapore, despite the latter's smaller geographical area. We therefore regard our inferred extinction estimates as conservative.

The differing magnitude of observed extinctions across taxonomic groups is probably due in part to a complex generational scaling effect on long-term population persistence. Larger organisms require more habitat area to support viable populations, but also tend to live longer²⁴. These taxa (including most remaining tree species) may persist long after habitat reduction²⁵, but carry the burden of a past habitat-loss debt²⁶ that consigns them to future extinction^{4,6}. Invertebrates (for example, butterflies) require relatively less habitat to persist, but have already passed through many generations of 'relaxation'⁸ since deforestation, and may therefore most closely reflect the equilibrium end-point for all taxa. Small vertebrates (for example, frogs and lizards) also need less pristine forest area than birds or mammals, but have longer generation times than invertebrates²⁴ and have therefore spent fewer generations near a critical extinction threshold. It is also likely that the existence and subsequent extinction of many smaller, more cryptic organisms simply went unrecorded. For example, four of the six species of

Table 1 Potential future biodiversity losses in Singapore and extrapolations to Southeast Asia

Taxon	Percentage of species restricted to Singapore's reserves*	Total percentage extinct with loss of reserves†	Projected percentage biodiversity loss in SE Asia by 2100‡
Vascular plants	Majority of native species ^{6,25} (not quantified)		12–44
Decapods [§]	81 (13)	87 (× 2.9)	14–50
Phasmids	100 (33)	100 (× 5.1)	9–38
Butterflies	63 (149)	77 (× 2.0)	19–43
Fish [§]	60 (21)	77 (× 1.8)	21–58
Amphibians	76 (19)	78 (× 10.5)	3–41
Reptiles	50 (59)	52 (× 10.7)	2–25
Birds	8 (12)	39 (× 1.1)	16–32
Mammals	46 (12)	69 (× 1.6)	21–48
Weighted Mean	50 (312)	66 (× 2.1)	13–42

*Reserves are Bukit Timah (71 ha), Nee Soon (935 ha), MacRitchie (484 ha), Lower Pierce forest (50 ha) and Botanic Gardens (7 ha). Numbers in parentheses are total number of species per taxon restricted to the reserves.

†Calculated as (number species extinct + number species restricted to reserves)/original number of species. Numbers in parentheses indicate (number species extinct + number species restricted to reserves)/number species extinct; for example, (×2.0) signifies a twofold increase in the extinction rate. Based on recorded extinctions only, so represents a minimum estimate of biodiversity loss.

‡Extrapolation of regional population extinctions based on a species–area curve scaling constant z fitted to each taxon's respective recorded and inferred habitat loss–extinction rate relationship in Singapore, proportion of original regional forest cover lost to date, and the present rate of deforestation in Southeast Asia as documented by ref. 10.

§Freshwater only (excludes marine species).

freshwater crabs on the island were discovered only over the last 20 years²².

Most extinctions occurred among those biota restricted to forest habitats (primary or secondary rainforest or mangrove forest interiors). The overall documented local extinction rate for forest specialists was 33% ($n = 2,542$), compared with only 7% ($n = 654$) for species that prefer or tolerate open or forest-edge habitats. These habitat-specific extinctions were particularly severe in freshwater fish, birds and mammals, which lost 53%, 67% and 59% of their forest species, respectively, compared with only 0%, 11% and 13% of their open-habitat counterparts.

Forest birds provide the best quantitative data on the rate and selectivity of the extinctions. Singapore's contemporary bird fauna is characterized by a predominance of open-habitat generalists, migrants and invasives²⁷, because since 1923, 61 of the 91 known forest-dependent species have become extinct¹⁶. Furthermore, up to 168 species may have once resided in Singapore (based on forest bird diversity in Peninsular Malaysia), implying extinction of up to 46% of species before the first reliable checklists were compiled (in strong agreement with other measures of relaxation rates in tropical bird communities⁸), and a total species loss of 82% since 1819. A binary logistic regression model relating the likelihood of extinction to habitat preference (forest interior, forest edge, open) and body length (mm) was highly significant ($G = 94.5$, d.f. = 4, $P < 0.001$) and provided strong concordance with the empirical extinction data (76.3% overall concordance, or 65.9% for habitat alone). Large forest-interior species were most vulnerable and small open-habitat-preferring species least so.

The predominant cause of Singapore's extinctions was undoubtedly rapid and large-scale habitat destruction, initially through deforestation for agriculture, and later, urban development⁵. Habitat loss, fragmentation and modification cause extinctions by reducing breeding and feeding sites, increasing predation, soil erosion and nutrient loss, limiting dispersal, and enhancing edge effects^{1,4,12,26}. However, factors such as over-hunting and collecting may have also been important^{4,14}, especially for the larger vertebrates—the last tiger (*Panthera tigris corbetti*) was shot in 1930. In addition, heavy shelling of the nature reserves during World War II had an undocumented but presumably detrimental impact on the forest fauna¹⁶.

The future prospects for Singapore's surviving biodiversity look bleak—77% of the island's species are considered 'threatened', based on the World Conservation Union (IUCN) regional listing criteria²². Furthermore, our estimates show that the few remaining protected nature reserves, which occupy only 1,547 ha (or 0.25% of the total land area)^{5,16}, harbour exclusively at least 50% (316) of species from the animal taxa we assessed, and a high (but unquantified) number of plant species. The loss of these reserves would more than double the observed fraction of species driven to extinction (Table 1). Birds are unusual among the taxonomic groups we examined in having few species dependent on the reserves, but only because most of the forest species are already extinct¹⁶. Of particular concern is the lack of redundancy in the present reserve system. For instance, a quarter of the surviving freshwater decapod crustacean and fish fauna are now restricted to only a small (5 ha) area in a single reserve (Nee Soon)²⁸, reinforcing the view that reserve designs that emphasise single representations of many species can be a poisoned chalice²⁹.

What can local extinctions in Singapore tell us about the larger biodiversity crisis now affecting the tropical forests of Southeast Asia^{4,7,12}, which support a comparable biota? Few other areas in Southeast Asia have hitherto suffered from such extensive habitat loss as Singapore (regional average is 46% loss of original forest cover⁷), yet projections of current rates of regional deforestation ($0.71\% \text{ yr}^{-1}$)¹⁰ imply an overall deforestation of 74% in Southeast Asia by the year 2100. We fitted our observed and inferred extinction data to the species–area relationship^{7–9,16}, and used this empirically

calibrated model to estimate the number of species likely to become extinct or consigned to extinction in Southeast Asia over the next century (see Methods). We predict the overall loss of 13–42% of regional populations due to the effects of deforestation in Southeast Asia by the end of the present century (see Table 1 for a taxonomic break down), at least half of which are likely to represent global species extinctions, given estimates of regional endemicity^{3,7,11}. Realized extinctions may be even higher, given the additional pressures of overexploitation, displacement by exotic species, climate change and loss of non-forest habitats^{1,4,14}, proportionally higher rates of deforestation in the biodiversity hotspots^{10,11}, and probable buffering of local populations in Singapore by recolonizations. Clearly, large-scale conservation efforts need to be implemented if these regional rates of extinction are to be abated. □

Methods

Quantifying local extinctions

The equatorial island of Singapore offers a unique opportunity to analyse the long-term phenomenological response of tropical biota to massive habitat loss, fragmentation and degradation, providing a 'microcosm' of the tropical biodiversity crisis. Its typically Southeast Asian terrestrial and freshwater biotas have been studied in detail by amateur naturalists and professional biologists for over a century^{5,16,30}, and modern biodiversity surveys have provided a relatively exhaustive coverage of the few remaining habitat areas²². Past and present taxonomic inventories from Singapore were compiled by sourcing all primary, secondary and 'grey' literature (checklists and scientific surveys) and the major contemporary biological reference material covering Peninsular Malaysia (see the Supplementary Information for a full listing). Recorded extinctions were defined using standard IUCN guidelines^{6,22}. Observed proportional extinctions were calculated as $(H - M)/H$ and inferred extinctions as $(P - M)/P$, where H and M are the size of the historical and modern Singaporean checklists, respectively, and P is the size of the modern checklists of Peninsular Malaysia.

We excluded montane, savanna, lacustrine and large river taxa from the species list for Peninsular Malaysia because Singapore lacks these habitats. Singapore has been separated from Peninsular Malaysia by a narrow (600-m wide), shallow (10-m deep) strait for only a few thousand years⁵, resulting in very low endemism, with only three endemic decapod crustacean species and one endemic subspecies of bird from the taxa studied. Therefore, the extinctions that we are reporting are population extinctions^{19,20}. These compiled data show that Singapore possessed a minimum (if we consider only documented records) of 37% of the biodiversity of Peninsular Malaysia (63% for birds).

Simulation of the uncertainty distribution of extinctions

Our estimates of the observed and inferred total species losses were combined by assuming: (1) that the true point estimate of the fraction of extinct biota for each taxon falls somewhere between these two bounds, with equal probability (that is, a uniform distribution); and (2) that the position of the extinction fraction within these bounds was independent across taxa. Repeated computer-aided re-sampling of point estimates within the extinction bounds data for each taxonomic group was combined across all represented taxa (and separately, just the animal taxa) and used to construct a probability–frequency distribution of species loss (Fig. 1b, based on 30,000 simulation replicates). Vascular plants comprised 71–77% of Singapore's total original biodiversity of these groups, and thus had a strong influence on the shape and uncertainty of the resulting probability distribution.

Extrapolation to Southeast Asia

Previous estimates of possible future biodiversity loss in Southeast Asia^{7,15,16} have relied on extrapolations using the species–area relationship (SAR), defined as $S = cA^z$, where S is the ratio of contemporary to original species composition, A is the ratio of present to original habitat area, and c and z are constants^{8,9}. Previous extrapolations have assumed a value of $z = 0.25$. We built on this approach by using our empirical data to 'calibrate' z for each of the nine taxonomic groups we studied, and used both the observed and inferred local extinction estimates to encompass the major uncertainties.

To solve the SAR for z , we used a different S for each taxonomic group and set A for Singapore as $4.3\%^{5,6,13}$, resulting in values of z and S (observed, inferred) as follows: vascular plants, $z = (0.10, 0.43)$ and $S = (0.74, 0.26)$; freshwater decapod crustaceans, $z = (0.11, 0.51)$ and $S = (0.70, 0.20)$; phasmids, $z = (0.07, 0.35)$ and $S = (0.80, 0.33)$; butterflies, $z = (0.15, 0.42)$ and $S = (0.62, 0.27)$; freshwater fish, $z = (0.18, 0.65)$ and $S = (0.57, 0.13)$; amphibians, $z = (0.02, 0.40)$ and $S = (0.93, 0.29)$; reptiles, $z = (0.02, 0.22)$ and $S = (0.95, 0.51)$; birds, $z = (0.13, 0.28)$ and $S = (0.66, 0.41)$; mammals, $z = (0.17, 0.48)$ and $S = (0.58, 0.22)$; weighted average, $z = (0.11, 0.42)$ and $S = (0.73, 0.28)$. Extrapolations for Southeast Asia from 1997 to 2100 (a 103-year period) assumed an annual regional deforestation rate¹⁰ of $0.71\% \text{ yr}^{-1}$ and $A_{(1997)} = 46\%$, giving $A_{(2100)} = 0.54(1 - 0.0071)^{103}$.

Our approach has the advantage of incorporating regional- and taxon-specific information into the projections (than rather than assuming a single universal value of z for all groups), and emphasises the complementary way in which local extinction and regional habitat-loss studies can be combined to produce biologically and empirically

grounded estimates of future biodiversity loss. Limitations on the reliability of this method include the difficulty in estimating the proportion of contemporary biota in Singapore that has not yet reached relaxation (that is, presently surviving, but committed to future extinction)^{13,25}, the unknown extent to which supplemental migration from mainland Malaysia may have buffered local populations in Singapore from extinction, the uncertainties in estimating the true pristine biodiversity of the island, given the likelihood of past habitat-loss-related extinctions in Peninsular Malaysia, and the uneven geographical distribution of endemic biodiversity 'hotspots'²¹, which currently suffer from higher rates of deforestation and degradation than the average of the entire region¹⁰. Collectively, these potential biases suggest that our projected regional losses are likely to be conservative.

Received 10 January; accepted 9 May 2003; doi:10.1038/nature01795.

1. Novacek, M. J. & Cleland, E. E. The current biodiversity extinction event: scenarios for mitigation and recovery. *Proc. Natl Acad. Sci. USA* **98**, 5466–5470 (2001).
2. Heywood, V. H., Mace, G. M., May, R. M. & Stuart, S. N. Uncertainties in extinction rates. *Nature* **368**, 105 (1994).
3. Pitman, N. C. A. & Jørgensen, P. M. Estimating the size of the world's threatened flora. *Science* **298**, 989 (2002).
4. Heywood, V. H. & Stuart, S. N. in *Tropical Deforestation and Species Extinction* (eds Whitmore, T. C. & Sauer, J. A.) 91–117 (Chapman and Hall, London, 1992).
5. Corlett, R. T. The ecological transformation of Singapore, 1819–1990. *J. Biogeogr.* **19**, 411–420 (1992).
6. Turner, I. M. *et al.* A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. *Conserv. Biol.* **8**, 705–712 (1994).
7. Brooks, T. M., Pimm, S. L. & Collar, N. J. Deforestation predicts the number of threatened birds in insular Southeast Asia. *Conserv. Biol.* **11**, 382–394 (1997).
8. Brooks, T. M., Pimm, S. L. & Oyugi, J. O. Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* **13**, 1140–1150 (1999).
9. May, R. M. & Stumpf, M. P. H. Species-area relations in tropical forests. *Science* **290**, 2084–2086 (2000).
10. Achard, F. *et al.* Determination of deforestation rates of the world's humid tropical forests. *Science* **297**, 999–1002 (2002).
11. Myers, N., Mittermeier, C. G., Mittermeier, G. A., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
12. Laurance, W. F. Reflections on the tropical deforestation crisis. *Biol. Conserv.* **91**, 109–117 (1999).
13. Corlett, R. T. in *The Ecological Consequences of Environmental Heterogeneity* (eds Hutchings, M. J., John, E. A. & Stewart, A.) 333–355 (Blackwell Science, Oxford, 2000).
14. Milner-Gulland, E. J. & Akçakaya, H. R. Sustainability indices for exploited populations. *Trends Ecol. Evol.* **16**, 686–692 (2001).
15. Russell, G. J., Brooks, T. M., McKinney, M. M. & Anderson, C. G. Present and future taxonomic selectivity in bird and mammal extinctions. *Conserv. Biol.* **12**, 1365–1376 (1998).
16. Castelletta, M., Sodhi, N. S. & Subaraj, R. Heavy extinctions of forest avifauna in Singapore: lessons for biodiversity conservation in Southeast Asia. *Conserv. Biol.* **14**, 1870–1880 (2000).
17. Sodhi, N. S. & Liow, L. H. Improving conservation biology research in Southeast Asia. *Conserv. Biol.* **14**, 1211–1212 (2000).
18. Droege, S., Cyr, A. & Larivee, J. Checklists: an under-used tool for the inventory and monitoring of plants and animals. *Conserv. Biol.* **12**, 1134–1138 (1998).
19. Williamson, M. Natural extinction on islands. *Phil. Trans. R. Soc. Lond. B* **325**, 457–468 (1989).
20. Ceballos, G. & Ehrlich, P. R. Mammal population losses and the extinction crisis. *Science* **296**, 904–907 (2002).
21. Diamond, J. M. Extant unless proven extinct? Or, extinct unless proven extant? *Conserv. Biol.* **1**, 77–79 (1987).
22. Ng, P. K. L. & Wee, Y. C. (eds) *The Singapore Red Data Book* (The Nature Society, Singapore, 1994).
23. Bierregaard, R. O. J., Lovejoy, T. E., Kapos, V., dos Santos, A. A. & Hutchings, R. W. The biological dynamics of tropical rainforest fragments. *BioScience* **42**, 859–866 (1992).
24. Peters, R. H. *The Ecological Implications of Body Size* (Cambridge Univ. Press, New York, 1983).
25. Turner, I. M. & Corlett, R. T. The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends Ecol. Evol.* **11**, 330–333 (1996).
26. Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994).
27. Lim, K. S. & Gardner, D. *Birds: An Illustrated Field Guide to the Birds of Singapore* (Sun Tree Publishing Limited, Singapore, 1997).
28. Ng, P. K. L. & Lim, K. K. P. The conservation status of the Nee Soon freshwater swamp forest of Singapore. *Aquat. Conserv.* **2**, 255–266 (1992).
29. Araujo, M. B. & Williams, P. H. Selecting areas for species persistence using occurrence data. *Biol. Conserv.* **96**, 331–345 (2000).
30. Ridley, H. N. The flora of Singapore. *J. Straits' Branch R. Asiatic Soc.* **33**, 27–196 (1900).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank I. Turner, K. Lim and T. Leong for providing timely answers to our taxonomic queries, and D. Bowman, R. Corlett, P. Whitehead, K. Winker and N. Yamamura for comments on the manuscript. This research was funded by grants from the Raffles Museum of Biodiversity Research, National University of Singapore, Australian Research Council and the Center for Ecological Research Visiting Research Scholar Programme.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to B.W.B. (barry.brook@ntu.edu.au) or N.S.S. (dbsns@nus.edu.sg).

Productivity–biodiversity relationships depend on the history of community assembly

Tadashi Fukami* & Peter J. Morin†

* Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610, USA

† Department of Ecology, Evolution, and Natural Resources, 14 College Farm Road, Rutgers University, New Brunswick, New Jersey 08901-8551, USA

Identification of the causes of productivity–species diversity relationships remains a central topic of ecological research^{1,2}. Different relations have been attributed to the influence of disturbance^{3,4}, consumers^{5,6}, niche specialization⁷ and spatial scale^{8–14}. One unexplored cause is the history of community assembly, the partly stochastic sequential arrival of species from a regional pool of potential community members. The sequence of species arrival can greatly affect community structure^{15–19}. If assembly sequence interacts with productivity to influence diversity, different sequences can contribute to variation in productivity–diversity relationships. Here we report a test of this hypothesis by assembling aquatic microbial communities at five productivity levels using four assembly sequences. About 30 generations after assembly, productivity–diversity relationships took various forms, including a positive, a hump-shaped, a U-shaped and a non-significant pattern, depending on assembly sequence. This variation resulted from idiosyncratic joint effects of assembly sequence, productivity and species identity on species abundances. We suggest that the history of community assembly should be added to the growing list of factors that influence productivity–biodiversity patterns.

Productivity, the amount of energy available for ecosystem development in a given location, has a major effect on species diversity^{20–22}. Until recently, hump-shaped relationships, in which diversity peaks at intermediate productivity levels, were the most widely observed pattern^{23–25}. We now know that the relationship takes many forms, including hump-shaped, U-shaped, positive, negative and flat (non-significant) patterns, and that none of these patterns predominates¹. Possible causes of variation include the influence of disturbance^{3,4}, consumers^{5,6}, niche specialization⁷ and spatial scale^{8–14}, which can create variation between taxonomic groups and habitat types^{1,13}. A few studies suggest that productivity might control the probability that alternative community states are produced through assembly^{14,26–28}.

Table 1 Introduction sequences used to assemble communities

	Sequence			
	A	B	C	D
First introduction	Set 1	Set 1	Set 2	Set 2
Second introduction	Set 2	Set 3	Set 1	Set 3
Third introduction	Set 3	Set 2	Set 3	Set 1
Set 1	Set 2		Set 3	
<i>Blepharisma americanum</i> *‡	<i>Colpidium striatum</i> *		<i>Aspidisca</i> sp.*	
<i>Chilomonas</i> sp.*	<i>Colpoda cucullus</i> *		<i>Holosticha</i> sp.*	
<i>Colpoda inflata</i> *	<i>Euplotes</i> sp.*†‡		<i>Lepadella</i> sp.* (r)	
<i>Loxoxecephalus</i> sp.*	<i>Paramecium tetraurella</i> †		<i>Rotaria</i> sp.* (r)	
<i>Paramecium caudatum</i> †	<i>Tetrahymena vorax</i> *‡		<i>Spirostomum</i> sp.*	
<i>Tetrahymena thermophila</i> *	<i>Uronema</i> sp.*		<i>Tillina magna</i> *	

The natural history of these rotifers (marked with (r)) and protozoans (all others) indicates that they consume bacteria and/or microflagellates (*), algae (†), and/or small ciliates (‡). Regardless of their diets, all the species can sustain their population solely on bacteria and/or microflagellates and thus potentially compete with one another.

Supplementary Information

Brook, B.W., Sodhi, N.S., Ng, P.K.L. Catastrophic extinctions follow deforestation in Singapore. *Nature* **424**, 420–423 (2003).

Data sources

Below¹⁻³¹ is a list of all primary and secondary literature used to evaluate species extinctions in Singapore and the comparative biodiversity of Peninsular Malaysia (excluding those publications cited in the main paper).

1. Bransbury, J. *A Birdwatcher's Guide to Malaysia* (Waymark Publishing, Singapore, 1993).
2. Brock, P. D. *Stick and Leaf Insects of Peninsular Malaysia and Singapore* (Malaysian Nature Society, Kuala Lumpur, 1999).
3. Chasen, F. N. An introduction to the birds of Singapore Island. *Singapore Nat.* **2**, 87-112 (1923).
4. Chasen, F. N. Remarks on the ornithology of Singapore. *Singapore Nat.* **3**, 22-36 (1924).
5. Chasen, F. N. A preliminary account of the mammals of Singapore Island I. *Singapore Nat.* **3**, 76-86 (1924).
6. Chasen, F. N. Further remarks on the birds of Singapore island. *Singapore Nat.* **5**, 71-73 (1925).
7. Chasen, F. N. A preliminary account of the mammals of Singapore Island II. *Singapore Nat.* **5**, 74-89 (1925).
8. Corbet, G. B. & Hill, J. E. *The Mammals of the Indomalayan Region* (Oxford University Press, Oxford, 1992).
9. Corlett, R. T. The naturalized flora of Singapore. *J. Biogeogr.* **15**, 657-663 (1988).
10. Corlett, R. T. The Angiosperm flora of Singapore 1. Introduction. *Gardens' B. Singapore* **44**, 3-21 (1992).
11. Corlett, R. T. The vegetation in the nature reserves of Singapore. *Gardens' B. Singapore* **49**, 147-159 (1997).
12. Gibson-Hill, C. A. A checklist of the birds of Singapore Island. *B. Raffles Mus.* **31**, 132-183 (1949).
13. Khew, S. K. & Neo, S. S. H. Butterfly biodiversity in Singapore with particular reference to the Central Catchment Nature Reserve. *Gardens' B. Singapore* **49**, 273-296 (1997).
14. Lim, K. K. P. Checklist of Singapore birds. *Iora* **1**, 172-184 (1994).
15. Lim, K. K. P. & Chou, L. M. in *Essays in Zoology 1990* (eds. Chou, L. M. & Ng, P. K. L.) 49-59 (Department of Zoology, National University of Singapore, Singapore, 1990).
16. Lim, K. K. P. & Ng, P. K. L. *A Preliminary Working List of Freshwater Fishes of Peninsula Malaysia* (ASEAN Wetland Bureau Publication No. 94., Singapore, 1993).
17. Medway, L. *The Wild Mammals of Malaya (Peninsular Malaysia) and Singapore* (Oxford University Press, Kuala Lumpur, 1983).
18. Moshin, A. K. M. & Ambok, M. A. *Freshwater Fishes of Peninsular Malaysia* (University Pertanian Press, Kuala Lumpur, Malaysia, 1983).
19. Ng, P. K. L. & Lim, K. K. P. The conservation status of the Nee Soon freshwater swamp forest of Singapore. *Aquat. Conserv.* **2**, 255-266 (1992).
20. Ng, P. K. L. & Lim, K. K. P. The freshwater fishes of Singapore. *J. Singapore Natl. Acad. Sci.* **22-24**, 109-124 (1996).
21. Ng, P. K. L. & Lim, K. K. P. The diversity and conservation status of fishes in the nature reserves of Singapore. *Gardens' B. Singapore* **49**, 245-265 (1997).
22. Seow-Choen, F. Stick and leaf insect (Phasmida: Insecta) biodiversity in the Nature Reserves of Singapore. *Gardens' B. Singapore* **49**, 297-312 (1997).
23. Sodhi, N. S. A comparison of bird communities of two fragmented and two continuous southeast Asian rainforests. *Biodivers. Conserv.* **11**, 1105-1119 (2002).
24. Sworder, G. H. On a few reptiles and batrachians from Singapore. *Singapore Nat.* **3**, 15-20 (1924).
25. Sworder, G. H. An addition to the list of Singapore snakes and a few notes on species already included. *Singapore Nat.* **3**, 21-22 (1924).
26. Sworder, G. H. The lizards of Singapore Island. *Singapore Nat.* **5**, 61-68 (1925).
27. Teo, R. C. H. & Rajathurai, S. Mammals, reptiles and amphibians in the Nature Reserves of Singapore - Diversity, abundance and distribution. *Gardens' B. Singapore* **49**, 353-425 (1997).
28. Turner, I. M. A checklist of the native and naturalized vascular plants of the Republic of Singapore. *J. Singapore Natl. Acad. Sci.* **18-19**, 58-88 (1990).
29. Turner, I. M. A catalogue of the vascular plants of Malaya. *Gardens' B. Singapore* **47**, 1-757 (1995).
30. Wee, Y. C. & Ng, P. K. L. (eds.) *A First Look at Biodiversity in Singapore* (National Council on the Environment, Singapore, 1994).
31. Yang, C. M., Yong, K. & Lim, K. K. P. in *Essays in Zoology 1990* (eds. Chou, L. M. & Ng, P. K. L.) 1-23 (Department of Zoology, National University of Singapore, Singapore, 1990).