We are now accepting email submissions. The form below must be filled out and attached in an email and sent to ifoa.remake@epa.nsw.gov.au If this form is not attached or incomplete the submission will be lodged as confidential and will not be published.

Make a submission – Contact Details

First Name*: Alan

Last Name*:Roberts

Phone: [redacted]

Mobile*:

Email* [redacted]

Postcode* [redacted]

Country*:Australia

Stakeholder type (circle)*: Community member

Community group	Local Government	Aboriginal group
Industry group	Other government	Forest user group
Environment group	Individual	Staff

Other, please specify:

Organisation name: NEFA, Nimbin Environment Centre

What is your preferred contact method (circle): Mobile, Email or phone? Email

Would you like to receive further information and updates on IFOA and forestry matters? Yes

Can the EPA make your submission public* (circle)?Yes

Yes No Yes, but anonymous

Have you previously engaged with the EPA on forestry issues?

Make a submission – Form

1. **What parts of the draft Coastal IFOA are most important to you? Why?**

Its impacts on ecological values, threatened species, the degredation of the forest estate from over logging, soil loss from reduced stream protection and much more.

Why – because it's my planet, we're into its 6th great extinction this one caused by us and we have no right to extinguish other species or even ourselves. We have obligations to future generations to leave the planet in a better state and I'm disgusted with the life extinguishing neoliberal system that has no values.

2. **What parts of the draft Coastal IFOA do you think have a positive outcome on the management of environmental values or the production of sustainable timber? Why?**

None – see my attachments

3. **What parts of the draft Coastal IFOA do you think have a negative outcome on the management of environmental values or the production of sustainable timber? Why?**

All of it – see my attachments

4. **What are your views on the effectiveness of the combination of permanent environmental protections at the regional, landscape and operational scales (multi-scale protection)?**

I can only imagine this scheme was proposed by a deluded accountant unfamiliar with forests. As well it seems that the bureaucracy is scrapping protections on the original reserve system wiping out any trust in the proponents. A temporary permanent proposal – the system has no credibility. This whole multiscale thing is so inept just scrap it and do the science first, forget the economists.

5. **In your opinion, would the draft Coastal IFOA be effective in managing environmental values and a sustainable timber industry? Why?**

No it's a total failure both environmentally and sustainably.

Why?: the original RFAs offered unsustainable timber supply agreements and now you're offering 30% more timber, with nothing left of forests (or forest environments) by 2023. Loggers are almost down to harvesting sticks now so the proposal is to get stuck into the original CARRS until there's nothing left of those either – not going to happen.

6. General comments

The proposed new IFOAs will get nowhere fast if you follow this line. Your line of least resistance will be to stop for as long as it takes to do credible scientific assessments on the ecology, the potential carbon sequestration potential and include all the values that forests provide. Then to properly involve the community in the decision making. If you don't do both it will be mayhem.

Taking our time is necessary and no loss. If it takes long enough the little trees might grow big and threatened species like Koalas might recover.

Included with my submission are 5 attachments:

1. **AlanSubAttach1**
2. **AlanSubAttach2**
3. **Carbon emissions from tropical forest degradation caused by logging**
   Timothy R H Pearson, Sandra Brown and Felipe M Casarim
4. **The Effect of Harvest on Forest Soil Carbon: A Meta-Analysis**
   Jason James * and Rob Harrison
5. **Paleo-antarctic rainforest into the modern old world tropics: the rich past and threatened future of the "southern wet forest survivors"1**
   Robert m. Kooyman,

Submission on the draft NSW Coastal IFOA

From:
Alan Roberts
[redacted]
NSW [redacted]

To:
DPI, EPA, NRC, NSW government

Congratulations to you all for what, even in a draft form, is a masterful piece of work that shows:

- how thoroughly the legislature has been captured by the plutocracy and oligarchy as represented in the current case by the logging juggernaut
- as a consequence how well protected from any interference by the demos the legislature now is (the demos is barred from taking court action on environmental breaches)
- how deceitfully misinformation can be deployed as exemplified by the justifications for remapping, because the original mapping was “mistaken”, which becomes a guise for stealing nearly all of the CARRS
- how compliant the bureaucracy now is regardless of how unconscionable that compliance is
- that the history of failure to prosecute breaches of the first RFA is to be obliterated and thus to be repeated if we are stupid enough accept a second RFA round
- which we’re not

Submission 2 on the draft NSW Coastal IFOA

From:
Alan Roberts
[redacted] NSW [redacted]

With hindsight it turns out to be a mistake for the 1992 Rio earth summit to have given the Australian governments care of the environment. These governments now only view the environment as a natural resource to be plundered for commercial gain. Anything that hinders this plundering is being swept aside. Especially swept aside is the incorporation of evidence based science in a review of the RFAs. In the intervening 20 years since the first RFAs Australia's fossil carbon burning has continued unabated resulting in native forest establishment becoming imperative to sequester some of the fossil carbon – this needs scientific assessment (see 2 attachments on forestry associated carbon loss to the atmosphere). Also in those intervening years it's been discovered that these forests are the only refuge on the planet where so much (10 times more than anywhere else) of the original Gondwanan species survive (see attached – Rob Kooyman paper) – this is an ongoing research project which any resumption of logging in the Northern Rivers will jeopardise and risk further extinctions.

Thus we do not have any trust in the review of the RFAs process. This is because 20 years of experience in the initial RFA trial resulted in:

1. Loggers finding it was more economic for them either not to look for, or to ignore, evidence of threatened species. If loggers were caught by the community breaching these rules, either no action was taken or a slap on the wrist and maybe a small fine was given – none of which discouraged repeat offences.
2. The 2 components of the RFA were never achieved namely the Comprehensive, Adequate and Representative Reserve System (CARRS) and the Ecologically Sustainable Forest Management (EFSM).
3. The reserve system now only caters for a fraction of the necessary ecology required for a multitude of threatened species and even this inadequately small area that's been reserved has resulted in much whinging by the timber industry prompting politicians to propose ignoring tenure and logging anything still standing. The fact that it's safe to make this threat and that the timber industry holds a strong political influence and there's no countervailing political support for ecological reserves results in no trust by the community for the IFOA promotion.
4. Forest management by accountants or economists has been a series of multiple disasters. Sawmillers and loggers knew that the promised quotas were not available resulting in huge payouts from the public to the timber industry. Since these wood supply agreements are proposed to be rolled over in increased quantities the only logical conclusion is that it's a deliberate boondoggle to transfer public money to the private sector for nothing.
   (a) The timber industry acknowledges that the wrong timber species have been planted in plantations which have now failed resulting in many plantations being cleared.
   (b) State forests are being converted over to monoculture plantations by stealth. The species being planted are fast growing lower quality light timbered wood that looks suspiciously like they're headed for the pulp mill.
   (c) There is no planting of the real timber species like Tallowwood or Ironbarks so that causes the timber industry to squeal that the "greenies" have commandeered all the real trees in National Parks. Clearly the timber industry finds it easier to steal from the public resource instead of planting real trees and being patient.

(d) The madness of the wood supply agreements has resulted in no decent sized trees remaining so that allocations are being filled by large numbers of small trees to get the volumes. This produces proportionately more waste. Instead a sensible plan would leave these trees time to grow, such is the idiocy of capitalism.

Hence we are not agreeing to any rolling over of RFAs especially after 20 years of seeing bureaucracies trashing a priceless ecology and now presenting a more thorough trashing version. The change in rules about what's old growth or rainforest pays no regard to the CARRS which the cunning "remapping" plan would eliminate. Thank you for such an explicit exposure of your environmental values.

They're our forests and it's our planet, the health of which is too important to be left to compromised idiots of which we've seen too much. So before any more RFAs we need to sit down for as long as it takes to go through the science and, with the whole community, work out a way forward based on evidence.

Carbon emissions from tropical forest degradation caused by logging

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Carbon emissions from tropical forest degradation caused by logging

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Abstract

The focus of land-use related efforts in developing countries to reduce carbon emissions has been on slowing deforestation, yet international agreements are to reduce emissions from both deforestation and forest degradation (REDD). The second 'D' is poorly understood and accounted for a number of technical and policy reasons. Here we introduce a complete accounting method for estimating emission factors from selective timber harvesting, a substantial form of forest degradation in many tropical developing countries. The method accounts separately for emissions from the extracted log, from incidental damage to the surrounding forest, and from logging infrastructure, and emissions are expressed as units of carbon per cubic meter of timber extracted to allow for simple application to timber harvesting statistics. We applied the method in six tropical countries (Belize, Bolivia, Brazil, Guyana, Indonesia, and Republic of Congo), resulting in total emission factors of 0.99–2.33 Mg C m^{-3}. In all cases, emissions were dominated by damage to surrounding vegetation and the infrastructure rather than the logs themselves, and total emissions represented about 3–15% of the biomass carbon stocks of the associated unlogged forests. We then combined the emission factors with country level logging statistics for nine key timber producing countries represented by our study areas to gain an understanding of the order of magnitude of emissions from degradation compared to those recently reported for deforestation in the same countries. For the nine countries included, emissions from logging were on average equivalent to about 12% of those from deforestation. For those nine countries with relatively low emissions from deforestation, emissions from logging were equivalent to half or more of those from deforestation, whereas for those countries with the highest emissions from deforestation, emissions from logging were equivalent to <10% of those from deforestation. Understanding how to account emissions and the magnitude of each emissions source resulting from tropical timber harvesting practices helps identify where there are opportunities to reduce emissions from the second 'D' in REDD.

Keywords: REDD+, carbon, timber, degradation, selective logging

S Online supplementary data available from stacks.iop.org/ERL/9/034017/mmedia

1. Introduction

The international community has come to accept that confronting global climate change cannot succeed without considering actions that reduce carbon emissions from deforestation and forest degradation (Stern 2007, UNFCCC 2007). Now known as REDD+ (reducing emissions from deforestation and forest degradation in developing countries; and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries), the topic has been the subject of intense negotiations since 2005 at COP 11 (the 11th Conference of the Parties to the United Nations Framework on Climate Change).

To date, the main focus has been on the first 'D', deforestation, in terms of emissions quantification (Achard *et al* 2002, DeFries *et al* 2002, 2007, Baccini *et al* 2012, Harris *et al* 2012) and the kinds of policies and programs that could be put in place to reduce these emissions (Meridian Institute 2009). Emissions related to the second 'D', representing those from forest degradation, are poorly quantified. Many studies have examined selective logging in tropical forests, but these have focused largely on the extent of damage to the residual stand (e.g. Uhl and Vieira 1989, Uhl *et al* 1991, Verissimo *et al* 1992, White 1994). The studies of Pinard and Putz (1996), Feldpausch *et al* (2005) and Medjibe *et al* (2011) detailed the carbon impact of timber harvesting but did not include all emissions source. Selective logging as a source of forest degradation should not be ignored, however, as in the Brazilian Amazon alone, Asner *et al* (2005) estimated that emissions caused by selective logging were equivalent to between 60 and 123% of previously reported deforestation emissions.

In tropical humid forests, selectively harvesting trees for timber and/or fuelwood can degrade the forest because the loss in live biomass resulting from harvesting practices often exceeds biomass accumulation by regrowth over many years. The loss of live biomass is due to the immediate damage that occurs by felling the selected trees, the incidental damage to surrounding trees caused by the felled trees, and the infrastructure built for removing the logs out of the forest. For commercial timber operations, infrastructure can be extensive and is composed of skidding trails (caused by use of bulldozers or other equipment to transport the logs from the felling area to roads), logging decks or landings (areas where the logs skidded out from the forest are piled awaiting transport) and logging roads (used by motor vehicles to transport the logs out of the forest).

Although techniques are being developed for detecting the extent of forest degradation, little has been done to estimate associated carbon emissions from degrading activities. The basic method recommended by the Intergovernmental Panel on Climate Change (IPCC 2006) is to derive the product of activity data (e.g. areal extent of loss in forest cover in ha yr^{-1}) and the emission factor (e.g. change in carbon stock as a result of the activity, as Mg C ha^{-1}). For deforestation, activity data can be readily obtained from the use of remote sensing imagery (GOFC-GOLD 2013) and the methods for this are well established and commonly used for many parts of the tropical world (e.g. Achard *et al* 2002, DeFries *et al* 2007, Hansen *et al* 2010). For estimating emission factors for deforestation, field data collection and analyses are based on well-established methodologies (Brown 1997, Pearson *et al* 2005, 2007, GOFC-GOLD 2013).

The IPCC (2006) guidance for estimating emissions and removals for forest degradation is covered in the section referred to as 'Forests Remaining as Forests', and although similar to that for deforestation, obtaining the activity data and estimating the emission factors is not so straightforward. The goals of our work were therefore to: (1) develop a new and complete methodology to estimate carbon emissions resulting from selective timber harvesting operations in tropical forests, (2) demonstrate the application of the methodology by producing emission factors for example logging operations in several key tropical timber producing countries, and (3) determine the relative significance of each emission source from the logging operations in relation to total emissions. We then use the results from our analysis to produce a first order estimate of the magnitude of emissions from degradation due to logging versus those from deforestation for key timber producing countries represented by our study sites. The methodology is designed to provide emission factors for all emissions sources as a function of the unit of timber production as recommended by the IPCC (2006).

2. Methods

2.1. Carbon accounting methodology

The methodology that we present here for estimating emissions caused by selective logging practices in tropical forests was originally conceived for one of the earliest forest-based carbon offset projects—the Noel Kempff Climate Action project (Brown *et al* 2000). We used the IPCC gain–loss approach that focuses on the direct losses in live biomass caused by the felled trees, incidental damage to other trees caused by the felling, and related logging infrastructure, and the gains from regrowth in and around the gaps caused by the felled and damaged trees and infrastructure (figure 1). In this sense, it is more appropriate to estimate the change in live and dead biomass pools due to logging impacts directly in the harvested areas as opposed to estimating the difference in the carbon stocks of the pre- and post-logged forest.

The total emission factor from selective logging is estimated as the sum of three factors: (1) emissions relative to extracted volume; (2) damaged biomass in the process of logging; and (3) damaged biomass resulting from infrastructure necessary for logging:

$$\mathrm{TEF} = (\mathrm{ELE} + \mathrm{LDF} + \mathrm{LIF}) \quad (1)$$

where TEF is the total emission factor resulting from timber harvest (Mg C m^{-3}), ELE is the extracted log emissions (Mg C m^{-3} extracted), LDF is the logging damage factor—dead biomass carbon left behind in gap from felled tree and incidental damage (Mg C m^{-3} extracted), LIF is the logging infrastructure factor—dead biomass carbon caused by construction of infrastructure (Mg C m^{-3}).

We did not include carbon emissions from soil as selective logging has been shown to have no impact on soil carbon over large concessions because of the relatively small area impacted, the short duration of impact and the retention of vegetative cover (Johnson and Curtis 2001). And although we do recognize that there will be carbon emissions from the construction of the unpaved logging roads, these emissions are not included in our analysis.

Extracted log emissions (ELE). Extracted log emissions are equal to the emissions resulting from conversion of the log to wood products and the subsequent emissions from retired wood products. Emissions can be estimated to occur fully at time of harvest (committed emissions) or they can be estimated

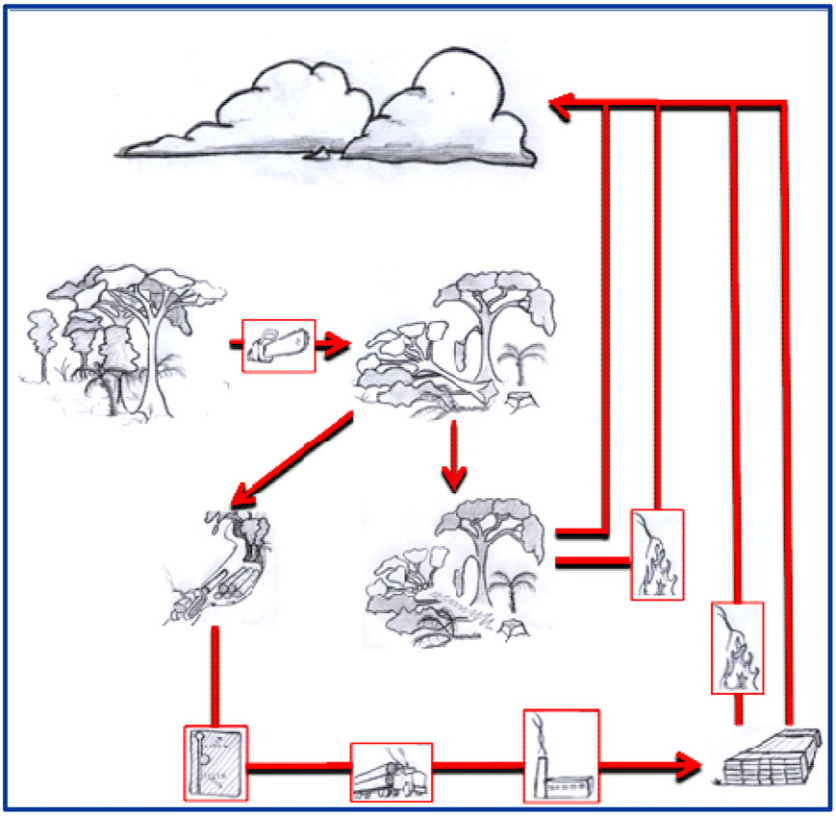

Figure 1. Illustration of the carbon cycle within tropical timber harvest. During felling surrounding trees are incidentally damaged and killed, this dead material plus the top, stump and roots of the felled tree decompose through time and return to the atmosphere. The log is extracted from the forest and converted into wood products. Waste during conversion and retired products return to the atmosphere either through burning or through decomposition.

for specific years after harvest to account for emissions that happen over a prolonged period (well over 100 years for some products as timber is stored in long-lived wood products and in landfills, e.g. IPCC 2006). Here we focus on committed emissions to simplify the carbon accounting process, and also adopt the simplifying IPCC Tier 1 assumption that all extracted carbon is emitted at the time of the event. In application for REDD+ accounting, it is possible that annual emission accounting rather than committed emissions would be required.

Logging damage factor (LDF). The logging damage factor reflects the emissions that occur at the location (gap) where the specific tree(s) are felled caused by the decomposition of all the dead wood produced as a result of felling the tree(s). This represents the carbon in the aboveground and belowground biomass of the stump and top of the timber tree felled and left as dead wood in the forest, trees incidentally killed or severely damaged (i.e. uprooted or snapped), and large branches broken off from surviving trees during tree felling.

The dead wood stocks in the logging gap are equal to the total biomass of the felled tree minus the biomass of the extracted log, plus the biomass of trees incidentally uprooted or snapped (i.e. killed), and the biomass of any broken branches from surviving trees during tree felling. This is expressed on the per extracted timber volume and averaged over all sampled gaps:

$$\mathrm{DW} = \left\{ \sum_{\mathrm{Gaps}} ([(f\ (\mathrm{dbh}) - (\mathrm{GAPVol} \times \mathrm{WD} \times \mathrm{CF})) + (\mathrm{BI} \times \mathrm{CF})]/\mathrm{GAPVol}) \right\} \{\mathrm{Number\ of\ Gaps}\}^{-1} \quad (2)$$

where DW is the dead wood carbon stock (Mg C m^{-3}), f (dbh) is the allometric function for calculation of tree biomass based on diameter at breast height (dbh) and species specific wood density (Mg biomass), GAPVol is the volume of timber over bark extracted in gap G (m^3 gap^{-1}), WD is the wood density of felled trees (Mg m^{-3}), CF is the Carbon fraction (0.47 Mg dry mass), BI is the biomass of incidentally killed/damaged trees (Mg C gap^{-1}), Number of Gaps is the the total number of gaps inventoried.

Logging infrastructure factor (LIF). Logging infrastructure emissions include emissions resulting from the creation of logging roads, skid trails and logging decks. Under some accounting schemes, roads and decks will be counted as deforestation because they will show up in moderate resolution imagery analysis (e.g. Landsat), and their emissions can be addressed through stock-difference approach (e.g. area of change multiplied by emission factor derived from C stocks of unlogged forest); however the direct correlation with logging makes it logical to include all sources of emissions under timber management.

Infrastructure emissions are considered to occur at time zero (i.e. committed emissions):

$$\mathrm{LIF} = \frac{((\mathrm{RF} \times \mathrm{RL}) + (\mathrm{DF} \times \#\mathrm{D}) + (\mathrm{SF} \times \mathrm{SL}))}{\mathrm{TotSampleVol}} \quad (3)$$

where LIF is the logging infrastructure factor—dead biomass carbon caused by construction of infrastructure (Mg C m^{-3}), RF is the road factor—emissions per km of road construction (Mg C km^{-1}), RL is the road length (km), DF is the decks factor—emissions per deck constructed (Mg C $deck^{-1}$), #D is the number of decks, SF is the skid trail factor—emissions per km of trail (Mg C km^{-1}), SL is the skid length (km), TotSampleVol is the total extracted volume across the area sampled for infrastructure (m^3).

Where road and deck areas are obtained from interpretation of remote sensing imagery then areas are used directly rather than length resulting in the RL being in hectares and the RF in Mg C ha^{-1}. In such a case, roads and decks are combined.

2.2. Field data collection

Data were collected in 13 commercially operated forest concession areas within the tropical moist climate zone of six countries (five concessions in Indonesia, four in Guyana, and one in each of the other four countries). These were selected to cover a wide range of extraction rates, logging practices, and forest carbon stocks in aboveground and belowground biomass (table 1). The dominance of specific timber species differed among sites (supplemental information available at stacks.iop.org/ERL/9/034017/mmedia). In some sites, aerial imagery and/or high resolution satellite imagery was used to supplement field measurements.

Measurements for assessing the carbon impacts in the logging gaps (volume of felled timber tree, biomass from crown and stump left in the forest, and incidentally killed trees and broken branches due to timber-tree felling), were made across all sites. Logging infrastructure measurements occurred in the Republic of Congo (ROC), Indonesia, and Guyana, with methods varying slightly across sites because this component of the methodology has evolved through time. Aerial imagery and/or high resolution satellite imagery were used to supplement field measurements in these three countries. Detailed information on the field measurements and conversion of field measurements into estimates needed for application of the carbon accounting equations given above are presented in the supplemental material (available at stacks.iop.org/ERL/9/034017/mmedia).

3. Results

3.1. Field measurements

A total of 944 logging gaps were examined across the concessions in the six countries including 1101 harvested trees (table 1). In all sites more than 75% of the gaps were formed by a single felled tree with this proportion as high as 90% in Bolivia. The largest trees harvested in terms of DBH and extracted volume were on average in ROC, followed by Indonesia, Brazil, Guyana, Bolivia, and Belize (table 2). The longest logs were in Indonesia and ROC (≥22 m long) and these two countries also had the highest proportion of total tree biomass extracted in logs (>40%).

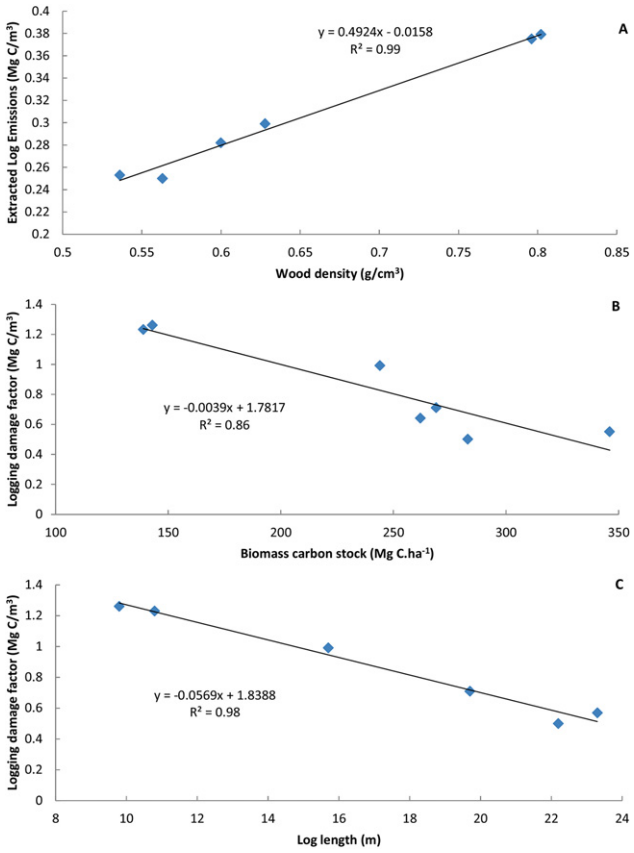

Figure 2. Predictive correlations in the data between: (A) wood density and extracted log emissions (ELE); (B) forest carbon stock and logging damage factor (LDF); (C) mean log length and logging damage factor (LDF).

The area of gaps was highly variable among sites with the largest gaps formed in the felling of trees in ROC and Indonesia where the average felled tree was also the largest (table 2). Expressing the gap area on a per unit of timber extracted results in values of more than 28 m^2 m^{-3} for ROC, Brazil, and Guyana, but only 18 m^2 m^{-3} for Indonesia. Volumes extracted per gap ranged from 25 m^3 (ROC) to just 3.7 m^3 (Belize) giving extracted biomasses of 6.4 Mg (ROC) to 1.0 Mg (Belize) (table 2). Extracted log emission factors (ELE) were highly correlated with the mean wood density of the harvested trees (figure 2(A)).

The mean total damaged biomass in the logging gaps varied by a four-fold factor between the lowest damage in Guyana to the highest in ROC (table 3). The biomass carbon in the roots, stump and tree top of the felled tree accounted for between 55 and 84% of the total damaged biomass recorded in the gaps by site. The logging damage factors (LDF) ranged from 0.50 to 1.26 Mg m^{-3}, and are negatively related to the biomass carbon stock (figure 2(B)) and to the mean total length of the extracted logs (figure 2(C)).

Logging infrastructure factors for the three countries varied by almost a four-fold factor between the lowest and highest value (table 4). In all cases roads and decks dominated total infrastructure emissions representing 96% of emissions

Table 1. Key characteristics of the concessions areas in six countries used for estimating total emissions from selective logging.

Site name	Province	Year sampled	Number of gaps & trees sampled	Extraction rate (m^3 ha^{-1})
RO Congo	Sangha	2004	99 & 120	9
Indonesia	East Kalimantan	2006 and 2009	413 & 481	34[a]
Belize	Orange Walk	2001	47 & 66	2
Bolivia	Santa Cruz	1999	97 & 108	<5
Brazil	Para	2005	105 &123	5
Guyana	Upper Demerara/Berbice	2010–2012	183 & 203	13

[a] Average rate across the five concessions (range of 26–38 m^3 ha^{-1}).

Table 2. Estimates of the mean gap related metrics (with 90% CI) and the resulting extracted log emissions (ELE) factor. The number of gaps measured at each of the six areas is given in table 1.

Country	Mean DBH (cm)	Mean log length (m)	Mean gap area (m^2)	Volume extracted per gap (m^3)	Biomass extracted per gap (Mg C)	ELE (Mg C m^{-3})[a]	Percent of felled tree extracted
RO Congo	123 (3)	22 (1)	719 (85)	25.1 (2.4)	6.4 (0.6)	**0.25**	43 (1)
Indonesia	103 (3)	22 (1)	309 (29)	17.3 (1.5)	4.7 (0.4)	**0.25**	47 (0)
Belize	63 (3)	10 (1)	n/m	3.7 (0.9)	1.0 (0.3)	**0.28**	25 (2)
Bolivia	69 (2)	11 (1)	n/m	4.5 (0.5)	1.3 (0.2)	**0.30**	28 (2)
Brazil	86 (3)	20 (1)	340 (40)	10.7 (1.1)	4.0 (0.4)	**0.38**	43 (2)
Guyana	54 (2)	16 (0.4)	111 (15)	3.5 (0.3)	1.3 (0.1)	**0.36**	44 (2)

[a] For ELE the 90% CI in all cases was less than 0.005.

Table 3. Estimates of the mean (with 90% CI) amount of damage and dead biomass produced per gap and the resulting logging damage factor (LDF). The number of gaps measured at each of the six concession areas is given in table 1.

Country	Top, stump, and root biomass per gap (Mg C)	Incidental damage biomass per gap (Mg C)	Total damage per gap (Mg C)	LDF (Mg C m^{-3})
RO Congo	8.6 (0.9)	3.9 (0.6)	12.4 (1.3)	0.50 (0.04)
Indonesia	7.8 (1.0)	1.7 (0.2)	9.5 (1.0)	0.57 (0.03)
Belize	3.3 (0.8)	0.9 (0.2)	4.2 (0.9)	1.26 (0.14)
Bolivia	3.5 (0.4)	1.7 (0.4)	5.2 (0.7)	1.23 (0.08)
Brazil	5.3 (0.5)	1.4 (0.2)	6.7 (0.6)	0.71 (0.05)
Guyana	1.8 (0.2)	1.5 (0.2)	3.3 (0.3)	0.99 (0.08)

Table 4. Mean estimates (and 90% CI where relevant) for each parameter used to estimate the logging infrastructure factor (LIF) for three of the concession areas for which we had the relevant data.

Country	Skid trail factor (Mg C m^{-3})	Deck factor (Mg C m^{-3})	Road factor (Mg C m^{-3})	LIF (Mg C m^{-3})
RO Congo	0.01 (0.00)	Included with roads	0.23 (0.04)	**0.24**
Indonesia	0.20	0.02	0.45	**0.67**
Guyana[a]	0.17	Included with roads	0.81	**0.98**

[a] Data are the national 5 yr average for the period 2006–2011 for length of skid trails and area of roads.

in ROC, 70% in Indonesia and 83% in Guyana. Emissions from skid trails differed markedly, however, with the skids representing just 4% of the LIF in ROC but 17% in Guyana and 30% in Indonesia.

3.2. Logging emission factors

Of the three sites for which we have complete data, the total emission factor (TEF) varied by a more than two-fold factor, with the lowest for ROC and highest for Guyana (table 5). The committed emissions from the logging gaps per cubic meter extracted (ELE plus LDF) accounted for 76% of the TEF for ROC and 55–58% of TEF for Indonesia and Guyana.

The emissions associated with the extracted logs were consistently the smallest proportion of the total emissions (even without considering sequestration in wood products) representing between 15 and 25%. The emissions associated with logging damage (LDF) varied more widely and were

Table 5. Summary of all logging emission factors and the total emission factor (TEF), all in units of Mg C m^{-3}, for each of the six concession areas.

Country	ELE	LDF	ELE + LDF	LIF	TEF
RO Congo	0.25	0.50	0.75	0.24	0.99
Indonesia	0.25	0.57	0.82	0.67	1.49
Belize	0.28	1.26	1.54	NA	NA
Bolivia	0.30	1.23	1.53	NA	NA
Brazil	0.38	0.71	1.09	NA	NA
Guyana	0.36	0.99	1.35	0.98	2.33

governed by the amount of dead wood produced during timber harvest, itself dominated by the top and stump of the timber tree. The logging damage emissions were a significant proportion of the total logging emissions, accounting for between 38 and 51%. The infrastructure emissions (LIF) varied widely depending upon the width and length of logging roads and decks mainly, but also on the density of skid trails and type of skidding machinery used. In Indonesia and Guyana, where bulldozed skid trails are combined with wide roads, most emissions are caused by construction of infrastructure.

3.3. Carbon emissions from tropical timber harvesting

To determine the relative significance of each emission source from logging operations across the study sites (excluded Belize where we had no means of estimating infrastructure emissions with confidence), we have combined the emission factors on a per cubic meter of timber extraction with the extraction rates (table 6). Despite the often perceived notion that logging in tropical forests is very damaging, the proportion of the above and below ground biomass carbon of the unlogged forest that is emitted from all logging sources represents only about 15% for the highest intensity of logging sites in Indonesia and as little as 3% for Brazil and ROC (table 6). These emissions will be offset to some degree depending on the rate of regrowth during recover—this is discussed further in the next section.

4. Discussion

4.1. Comparison with other studies

Very few comparable results exist because timber harvesting and associated emissions have not been considered in this context of tackling emissions per unit of production. Many studies exist detailing the relative coverage of roads, decks and skid trails (e.g. Jackson *et al* 2002, Iskandar *et al* 2006), number of trees or areas disturbed by timber harvest (e.g. Verissimo *et al* 1992, Uhl *et al* 1991, Holmes *et al* 2002, Schulze and Zweede 2006, White 1994, Pereira *et al* 2002) and even carbon stock changes associated with timber harvest (e.g. Medjibe *et al* 2011, Pinard and Putz 1996, Feldpausch *et al* 2005). However, to our knowledge no published literature systematically developed emission factors for timber harvest, but we were able to estimate the relevant emission factors from data presented in Feldpausch *et al* (2005) and Pinard and Putz (1996).

In the Feldpausch *et al* study in the Brazilian Amazon, the mean DBH of the harvested trees was 75 cm, a mean wood density of 0.69 g cm^{-3} and 6.2 m^3 ha^{-1} were extracted. We estimated the logging damage factor to be 0.84 Mg C m^{-3}, the extracted log emission 0.36 Mg C m^{-3} and the logging infrastructure factor 0.27 Mg C m^{-3}, for a total emission factor of 1.5 Mg C m^{-3}. The estimated LDF is about 20% higher than our result for Brazil; the ELE is within 10% of our estimate for Brazil and identical to the estimate for Guyana; and the LIF was very close to our estimate for ROC and significantly lower than those we obtained for Guyana and Indonesia. Fifty-three percent of infrastructure emissions in the Feldpausch *et al* study were from roads compared to 67% and 83% for Indonesia and Guyana, respectively.

In the Pinard and Putz (1996) study of conventional logging in Sabah, Malaysia, the mean extraction was 154 m^3 ha^{-1} and the minimum harvest DBH was 60 cm in a forest with a mean stock of 200 Mg C ha^{-1}. We estimated their ELE to be 0.21 Mg C m^{-3}, and the LDF to be 0.46 Mg C m^{-3}; insufficient data were available for estimating the LIF. These two factors from the Pinard and Putz study are comparable to those we obtained for Indonesia despite the extremely high extraction rate per ha.

4.2. Consideration of factors affecting the net emissions profile through time

The method and factors presented here assume, like the IPCC Tier 1 method, that all emissions associated with the conversion of live to dead biomass occur in the year of

Table 6. Gross carbon emissions from logging (ELE = extracted log emissions, LDF = logging damage factor, LIF = logging infrastructure factor) compared to the carbon stock, both normalized to a hectare of forest for five key timber producing areas (excludes Belize where no estimation of infrastructure emissions were possible). The emissions were estimated as the product of the extraction rate and each emission factor.

Country	Timber extraction rate (m^3 ha^{-1})	ELE (Mg C ha^{-1} $harvest^{-1}$)	LDF (Mg C ha^{-1} $harvest^{-1}$)	LIF (Mg C ha^{-1} $harvest^{-1}$)	Total logging emissions per harvest (Mg C ha^{-1})	Forest carbon stock (Mg C ha^{-1})
RO Congo	9	2.3	4.5	2.2	8.9	283
Indonesia	34	8.5	19.4	22.8	50.7	332
Bolivia	5	1.5	6.2	1.4[a]	9.0	139
Brazil	5	1.9	3.6	1.4[a]	6.8	269
Guyana	13	4.7	12.9	12.7	30.3	244

[a] We used the LIF of 0.27 Mg m^{-3} estimated from data in Feldpausch *et al* (2005) for Bolivia and Brazil.

the event, and thus are considered committed. In reality, however, more research is needed to understand the trajectory of carbon pathways through time and how these aspects are best addressed in an accounting framework to develop more detailed logging emission factors. The IPCC (2006) requires annual reporting by developed countries, but whether annual reporting will be required for REDD+ reporting is unclear at present. If reporting annually rather than reporting as committed emissions will be required, several challenges will need to be overcome, such as: robust decomposition rates for lying deadwood created from felling of timber trees, decomposition rate for roots, and retirement rate of wood products for estimating long-term wood product carbon storage.

First, research shows that dead wood decomposes relatively slowly in tropical forests, although its rate of decomposition through time is very poorly known (Brown 1987, Delaney *et al* 1998). Most of the logging slash of tropical species is large in size, composed of the tree top and large branches, and generally low in nutrients and high in secondary compounds (Brown 1987). For a tropical moist climate typical of our study sites, the half-life of dead wood has been shown to range from 1 to 69 yr (Delaney *et al* 1998, Chambers *et al* 2000), with slower rates generally associated with larger diameter tree boles and branches. Given the high variability in rates of wood decomposition and the highly variable sizes of the dead wood in logging gaps (from twigs to large diameter boles), accounting for all emissions from dead wood as committed emissions would be a consistent and comparable approach for national level accounting.

Second, the delayed mortality of trees impacted by harvesting practices also has a time component that is not considered in our analysis. Our method considers that all trees snapped or uprooted are killed and, even if they do survive, they still contribute to emissions from the dead wood produced. However, there will be additional trees that are merely scraped or leaning that may subsequently die, and there are suggestions that this quantity is significant. The re-measurement of about 100 paired plots (one plot around a logging gap and the other same size plot in an adjacent unlogged area) four years after initial logging at our site in Bolivia showed that 28% of trees recorded as leaning after timber harvest were dead. Pinard and Putz (1996) re-measured their plots 8–12 months after timber harvest and found that for trees with 'other damage' resulting from logging (i.e. neither snapped nor uprooted), 8–10% had died. Thus our focus on just snapped and uprooted incidentally damaged trees will underestimate total mortality and thus emissions resulting from logging.

Third, we assume that all felled trees are extracted, while in reality trees could be felled and then not extracted for a variety of reasons (e.g. too damaged, hollow, misidentified, could not re-locate to skid out). In this situation the ELE factor would be zero but the total dead wood created (LDF) would include the biomass of the whole tree. Where this practice is common and not monitored (e.g. such trees can be difficult to locate if no skid trail is present), the method described here will underestimate the total emissions associated with timber harvesting.

Fourth, on the carbon *gain* side of the equation, carbon will accumulate in and around the gaps in existing trees and in new trees that in-grow after logging activities, and we do not account for this potential stimulation in carbon sequestration rates. Carbon storage of old-growth forests across tropical forests in Amazonia and Africa has been shown to occur (Phillips *et al* 2008, Lewis *et al* 2009), and we refer to this growth as the background rate of carbon accumulation. In contrast, we refer to the carbon accumulation that occurs only in the gaps caused by logging as the human-induced potential carbon accumulation rate. The opening of the canopy with associated light penetration and decreased competition for water and nutrients could lead to higher sequestration rates in these areas than would occur in the absence of harvest, and this is the quantity of interest for estimating the potential net gain of carbon from logging. In the gaps, large trees are felled and removed. Although the radial increment of the remaining trees may increase, the biomass carbon increment of many smaller trees will often be lower than the biomass increment of the single missing large trees. Thus the loss of a large timber tree with large canopy area could actually lead to a net *reduction* in absolute carbon sequestration rate.

Studies have shown that the recovery of a logged stand to conditions similar to the pre-logged forest can take 150 years or more (Meijer 1970, Riswan *et al* 1986) suggesting that growth cannot be greatly elevated. Kartawinata *et al* (2001) suggested that logging can affect natural drainage leading to flooding and ongoing tree mortality and/or climbers can invade bare ground and overgrow regenerating and residual trees suppressing growth. Silva *et al* (1995) in Brazil showed that logging did stimulate growth in the residual stand but that this effect only lasted 3 years with subsequent rates similar to unlogged forest. A similar trend was found for logged plots in our Bolivia study site, where we measured the rates of carbon accumulation in the 100 paired plots and found that there was no difference in the rates between the two sets of plots (unpublished data). Pinard and Cropper (2000) in Sabah, Malaysia showed that when 20–50% of the stand was killed during logging, subsequent replacement with pioneer species reduced a site's potential for carbon storage by 15–28% over 60 years. Thus it is likely that in many cases timber harvesting leads to minimal elevation in sequestration rates, and that regrowth will occur but likely it will take many decades for the forest to reach the carbon stocks of the pre-logged forest, and longer than the typical 30 year re-entry time used in the management of many tropical humid forests. It is likely therefore that managed forests with relatively high extraction rates such as those in Indonesia and Malaysia will not recover to their former unlogged state before they are logged again and thus the carbon stock will gradually decline over repeated cycles. Further detailed studies on a chronosequence of previously logged areas could determine whether or not a positive regrowth factor exists.

Finally, within our accounting methodology, all harvested wood is assumed to be emitted immediately (i.e., within the ELE factor), and thus we do not allow for the potentially significant proportions that are stored long term or even permanently sequestered in products or in landfills. During

the processing of harvested logs into wood products, a portion of the log is converted to waste (e.g. sawdust and offcuts) and emitted immediately to the atmosphere, and another portion converted to long-lived products that represent a carbon sink (Winjum *et al* 1998). For tropical developing countries, Winjum *et al* (1998) estimated that on average 45% of harvested logs end up as waste and short-lived (<5 yr life) products and are essentially emitted to the atmosphere at the time of the event. The remaining wood is processed into a variety of products. Carbon is sequestered in these products over different time periods, with some fraction sequestered permanently in, e.g., a piece of furniture or a landfill, or because its sequestered life exceeds that of carbon dioxide in the atmosphere (Skog and Nicholson 2000). Using the factors in Winjum *et al* (1998) for tropical timber, about 10% or less of the carbon in extracted logs is essentially permanently sequestered in long-term products (life >100 yr). Thus the assumption of immediate emissions from the ELE factor will overestimate both emissions in the year of harvest and ultimate total emissions.

4.3. Implications for forest management

Knowledge of the relative magnitude of each emission source from logging provides the information needed to design possible actions for reducing emissions by improving the logging practices. Emissions from logging damage (LDF) are generally the largest source of emission for most sites, followed by infrastructure damage in Guyana and Indonesia. The emissions from the extracted log, for comparison, are between 24 and 53% of the in-forest logging damage emissions. Efforts to reduce these emission sources could include, e.g., extracting more timber per felled tree and reducing waste; improving directional felling and thus reducing incidental damage to surrounding trees; planning infrastructure more effectively in areas with greater concentration of timber trees; and use of cable extraction of timber instead of creating skid trails up to the stump of the felled trees. In several of the logging study sites, most notably Indonesia and ROC, the diameter at the base of the top of many of the trees left in the forest to decompose was 80 cm or more containing more than 50% of the tree carbon. With respect to replacing skidding trails with cable extraction—this could potentially reduce the infrastructure emissions by up to 30%. Many such practices and thus emission reductions can be associated with Reduced Impact Logging (RIL). The ability to reduce emissions through changes in practices highlights the need for multiple emission factors with changes in practices leading to new emission factors to apply to activity data. The need to develop emission factors for both conventional and reduced impact logging will be particularly important for rewarding countries efforts to implement sustainable forest management under REDD+.

4.4. Comparison of gross carbon emissions from selective logging with those for deforestation

Although we have shown that selective logging in tropical humid forests has a relatively low impact on the biomass carbon stocks on a per hectare basis, selective logging takes place over large areas, and at a country level, the total emissions could be significant (Asner *et al* 2005). To produce an initial estimate of logging emissions at a national scale we used estimates of industrial roundwood production from the FAO-FRA 2010, cross checked with each country report and FAOSTAT, for five countries covered by our study sites (excluding Belize) plus a further four key timber producing countries (Democratic Republic of Congo, Gabon, Malaysia, and Suriname) represented by the data collected in our study sites; and applied the relevant emission factors obtained in this study (table 7). Although we recognize that the emission factors can be expected to vary geographically, these four additional countries were selected because we assumed, that given their location, physiognomy of their forest types, and their selective logging practices (including extraction rates per ha), that their emission factors would be very similar to those obtained in our study sites. We compared these gross emissions with those from gross tropical deforestation for these nine countries using the data reported in Harris *et al* (2012).

The purpose of this analysis is to demonstrate the scale of emissions from logging relative to deforestation rather than to give definitive estimates. Such estimates would require emission factors that are country specific and rely on accurate estimates of harvested volumes from non-plantation forests. We are confident that the FAO-FRA estimates for the given countries capture extraction rates only from natural forests. Although the three emission factors will likely vary somewhat within countries, we further argue that given the robustness of the emission factors (e.g. 90% confidence intervals for individual factors <10% of the mean) and the strong relationships between LDF and forest biomass and log length, and ELE and wood density (figure 2) restricts the possible variation within timber harvesting areas in a country. To be conservative in the comparison we exclude roads and decks from the LIF because in some cases the gross deforestation data used by Harris *et al* may have already included these areas as deforestation. This is very conservative as many roads and decks are likely too small to be captured in the remote sensing imagery and countries may not consider thin lines of tree cover loss within the forest to be deforestation. However, the total emissions from tropical timber harvesting practices must include emissions from all infrastructure; only in this comparison with deforestation do we exclude roads and decks to reduce the risk of double counting.

Extraction spanned one order of magnitude between the nine countries leading to a similar variation in harvesting emissions. Comparison with deforestation emissions clearly illustrates the significance of timber harvest from native forests as an emissions source. For the nine countries included, emissions from logging were on average equivalent to about 12% of those from deforestation (with a range from 6% to 68%).

We found that for those countries with high deforestation emissions, such as Indonesia and Brazil, emissions from logging were relatively small and were equivalent to <10% of those from deforestation. On the other hand, for several of the countries with relatively low deforestation emissions

Table 7. Gross carbon emissions from logging (ELE = extracted log emissions, LDF = logging damage factor, LIF = logging infrastructure factor) and from deforestation for some key tropical timber producing countries. Estimates of industrial roundwood production for 2005 (most recent reporting year) for each country are from the FAO-FRA 2010, cross checked with each country report. Total emissions from deforestation are the median values from Harris *et al* (2012). Countries selected are considered those appropriate for the emission factors calculated in this study.

Country	Industrial roundwood production (10^3 m^3 yr^{-1})	ELE (Tg C yr^{-1})	LDF (Tg C yr^{-1})	LIF (Tg C yr^{-1})	Total emissions from logging (Tg C yr^{-1})	Total emissions from logging excluding roads and decks[d] (Tg C yr^{-1})	Total emissions from deforestation (Tg C yr^{-1})	Ratio of logging to deforestation emissions (excluding roads and decks)
DRC[a]	4 208	1.05[e]	2.10[e]	1.01[e]	4.17	3.20	22.5	0.14
Gabon	1 098	0.27[e]	0.55[e]	0.26[e]	1.09	0.83	3.97	0.21
ROCongo	1 450	0.36	0.73	0.35	1.44	1.10	3.29	0.33
Indonesia	5 839[b]	1.46	3.33	3.91	8.70	5.96	104.6	0.06
Malaysia	26 706	7.48[f]	14.7[f]	17.9[f]	40.1	27.51	40.8	0.68
Brazil	18 303[b]	6.96	13.0	4.94[c]	24.9	21.73	339.2	0.06
Bolivia	871	0.26	1.07	0.24[c]	1.57	1.33	10.6	0.13
Guyana	395	0.14	0.39	0.39	0.92	0.60	1.41	0.43
Suriname	181	0.07[g]	0.18[g]	0.18[g]	0.42	0.28	0.83	0.33

[a] Democratic Republic of Congo, and data from FAOSTAT for 2005 (http://faostat.fao.org/site/626/DesktopDefault.aspx?PageID=626#ancor).
[b] From natural forests only; an additional 8.6 million m^3 are produced from plantations in Indonesia, and 98.7 million m^3 in Brazil (www.sidra.ibge.gov.br/bda/pesquisas/pevs/default.asp).
[c] We used the LIF of 0.27 Mg m^{-3} estimated from data in Feldpausch *et al* (2005) for Bolivia and Brazil.
[d] Roads and decks excluded for comparison with deforestation to give a conservative comparison taking into account the risk that roads and decks may have been captured in the deforestation analysis.
[e] Emission factors for Gabon and DRC from ROC.
[f] Emission factors for Malaysia from Indonesia.
[g] Emission factors for Suriname from Guyana.

of less than 5 Tg C yr^{-1} (e.g. Republic of Congo, Guyana, and Suriname) emissions from logging were significant and equivalent to about half or more of those from deforestation. We suggest, therefore, that such countries should place equal efforts on opportunities for reducing emissions in this sector. Understanding the magnitude of each emissions source resulting from tropical timber harvesting practices as presented in this paper helps identify where there are opportunities to reduce emissions from the second 'D' in REDD.

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The Effect of Harvest on Forest Soil Carbon: A Meta-Analysis

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Abstract: Forest soils represent a substantial portion of the terrestrial carbon (C) pool, and changes to soil C cycling are globally significant not only for C sequestration but also for sustaining forest productivity and ecosystem services. To quantify the effect of harvesting on soil C, we used meta-analysis to examine a database of 945 responses to harvesting collected from 112 publications from around the world. Harvesting reduced soil C, on average, by 11.2% with 95% CI [14.1%, 8.5%]. There was substantial variation between responses in different soil depths, with greatest losses occurring in the O horizon (−30.2%). Much smaller but still significant losses (−3.3%) occurred in top soil C pools (0–15 cm depth). In very deep soil (60–100+ cm), a significant loss of 17.7% of soil C in was observed after harvest. However, only 21 of the 945 total responses examined this depth, indicating a substantial need for more research in this area. The response of soil C to harvesting varies substantially between soil orders, with greater losses in Spodosol and Ultisol orders and less substantial losses in Alfisols and Andisols. Soil C takes several decades to recover following harvest, with Spodosol and Ultisol C recovering only after at least 75 years. The publications in this analysis were highly skewed toward surface sampling, with a maximum sampling depth of 36 cm, on average. Sampling deep soil represents one of the best opportunities to reduce uncertainty in the understanding of the response of soil C to forest harvest.

Keywords: forest management; harvest; soil carbon; soil order; deep soil; meta-analysis

1. Introduction

Forest ecosystems contain 1240 Pg C [1,2], which represents as much as 80% of aboveground terrestrial C and 70% of all soil organic C [3–5]. The relative proportion of forest C found in soils varies among biomes, ranging from roughly 85% of the terrestrial C pool in boreal forests, to 60% in temperate forests, to 50% in tropical rainforests [1,6]. The net balance of soil C in forests relies upon large rates of detrital inputs (61.4 Pg C year^{-1}) and respiratory losses (60 Pg C year^{-1}), which together represent substantial yearly turnover in the soil C pool [7]. By altering the rates of detrital inputs and respiratory outputs in soils, the extent and intensity of forest harvest can have substantial impacts not only on ecosystem function but also on atmospheric chemistry and global climate [6,8,9].

C is one of the principal components of soil organic matter (SOM), a key component of soil that plays an important role in many biological, chemical, and physical properties [10–12]. SOM provides a crucial source of energy and nutrients for soil microbes, buffers soil pH, and helps to stabilize soil structure [12,13]. Along with nitrogen and phosphorus, SOM is considered a critical indicator for soil health and quality.

Thus, soil C is an essential component of forest C accounting, yet many models assume that only surface soil responds to forest management and that soil C returns to equilibrium within 20 years after harvest [14]. Recent national or global assessments of forest C lack any mention of mineral soil

C [15–17], implicitly assuming that soil C remains constant after forest harvest. Furthermore, carbon monitoring programs include soil C inconsistently. For example, the American Carbon Registry [18] and the Verified Carbon Standard [19] do not require or specify protocols for soil C measurements. The Intergovernmental Panel on Climate Change (IPCC) inventory standards [20] assume constant mineral soil C in Tier 1, with an option for inclusion of national soil C inventories only if preferred by a particular agency, and the U.S. Forest Service Inventory and Analysis Program [21] specifically limits soil sampling to 20 cm depth. The inclusion of soil in models of ecosystem C following harvest can have significant effects. For example, in a model of the forest C pool change following intensive bioenergy harvest, Zanchi et al. [22] show that the inclusion of soil increases the C payback period by approximately 25 years when substituting forest bioenergy for coal. Thus, the inclusion or exclusion of soil in ecosystem C models and ecological monitoring programs can have a major impact on forest policy when attempting to mitigate climate change through forest management [14].

Ambiguity about the effect of forest harvesting on soil C has persisted in the literature, likely exacerbated by the inherent spatial and temporal variability in soil measurements that can obscure the results of even the most well-designed studies [23]. By gathering the results from many studies that apply similar treatments, meta-analysis can overcome the high levels of spatial and temporal variability to provide cumulative answers that may not have been evident within individual sites [23,24]. Previous meta-analyses on the effect of harvesting on soil C have found either minimal effects on soil C pools [25] or substantial (30%) loss to O horizon pools with little change to mineral soil C [9]. Variation in soil C response has been shown to significantly differ among soil types and different harvesting strategies [9].

Studies of soil C change due to harvest have historically been strongly biased toward surface sampling [26]. Nave et al. [9] reported a mixed response to harvest in deeper soil (20–100 cm depth), ranging from a slight average decrease (−5%) in studies that reported C pools to a large average increase (+20%) in studies that reported only C concentration. Several recent reviews have highlighted the need for greater sampling of deep soil [26–28], especially as the shifting paradigm of SOM research has come to reject the assumption that deep soil C cannot not change on timescales relevant to anthropogenic C emissions [29–31]. Resolving the response of deep soil horizons to harvesting is important because these horizons occupy a much greater volume than surface O and A horizons. Even small changes in subsurface C can exacerbate or compensate for changes in surface soil C, and neither the magnitude nor direction of subsoil C change is clear from previous research.

The process of meta-analysis is necessarily cumulative, with each iteration updating previous analyses to further constrain the error in effect size estimates and to extend the scope of analysis. Thus, the objective of our meta-analysis is to update and extend the findings of Nave et al. [9] with respect to five major research questions:

(1) What is the overall effect of forest harvesting on soil C pools?
(2) How does the effect of forest harvest on soil C change with soil depth?
(3) To what extent does the effect of harvesting differ among soil orders?
(4) Do site pretreatment strategies or increasing harvesting intensity (i.e., whole tree harvest) moderate or accentuate harvesting impacts on soil C?
(5) How long does soil C take to recover from harvest across different soil types?

2. Materials and Methods

Meta-analysis is a cumulative activity which builds upon previous research and meta-analyses on similar research questions. Our meta-analysis builds upon the work of Nave et al. [9] and Johnson and Curtis [25] by updating their results with studies published between 2008 and 2016. The database published by Nave et al. [9] was independently recreated from each of 75 references. Metadata for each study was verified, and additional metadata such as the sampling depth of each response ratio was gathered. A total of 8 effect sizes differed in our dataset from the Nave et al. [9] database, all of

which were either additional data for mineral soils or a split of one effect size into two based upon sampling depth.

To add to this database with studies published between 2008 and 2016, we searched the peer-reviewed literature for relevant studies using the online database Web of Science with combinations of the terms: forest, timber, harvest, logging, soil C, soil organic matter, and management. No climate criteria was used to screen studies. To be included in the meta-analysis, publications had to report both a control as well as harvested treatments. Both pretreatment soil C and unharvested reference stands were considered acceptable controls, and measurements of reference stands were considered the superior control. For forest chronosequence studies, soil C data from the oldest stand was used as the control. A minimum stand age of 30 years was considered acceptable for control stands, although most studies used controls of considerably greater age. Nave et al. [9] found that studies reporting only soil C concentration data yielded different conclusions about the direction of harvest effects than those studies reporting soil C pool data. Consequently, soil C pool data was used in our meta-analysis when both concentration and pool data were available.

We collected potentially useful predictor variables of soil C response from each publication, including soil order, geographic region, and time since harvest (Table 1). Binning of continuous predictor variables (such as precipitation) was carried out in the same intervals as Nave et al. [9] for ease of comparison. Each study was categorized by harvest, residue management, and site preparation strategies. Harvesting technique was categorized as sawlog when only the merchantable bole (stem) was removed from the site or whole tree harvest (WTH) when the tops, limbs, and foliage were removed in addition to the bole. To test the response of soil C at different depths, data from each study was separated into one of five groups: O horizon, top soil (0–15 cm), mid soil (15–30 cm), deep soil (30–60 cm), and very deep soil (60–100+ cm). A sixth group called whole soil was assigned to studies that aggregated mineral soil samples instead of reporting results at separate depths. Several studies aggregated soil data from 0–100 cm, which reduced the number of unique deep and very deep soil observations even though these depths were separately sampled.

Table 1. Factors gathered as potential predictor variables in this meta-analysis.

Factor	Levels	
Reporting units	Pool ($Mg \cdot ha^{-1}$), concentration (% or $mg \cdot g^{-1}$)	
Soil Depth	O horizon	Forest Floor
	Top Soil	0–15 cm
	Mid Soil	15–30 cm
	Deep Soil	30–60 cm
	Very Deep	60–100+ cm
Overstory species	Hardwood, conifer/mixed	
Soil order	Alfisol, Andisol, Entisol, Inceptisol, Mollisol, Spodosol, Oxisol, Ultisol	
Geographic group	NE North America, NW North America, SE North America, SW North America, Europe, Asia, Pacific (Australia, New Zealand)	
Harvest type	Clearcut, thin	
Harvest intensity	Stem only, whole tree	
Residue management	Removed, spread	
Site preparation	Broadcast burn, tillage/scarification	
Soil texture	Fine (mostly silt or clay), coarse (mostly sand), organic	
Time since harvest	Continuous	
Mean Annual Temperature	0–5, 5–7.5, 7.6–10, 10.1–15, 15.1–20, >20 (°C)	
Mean Annual Precipitation	<500, 500−750, 751−1000, 1001−1400, 1401−1800, >1800 (mm)	

Our meta-analysis estimates the magnitude of change in soil C using the ln-transformed response ratio R, which is defined as

$$\ln(R) = \ln\left(\frac{\overline{X_T}}{\overline{X_C}}\right) \quad (1)$$

where $\overline{X_T}$ is the mean soil C value of treatment (harvested) observations, and $\overline{X_C}$ is the mean soil C value of control observations for a given set of experimental conditions at a specific site and depth. Multiple response ratios were recorded for each publication, with the number of response ratios (k) depending upon the number of experimental conditions imposed and the number of samples taken by depth. For example, a publication that reports the results of two thinning treatments and two clear-cut treatments at three depth increments (forest floor, top soil, and mid soil) versus a control would yield 12 response ratios. R is a unit-less measure of effect size, which allows comparison among studies that report data in different units [24]. By back transforming ln(R), $[(e^{(\ln(R))} - 1) \times 100]$, mean response ratios can be interpreted as the percentage change in soil C relative to the control. Estimates of the standard deviation and sample size for each $\overline{X^T}$ and $\overline{X^C}$ were not available in several publications. Consequently, an accurate estimate of total heterogeneity (Q_T) for the dataset was not possible. Subsequent partitioning of Q_T into within- and among-group heterogeneity (Q_W and Q_A, respectively) for random and mixed effect models (as is customary for meta-analyses) was not possible [24]. Instead, we used nonparametric resampling techniques (bootstrapping) to estimate confidence intervals around mean effect sizes in an unweighted meta-analysis [9]. Adams et al. [32] recommend bootstrapping confidence intervals for ecological meta-analyses, and show that confidence bounds based on this method are more conservative than standard meta-analyses. Bootstrapping was implemented using the bootES package [33] in *R* [34]. For all statistical tests in our analysis, $\alpha = 0.05$.

Although not exhaustive, the database we compiled from the literature search contained 945 soil C response ratios from 112 publications published between 1979 and 2016. Roughly half the dataset was comprised of response ratios analyzed by Nave et al. [9]. The full dataset is available as Supplementary Material, including maximum sampling depth and the number of response ratios from each paper (Appendix A).

3. Results

3.1. Overall Effect and Change with Depth

Across all studies, harvesting led to a significant average decrease in soil C of 11.2% relative to control (Figure 1). Whether the response to harvest was reported as pools or concentrations had a large impact on the estimated effect of harvest on soil C, with mean response for studies reporting C concentration units (%, mg·g^{-1}, etc.) 16.2% higher (with a 95% CI [20.9%, 11.8%]) than studies reporting C pool units (Mg·ha^{-1}, tons·ha^{-1}, etc.). Concentration responses are higher than pool responses at all soil depths, except for very deep and whole mineral soil, which did not have enough concentration response ratios to construct separate confidence intervals (Figure 1). Consequently, all subsequent analyses focused on the subset of data reporting soil C pools.

Several different soil layers show significant losses of C due to harvesting. Overall, O horizons lost 30.2% of their carbon as a result of harvesting. Losses from top soil were much smaller, although the estimated loss when reported in pool units was significant (−3.3%). In mid (15–30 cm) and deep soil (30–60 cm), the average loss of soil C was greater than topsoil, although the smaller number of response ratios for these depths resulted in more poorly constrained estimates. Studies only reporting C concentration observed a 14.5% increase in deep soil (30–60 cm), although the sample size was relatively small. The overall effect in very deep soil (60–100+ cm) was significant, with an average loss of 17.7%. Unfortunately, this region of the profile was not frequently sampled (21 response ratios out of 945 total), and consequently the 95% confidence interval is quite wide.

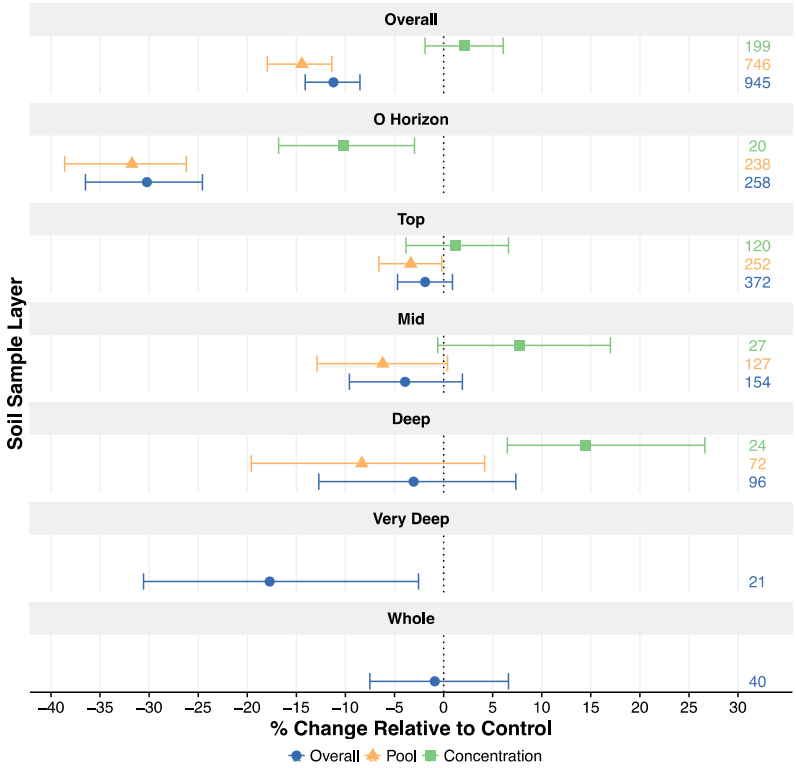

Figure 1. Response of soil C to forest harvesting, overall and faceted by soil depth. All points are back-transformed mean effect sizes ± 95% confidence intervals calculated by nonparametric bootstrap. The number of response ratios (*k*) that make up each mean effect is listed on the right. Mean effects with confidence intervals overlapping the dashed line (0%) show no significant change in soil C due to harvesting. Within each facet, mean effect sizes are shown for the overall effect as well as separately for studies reporting C pool units or concentration units.

3.2. Effect of Harvesting across Soil Orders

The effect of harvesting on soil C differs between soil orders (Figure 2). For the Alfisols and Inceptisols, there are significant losses in O horizon C pools (−12.0% and −45.4%, respectively), but no significant loss in the mineral soil. Mollisols lost an average of 17.7%, although neither O horizon nor mineral soil responses were significantly different from 0. In several cases, small samples sizes made separate testing of organic and mineral soil impossible within a single order (Andisols, Entisols, Oxisols). However, in each of these cases the overall effect was significant. Soil C increased by 24.5% on average in Andisols, but decreased by 18.8% in Entisols and 30.9% in Oxisols. The number of response ratios was more concentrated in the Alfisol, Inceptisol, Spodosol, and Ultisol orders, although a large number of publications did not report information on soil classification. The response to harvesting in Spodosols is substantial (−19.0% overall), with significant losses in both the O horizon (−36.4%) and moderately less in the mineral soil (−9.1%). Likewise, Ultisols lost significant soil C in response to harvesting (−24.7% overall), with the most substantial losses occurring in the O horizon (−66.0%) rather than in the mineral soil (−11.9%).

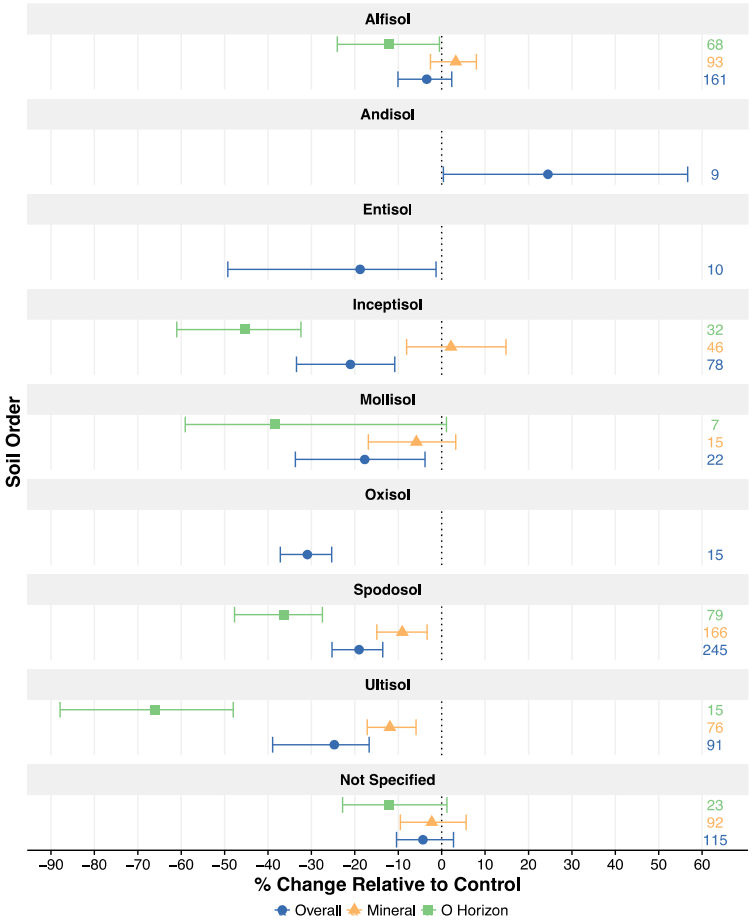

Figure 2. Response of soil C to harvesting in different soil orders. Mean effect sizes ± 95% confidence intervals calculated by nonparametric bootstrap are shown for all response ratios in each soil order (Overall) and broken out into mineral soil or O horizon. The number of response ratios (*k*) comprising each mean effect are listed on the right. Effect sizes were calculated only on response ratios reported in pool units ($k = 746$).

3.3. Differences in Response to Harvest between Forest Types

The response of soil C to harvest differs between hardwood and coniferous/mixed forest types (Figure 3). The decline in O horizon C pools is significantly greater in conifer/mixed forests (−38.1%) compared to hardwood forests (−25.4%). Differences between forest types were not significant for any mineral soil layer. However, the decline in soil C after harvest was significant for hardwood forests but not conifer/mixed forests in deep soil (30–60 cm) and in studies reporting whole mineral soil C pools. Also in these studies, the difference between hardwood and conifer/mixed forest response to harvest is marginally significant ($p < 0.1$). The number of observations are highly concentrated in O horizon and top soil, consequently limiting the precision of mean effect size estimates in deeper layers. No observations for hardwood forest were made in very deep soil (60–100+ cm).

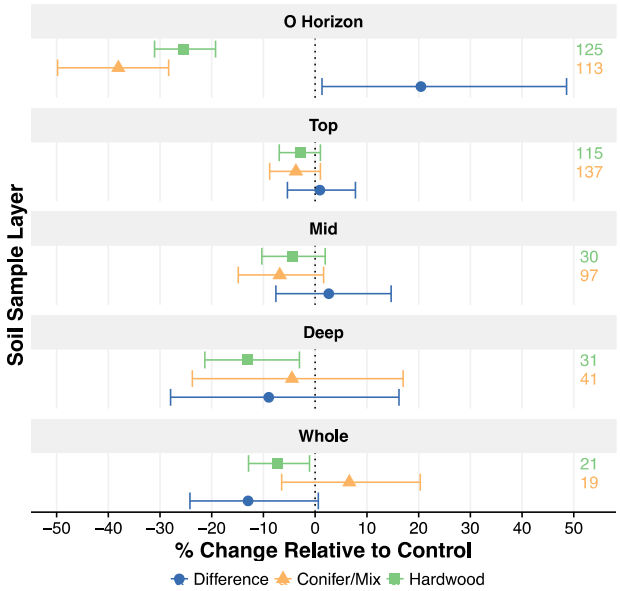

Figure 3. Response of soil C harvesting at different depths in soil, broken down by hardwood or conifer/mixed forest types. Mean effect sizes ± 95% confidence intervals calculated by nonparametric bootstrap are shown for hardwood and conifer/mixed forests. Blue circles show the mean difference between these forest types (Hardwood–Conifer/Mix) ± 95% confidence interval for the difference. Differences are calculated on the logarithmic effect size scale, and then back-transformed to % change, and thus do not necessarily add up on the % change scale. The number of response ratios (*k*) in each forest type at each depth is listed on the right. Data for very deep soil is not shown because there were no observations for this soil layer in hardwood forests.

3.4. Harvest Intensity, Residue Management and Site Pretreatment

Differences in forest management strategies can significantly impact the response of soil C to harvesting (Figure 4). While there was no significant overall difference observed between thinning and clear-cut harvesting, less C was lost from mineral soils under clear-cut harvesting compared to thinning (+9.3%). Likewise, harvest intensity significantly changed the response of mineral soil C, with soils undergoing whole tree harvesting losing 13.3% less C than bole-only harvesting. Possible mechanisms for these counter-intuitive results are considered in Discussion Section 4.5.

The practice of broadcast burning sites in preparation for planting after a harvest leads to significant additional losses of soil C, with burned soils losing 15.2% more C than soils with no pretreatment. This effect is especially severe in the O horizon (40.9% additional loss than if sites were not burned), and somewhat curtailed in the mineral soil (8.3% additional loss). The wide 95% CI for the estimate of differences in O horizon responses due to burning reflects disparities in burn severity and treatment implementation among different studies.

Spreading of residual materials across harvested sites (by chipping tops and limbs or other methods) resulted in significant additional loss of soil C (−10.9%), with these extra losses occurring mostly in the mineral soil (−17.5%). On the other hand, residue removal resulted in no significant additional losses to soil C.

Tillage is sometimes used to prepare soils for planting after harvest, either to create raised planting beds or to prepare the soil seed bed. This intensive style of site preparation did not result in significant losses in soil C, especially in the mineral soil. However, very large losses were reported in the O horizon (mean effect = −37.1%) with a very wide confidence interval due to a small number of observations. Additional study of the effect of tillage would help to reduce this error.

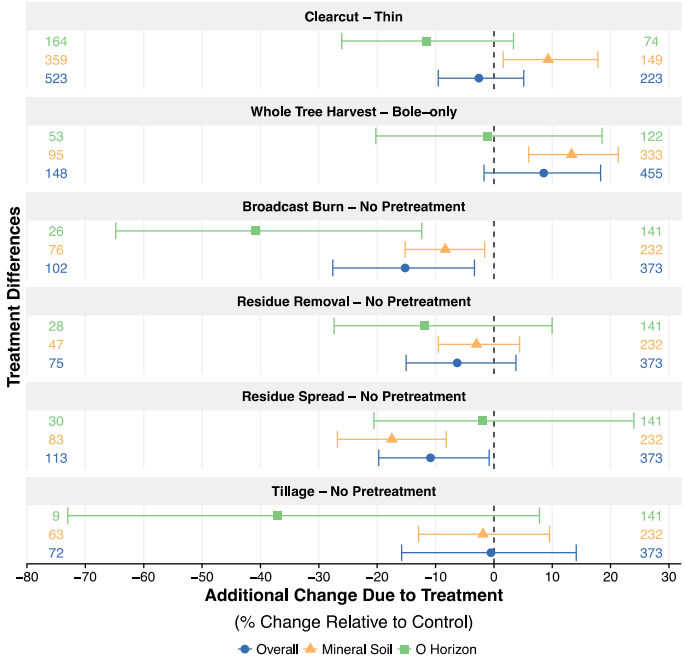

Figure 4. Differences in response of soil C to harvesting between treatment strategies. Differences are calculated by subtracting [more intensive treatment] − [less intensive treatment], such that positive differences represent reduced loss of C due to more intensive treatment, and negative differences represent increased losses of C due to more intensive treatment. Point estimates are back-transformed differences between mean effect sizes ± 95% confidence intervals calculated by nonparametric bootstrap. Mean effect differences with confidence intervals overlapping the dashed line (0%) show no significant difference between the harvesting, residual management, or pretreatment strategies. The number of response ratios (*k*) for the intensive treatment in each comparison appear on the left and for the less intensive treatment on the right.

3.5. Recovery of Soil C after Harvest

The recovery time for soil C following harvest differs among soil orders (Figure 5). Only 4 soil orders contained enough observations over time to model recovery times: Alfisols, Inceptisols, Spodosols, and Ultisols. We modeled time as a second degree polynomial (Time + Time^2) separately for O horizons and mineral soils for each soil order (Table 2).

Table 2. Linear regression coefficients and significance for second degree polynomial model of response of soil C to harvesting over time.

Coefficient	Estimate	SE	*t*-Value	*p*-Value
Intercept (Alfisol, mineral soil)	12.702	3.587	3.541	0.0004
O horizon	−21.475	3.766	−5.703	<0.0001
Inceptisol	−10.876	5.717	−1.902	0.0577
Spodosol	−14.717	4.320	−3.407	0.0007
Ultisol	−24.776	5.391	−4.596	<0.0001
Time	−67.834	41.56	−1.632	0.10325
Time^2	120.412	40.361	2.983	0.0030
Residual SE: 40.24 on 533 *DF*				
F-Statistic: 10.74 on 6 and 533 *df*, $p < 0.0001$			$R^2 = 0.108$	Adj. $R^2 = 0.098$

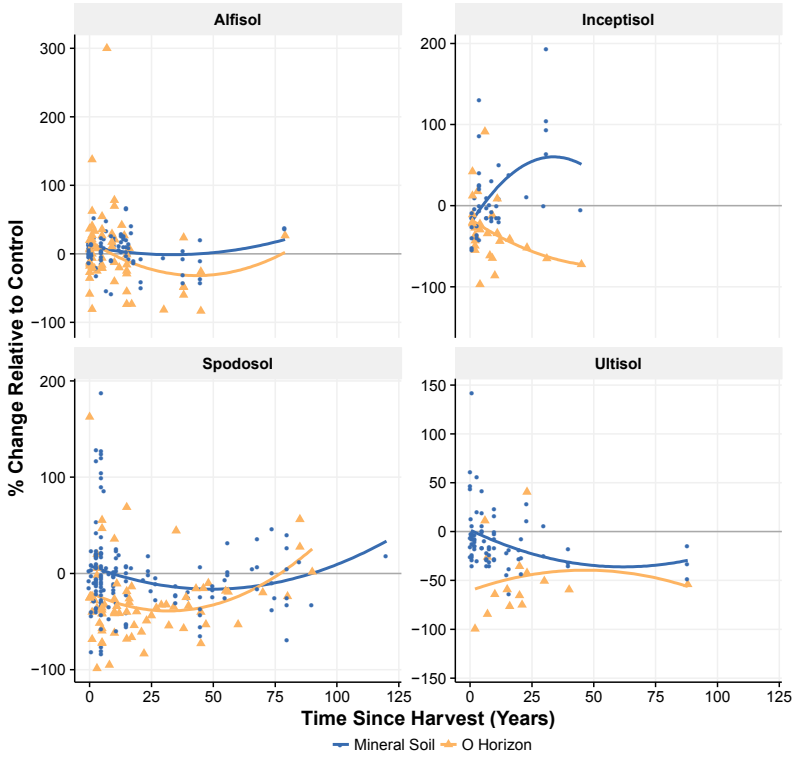

Figure 5. Temporal patterns in both O horizon (yellow triangle) and mineral soil (blue circle) C pools for Alfisol, Inceptisol, Spodosol, and Ultisol orders. Other soil orders are not shown due to an inadequate number of response ratios over time. Regression lines show trends with time using a second order polynomial. For the overall model, $F = 9.205$ on 7 and 532 degrees of freedom, Adj. $R^2 = 0.096$, and $p < 0.0001$ (Table 2).

4. Discussion

4.1. Overall Effect of Harvesting on Soil C

Our results reveal that across many publications in the literature there is a significant loss of soil C in response to harvest (−11.2% overall, −14.4% for studies reporting C pools). This estimate is slightly greater than that found by Nave et al. [9], who reported −8% change relative to control. The difference between these estimates derives from additional losses reported in mineral soil, since the effect of harvesting on O horizon C is identical between this study and Nave et al. [9] (−30%). Indeed, while no significant loss of soil C due to harvesting was reported in previous meta-analyses on the subject [9,25], this analysis reveals significant if small losses in various mineral soil layers. Our meta-analysis has roughly double the number of responses than previous meta-analyses on the subject, and consequently has greater statistical power. In particular, this has allowed us to break down the response of mineral soil C to harvest into more depth increments to better characterize how response is moderated or accentuated by depth.

4.2. Depth Distribution of Soil C Response to Harvest

The response of soil C to harvest differs among depths in the soil. O horizons show the most substantial declines (by percentage), although the O horizon is typically a smaller pool of C than mineral soil horizons. Consequently, smaller absolute declines in O horizon C pools can lead to larger response ratios. Forest type significantly alters the response of O horizons to harvesting, with hardwood forests undergoing less drastic losses than conifer and mixed forests (Figure 3). This result is in contrast with Nave et al. [9], who found that conifer O horizon soil C declines significantly less

than hardwood forest floors. Coniferous forest litter is thought to be more chemically recalcitrant to decomposition because of higher C/N and lignin/N, as well as slower N mineralization rates [35,36]. The trend for more soil C loss from coniferous forest floors could be due to differences in the harvesting techniques utilized for each forest type. On the other hand, less change in soil C in coniferous forests in deeper mineral soils could suggest that some of the additional loss in O horizon C pools is the result of translocation of C into mineral soil rather than mineralization to CO_2. Whatever the case, the mechanism for this difference is not clear and warrants additional study.

In mineral soils, the relative response to harvest is typically less than the O horizon, but this small relative loss might correspond to a larger absolute loss of C in the mineral soil in many forests. The major exception to this pattern are Spodosols, which can contain larger proportions of total soil C in deep, acidic O horizons. Declines in top soil C pools were modest (−3.3%) but still significant (Figure 1). Mean effect size estimates become more negative with soil depth, although these estimates are not significant. The overall estimate of change in very deep soil (60–100+ cm) shows substantial and significant loss of C (−17.7%). This estimate, however, only covers a small number of observations (21) from Spodosol, Ultisol, Alfisol, and Inceptisol soil orders and completely excludes hardwood forests. The lack of observations in deeper soil horizons leads to very wide confidence intervals.

On average, the maximum depth of soil sampled by the publications in this meta-analysis was 35.9 cm (Figure 6). The average depth of sampling for each response ratio in the database is even more surface-skewed at 21.3 cm. Many of the observations down to 100 cm in the literature only report treatment differences for the whole mineral soil profile (0–100 cm), which eliminates any possibility of understanding the relative response of different horizons or depths. The scarcity of observations in deep soil is incongruous with the increasing loss of soil C with depth relative to control observed in this analysis. More important than the magnitude or significance of the harvest response in very deep soil is the conclusion that much greater attention should be paid to deep soil C pools in both individual forest manipulation experiments and broad-scale C inventory.

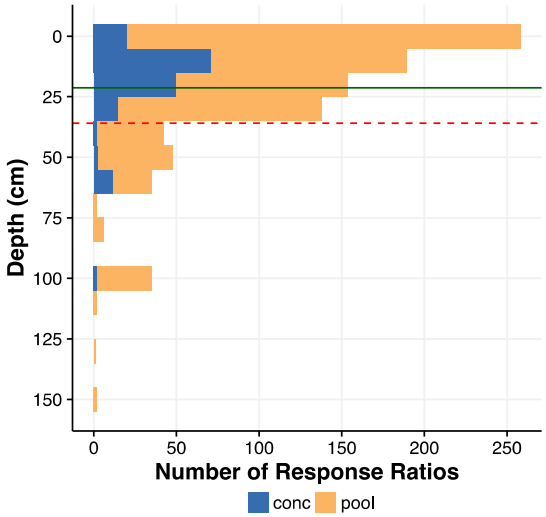

Figure 6. Number of response ratios plotted by the maximum depth of sampling for each observation. Response ratios calculated from concentration are in blue, and from pools in orange. The average depth of all response ratios is denoted by the solid green line (21.3 cm, n = 945). The average maximum sampling depth for all 112 publications in the meta-analysis is denoted by the dashed red line (35.9 cm).

While soil C in deep soil is much less concentrated than in O and A horizons, subsurface soil represents a much greater volume of soil than surface soil, especially in older/more well developed soil orders like Alfisols, Ultisols, and Oxisols. Some major regions for forestry contain substantial portions of total soil C in deep horizons. For example, 38% of total soil C was below 50 cm and 24.1% below

1 m in production forest soils in the Pacific Northwest [37]. The imprint of biological activity extends many meters into soil, even into the C horizon [38]. Globally, the average maximum rooting depth for trees is ~7 m [39], far outreaching even the deepest observations in this database. Harvesting disrupts the continued growth and turnover of roots extended deep into soil by mature trees, which in turn disturbs the steady state of C cycling in deep soil by changing environmental conditions (temperature, moisture) as well as the type and rate of C inputs. Furthermore, the flush of nitrate and dissolved organic matter that frequently follows harvest [40,41] could prime the breakdown of older, subsurface C by providing a spike in nutrient availability and labile energy sources [31,42,43]. Alteration of aboveground ecosystems can cause changes in subsurface soils. For example, Mobley et al. [44] observed that, over a period of several decades following afforestation of agricultural land, modest C gains in surface soil were more than offset by large losses in soil C below 30 cm. Neither the response of deep soil C to harvest nor the mechanisms for that change have been sufficiently resolved in the literature, and future work to address these questions are necessary.

4.3. Differences in Soil C Response to Harvest among Soil Orders

Substantial variation in response to harvest was observed among soil orders. Several soil orders had very few response ratios (Andisols, Entisols, Mollisols, and Oxisols), which greatly widens confidence intervals. Nonetheless, significant changes in soil C in response to harvest were observed for all four of these orders. Andisols were the only order to show a significant average increase in soil C in response to harvest. This likely stems from Andisols particular mineralogy, which is often characterized by short-range-order minerals like allophane and imogolite [45–47]. The capacity for these types of minerals to adsorb organic matter makes Andisol soil C especially resistant to loss after harvesting. Alfisols also appear to be resistant to loss of soil C after harvesting, with relatively small loss in O horizons (−12.0%) being the only significant effect. All other soil orders have significant overall losses in soil C, roughly −20% for Entisols, Inceptisols, Mollisols, Spodosols, and Ultisols. The uneven distribution of observations among soil orders (most response ratios in the database are from Alfisols, Inceptisols, Spodosols, and Ultisols) results in substantial differences in the size of confidence intervals among different orders. Unfortunately, many studies did not report soil taxonomic information, and thus 115 response ratios could not be assigned to a soil order. The lack of studies on Andisols is curious given the importance of these soils to forestry in several regions such as the Pacific Northwest, USA and New Zealand. Several studies on Andisol and other under-represented soil orders were excluded from this analysis because of a lack of appropriate controls.

4.4. Recovery of Soil C after Harvest

Recovery of soil C after harvesting can take several decades [9]. O horizon pools decline more severely than mineral soil pools, especially in the first several decades (Figure 5). In Spodosols, O horizons recovered from harvesting after 60–85 years, while mineral soil recovered over a longer period of 75–100+ years. While the response to harvest was less severe in mineral soils, the longer recovery period implies either lagged response time between forest floor and mineral soils or differences in the decay rate constants leading to longer-term changes in mineral soil C compared to the forest floor. In the case of Alfisols and Inceptisols, soil C in mineral pools increased or stayed the same after harvest, while O horizons declined. However, the observations of harvest effects on Alfisols, Inceptisols, and Ultisols were largely confined to within the first 50 years post-harvest. Consequently, an estimate for the recovery period of soil C pools in these soil orders cannot be assessed with much confidence. Continued observation of existing harvesting experiments in other soil orders must be made to better characterize changes in soil C over time. For Andisols, Entisols, Mollisols, and Oxisols, only a few time points have been documented, and much further study will be necessary to understand recovery of soil C after harvest.

The modeled recovery time has a fairly low adjusted R^2 (0.1) and thus a low predictive capacity. Substantial variation in the response to harvest exists within each soil order, reflecting differences in

tree species, harvest intensity, and pretreatment strategies, among other factors. Moreover, soil orders are hardly homogeneous, and differences in the response of soil C among lower levels of classification within each order could be as important as order-level differences. Nonetheless, the substantial and significant differences between orders considered in the model suggest that both the resistance of soil C to change and the recovery period of soil C following harvest (resilience) consistently varies among soil types. Compared with 20-year recovery periods assumed by many models [14], our results indicate that soil C recovery takes place over at least triple that time frame for both O horizons and mineral soil in many cases.

While forests >30 years of age were considered acceptable controls for this analysis, the preponderance of data in this meta-analysis show decreases in soil C relative to control at time = 30 years. Consequently, studies that use mature second growth stands barely over this threshold for experimental controls likely underestimate the response of soil C due to harvesting treatments. Depending upon the site conditions and soil order, control stands of at least 50–75+ years since harvest would be recommended, with older stands being more accurate controls.

4.5. The Effect of Harvest Strategies on Soil C

Differences in harvesting and soil pretreatment strategies significantly impact the loss of soil C after harvest. Curiously, despite the greater relative losses of soil C in O horizons, significant differences between harvest intensities and pretreatment strategies were only found in the mineral soil with the exception of broadcast burning (Figure 4). The reduced loss of soil C from mineral soil observed in treatments with greater harvest intensity (+9.3% for clearcut, +13.3% for whole tree harvest) runs counter to the intended effect of these experimental treatments on soil C. One possibility is that increased harvest intensity reduces the quantity of dissolved organic matter and inorganic nutrients leached into the mineral soil, thus reducing the priming [42,48,49] of mineral soil C mineralization through less addition of energy-rich substrates and nutrients. Another possibility is that response of soil C to increased harvest intensity is soil-type specific, and thus an aggregate analysis such as this is subject to bias by unequal sampling of different soil orders. Whatever the case, this dataset cannot identify the specific mechanism(s) driving this difference, and further study is warranted.

Tilling of forest soils prior to planting should intuitively disrupt O horizons to a greater extent than less intensive practices. However, due to the very small number of observations of this practice in the dataset, the large mean treatment effect on soil C was could not be differentiated from 0. By mixing organic material into the surface mineral soil, tilling could increase top soil C in the short term and possibly prime additional breakdown of C over time. In regions where this practice is used, additional research could help to reveal the mechanisms driving change in the soil C of O horizons and mineral following tillage.

Broadcast burning led consistently to additional loss of soil C in both O horizons and mineral soil. The large additional reduction in O horizon C (−40.9%) is expected given that such a treatment is intended to reduce slash on site to facilitate planting. The loss of carbon after harvest extends into deep soil, especially following slash burning (Figure 7). Although there are few observations in very deep soil (60–100+ cm), burning appears to especially exacerbate C losses in this layer. This result is despite the direct effects of fire (such as soil heating and nutrient volatilization) being highly attenuated with depth [50,51]. Levels of mineralized nitrogen (NH_4^+ and NO_3^-) and soluble sugars spike within the first year following fire, leading to increased microbial biomass N and N leaching loss [52]. Thus, the flush of nutrients and organic matter into deeper mineral soil following post-harvest broadcast burning has the potential to impact soil C dynamics throughout the soil profile. The number of observations in deep and very deep layers is small, and consequently additional research is necessary to better differentiate between harvesting and fire effects in deep soil horizons.

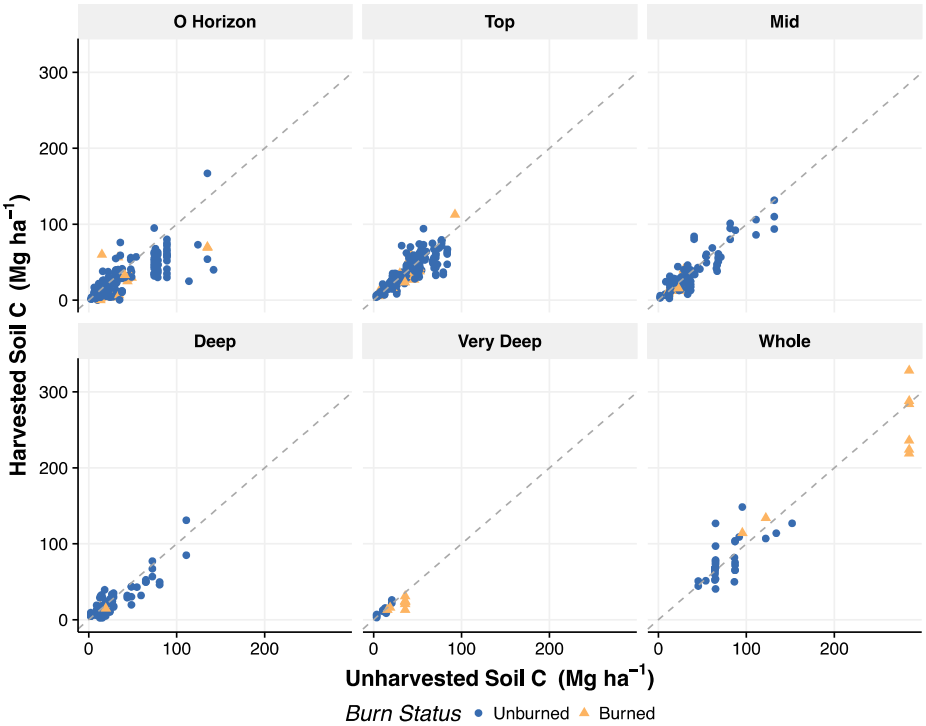

Figure 7. Absolute change in soil C due to harvest for each soil depth in this analysis (O horizon, top, mid, deep, very deep, and whole mineral soil). Different points show burned (yellow triangle) and unburned (blue circle) pretreatment strategies. Dashed 1:1 lines in each facet represent no response due to harvest. The total number of responses shown is $k = 746$.

5. Conclusions

We analyzed 945 studies from 112 publications to examine the effect of harvest on forest soil C around the globe. There is a significant overall reduction in forest soil C following harvest that occurs in both the O horizon and mineral soil. Significant variation in the response to harvesting was observed among different soil depths, among soil orders, between overstory forest types, and between different harvest intensities and pretreatment strategies. Broadcast burning, in particular, appears to exacerbate loss of soil C in both organic and mineral horizons following harvest. The recovery period of soil C following harvest depends upon soil type and takes at least 60 years in many production forests. One of the most important findings of this analysis is a significant loss (−17.7%) of soil C following harvest in very deep soil (60–100+ cm). Deep layers of the soil are greatly under-represented in the literature, and consequently, there is great uncertainty around this estimate. Examination of deep soil horizons in existing manipulative forest studies, in new studies, and in C inventory should be a clear objective for future research.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/7/12/308/S1, Table S1: Harvest meta-analysis database (Excel file).

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Appendix A. Publications Providing Response Ratios for This Analysis

Reference	Year	*k*	Max Depth (cm)	Time Since Harvest [a] (years)	Location
Alban and Perala [53]	1992	7	50	35	MN, USA
Bauhus et al. [54]	2004	6	40	9	Germany
Bisbing et al. [55]	2010	6	100	40	MT, USA
Black and Harden [56]	1995	15	20	23	CA, USA
Boerner et al. [57]	2006	4	10	2	SC, USA
Borchers and Perry [58]	1992	4	15	14	OR, USA
Bravo-Oviedo et al. [59]	2015	8	30	15	Spain
Cade-Menun et al. [60]	2000	12	26	5	BC, Canada
Carter et al. [61]	2002	8	15	2	LA, TX, USA
Chatterjee et al. [62]	2009	19	54	21	WY, USA
Chen et al. [63]	2013	24	100	29	China
Chiti et al. [64]	2016	24	100	24	Ghana, Cameroon, Gabon
Christophel et al. [65]	2013	6	30	15	Germany
Christophel et al. [66]	2015	18	30	33	Germany
Cromack et al. [67]	1999	1	100	10	OR, USA
Dai et al. [68]	2001	3	70	14	NH, USA
DeByle et al. [69]	1980	10	5	3	WY, USA
Deluca and Zouhar [52]	2000	6	8	5	MT, USA
Diochon et al. [70]	2009	28	50	35	NS, Canada
Edmonds and McColl [71]	1989	4	20	3	Australia
Edwards and Ross-Todd [72]	1983	6	45	1	TN, USA
Elliott and Knoepp [73]	2005	3	15	3	NC, USA
Ellis et al. [73]	1982	4	10	2	Tasmania
Ellis and Graley [74]	1983	2	10	1	Tasmania
Esquilin et al. [75]	2008	1	10	14	CO, USA
Falsone et al. [76]	2012	3	130	5	Russia
Fraterrigo et al. [77]	2005	1	15	30	NC, USA
Frazer et al. [78]	1990	4	14	12	CA, USA
Gartzia-Bengoetxea et al. [79]	2009	2	5	10	Spain
Gillon et al. [80]	1999	2	0	1	France
Goh and Phillips [81]	1991	4	60	2	New Zealand
Goodale and Aber [82]	2001	2	10	85	NH, USA
Gough et al. [83]	2007	15	80	41	MI, USA
Grady and Hart [84]	2006	2	15	12	AZ, USA
Grand and Lavkulich [85]	2012	6	80		BC, Canada
Gresham [86]	2002	6	30	10	SC, USA
Griffiths and Swanson [87]	2001	3	10	20	OR, USA
Gundale et al. [88]	2005	4	10	3	MT, USA
Gupta and DeLuca [89]	2012	12	50	5	Wales
Hart et al. [90]	2006	2	15	1	AZ, USA
Hendrickson and Chattarpaul [91]	1989	6	20	3	ON, Canada
Herman et al. [92]	2003	2	9	8	CA, USA
Holscher et al. [93]	2001	2	20	22	Germany
Hwang and Son [94]	2006	2	30	2	Korea
Jang and Page-Dumroese [95]	2015	8	30	38	MT, USA
Johnson [96]	1991	3	20	3	NH, USA
Johnson and Todd [97]	1998	6	45	15	TN, USA
Johnson [98]	1995	12		7	NH, USA
Johnson et al. [99]	1997	14	53	6	NH, USA
Johnson et al. [100]	2014	4	60	1	CA, USA
Jones et al. [101]	2011	12	30	15	New Zealand
Kaye and Hart [102]	1998	2	15	1	AZ, USA
Keenan et al. [103]	1994	1	20	4	BC, Canada
Kelliher et al. [104]	2004	4	50	22	OR, USA

Reference	Year	*k*	Max Depth (cm)	Time Since Harvest [a] (years)	Location
Kishchuk et al. [105]	2014	4	7	6	AB, Canada
Klockow et al. [106]	2013	9	20	1	MN, USA
Klopatek [107]	2002	6	20	30	WA, USA
Knoepp and Swank [108]	1997	4	30	33	NC, USA
Korb et al. [109]	2004	1	10	1	AZ, USA
Kraemer and Hermann [110]	1979	2	10	26	WA, USA
Kurth et al. [111]	2014	72	30	8	MI, MN, USA
Laiho et al. [112]	2003	5	22	5	NC, LA, USA
Latty et al. [113]	2004	2	15	90	NY, USA
Law et al. [114]	2001	3	100	21	OR, USA
Law et al. [115]	2003	9	100	62	OR, USA
Leduc and Rothstein [116]	2007	1	10	5	MI, USA
Maassen and Wirth [117]	2004	2	5		Germany
Mattson and Smith [118]	1993	30	10	11	WV, USA
Mattson and Swank [119]	1989	8	60	5	NC, USA
May and Attiwill [120]	2003	2	10	5	Australia
McLaughlin and Phillips [121]	2006	2	50	17	ME, USA
McKee et al. [122]	2013	8	60	24	AL, USA
McLaughlin [123]	1996	10	50	5	MI, USA
Merino and Edeso [124]	1999	6	15	1	Spain
Moreno-Fernandez et al. [125]	2015	54	50	60	Spain
Mu et al. [126]	2013	18	50	5	China
Murphy et al. [127]	2006	20	60	1	CA, USA
Neher et al. [128]	2003	3	20	2	NC, USA
Norris et al. [129]	2009	15	100	16	SK, Canada
O'Brien et al. [130]	2003	6	50	18	Australia
Powers et al. [131]	2011	20	30	13	MN, WI, USA
Prest et al. [132]	2014	5	50	35	NS, Canada
Prietzel et al. [133]	2004	4	0	1	WA, USA
Puhlick et al. [134]	2016	10	100		ME, USA
Rab [135]	1996	8	10	1	Australia
Riley and Jones [136]	2003	3	10	1	SC, USA
Roaldson et al. [137]	2014	16	20	5	CA, USA
Rothstein and Spaulding [138]	2010	6	30		MI, USA
Sanchez et al. [139]	2007	6	105	2	SC, USA
Sanscrainte et al. [140]	2003	4	70		WA, USA
Saynes et al. [141]	2012	8	5	11	Mexico
Selig et al. [142]	2008	3	30	14	VA, USA
Shelburne et al. [143]	2004	4	10	1	SC, USA
Sheng et al. [144]	2015	5	100	8	China
Skovsgaard et al. [145]	2006	12	30	0	Denmark
Slesak et al. [146]	2012	12	60	5	OR, WA, USA
Small and McCarthy [147]	2005	3	10	7	OH, USA
Stone et al. [148]	1999	1	15	1	AZ, USA
Stone and Elioff [149]	1998	4	30	5	MN, USA
Strong [150]	1997	8	40	18	MN, USA
Strukelj et al. [151]	2015	12	10	5	QC, Canada
Tang et al. [152]	2009	12	60	29	MI, WI, USA
Trettin et al. [153]	2011	6	150	11	MI, USA
Ussiri and Johnson [154]	2007	15	60	8	NH, USA
Vario et al. [155]	2014	6	60	49	NH, USA
Vesterdal et al. [156]	1995	9	0		Denmark
Waldrop et al. [157]	2003	3	0	1	CA, USA
Wu et al. [158]	2010	1	20	10	China
Xiang et al. [159]	2009	8	30	0	China
Yanai et al. [160]	2000	35	0	29	NH, USA
Zabowski et al. [161]	2008	2	20	25	OR, WA, USA
Zhong and Makeshin [162]	2003	2	10	16	Germany
Zummo and Friedland [163]	2011	15	60	3	NH, USA

[a] For chronosequence studies, time since harvest in this table is averaged across all response ratios for that study.

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Paleo-Antarctic rainforest into the modern Old World tropics: The rich past and threatened future of the "southern wet forest survivors"[1]

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- *Premise of study:* Have Gondwanan rainforest floral associations survived? Where do they occur today? Have they survived continuously in particular locations? How significant is their living floristic signal? We revisit these classic questions in light of significant recent increases in relevant paleobotanical data.
- *Methods:* We traced the extinction and persistence of lineages and associations through the past across four now separated regions—Australia, New Zealand, Patagonia, and Antarctica—using fossil occurrence data from 63 well-dated Gondwanan rainforest sites and 396 constituent taxa. Fossil sites were allocated to four age groups: Cretaceous, Paleocene–Eocene, Neogene plus Oligocene, and Pleistocene. We compared the modern and ancient distributions of lineages represented in the fossil record to see if dissimilarity increased with time. We quantified similarity–dissimilarity of composition and taxonomic structure among fossil assemblages, and between fossil and modern assemblages.
- *Key results:* Strong similarities between ancient Patagonia and Australia confirmed shared Gondwanan rainforest history, but more of the lineages persisted in Australia. Samples of ancient Australia grouped with the extant floras of Australia, New Guinea, New Caledonia, Fiji, and Mt. Kinabalu. Decreasing similarity through time among the regional floras of Antarctica, Patagonia, New Zealand, and southern Australia reflects multiple extinction events.
- *Conclusions:* Gondwanan rainforest lineages contribute significantly to modern rainforest community assembly and often co-occur in widely separated assemblages far from their early fossil records. Understanding how and where lineages from ancient Gondwanan assemblages co-occur today has implications for the conservation of global rainforest vegetation, including in the Old World tropics.

Key words: Antarctica; assemblage; Australia; biogeography; Gondwana; New Zealand; Old World tropics; paleobotany; Patagonia; rainforest.

The recognition of similar plant communities on isolated landmasses played an important role in the development of modern biogeography (Raven and Axelrod, 1974). Hooker (1853) first recognized elements of a circum-Antarctic flora in the forest and alpine habitats of Australia, New Zealand, and South America. An iconic example is the *Nothofagus* (Antarctic Beech)–conifer rainforest assemblages that occur today in cool, high-rainfall areas of those regions (Hill, 1994). The rich paleobotanical history of the *Nothofagus* assemblage—and many others like it—classically suggests persistence of Gondwanan rainforest associations from deep time to the present and provides strong support for the concept of phylogenetic biome conservatism (Crisp et al., 2009). For example, fossil discoveries from the Paleogene of Patagonia and Australia include many shared genera that are now extinct in Patagonia but are extant, often in association, in Australasian and southeast Asian rainforests (e.g., Hill et al., 1999, 2008; Wilf et al., 2013).

Differences in plant traits and climate tolerances that reflect abiotic gradients determine the success of plants under different environmental conditions (Schimper, 1903; Westoby and Wright, 2006). The timing of the Gondwanan breakup, the

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movement and isolation of the various landmasses, and subsequent shifts in global climate shaped Southern Hemisphere plant evolution, distribution, assembly, and extinction (Raven and Axelrod, 1974; Wilford and Brown, 1994; Sanmartín and Ronquist, 2004; Lawver et al., 2011; Weston and Hill, 2013; Wilf et al., 2013; Bowman et al., 2014). The loss of suitable habitat in middle to high latitudes since the early Paleogene, and subsequent (Neogene) movement into newly emerging moist upland habitats (often in lower latitudes), resulted in major shifts in the distributional ranges of rainforest components in the paleo-Antarctic Gondwanan flora. Survival was dependent on the positions of major continents in relation to suitable versus aridifying climatic zones, and the timing of opportunities that included the emergence of land (Lawver et al., 2011). New land emerged in orogenic events associated with the formation of volcanic arcs and trains of emerging islands, and with plate collisions and uplifts (Lawver et al., 2014). These geological forces have controlled the always changing distributions of less extreme (i.e., warm–cool, and generally frost-free), wet (perhumid) habitats, across a substantial range of global latitude and longitude.

Close geographic proximity between South America and Antarctica was still evident during the Late Cretaceous and continued until at least the early Eocene, after which isolation by formation of the Drake Passage began. Like Patagonia, Australia was still proximal to, but began to separate from, Antarctica during the middle to late Eocene (Wilford and Brown, 1994; Lawver and Gahagan, 1998; Lawver et al., 2011, 2014; Dalziel, 2014). After the Eocene, the Australia–Antarctica–South America corridor was severed, deep seaways formed (but see Dalziel, 2014), and Antarctic glaciation and the global transition from greenhouse to icehouse conditions were underway (e.g., Zachos et al., 2001; Francis et al., 2009).

Despite those abiotic changes, elements of the Gondwanan rainforest flora can now be found, usually at great distance from the fossil sites that document their early history, on both old and more geologically recent terrains. These include Australia, New Zealand, Patagonia, New Guinea, New Caledonia (Burbidge, 1960; Webb and Tracey, 1981; Hill, 2004), remote locations in the southwest Pacific such as Fiji and Vanuatu (Enright and Jaffré, 2011), and recently uplifted areas of Southeast Asia, including Mt. Kinabalu in northern Borneo (Kitayama et al., 2011). Each of those separate and geologically diverse regions contains areas with mesic climates that harbor plant communities with surviving Gondwanan lineages, thus hypothetically approximating the ancestral biome.

Some of the strongest signals for shifts in distribution of Gondwanan lineages come from the fossil and living southern conifers, which were among the first living Australasian taxa recognized in Patagonian fossil floras (Berry, 1938; Florin, 1940a, b; Brodribb and Hill, 1999). Recent studies have identified physiological traits in many of the broad-leaved southern conifers related to water balance, and shade and freezing tolerance, which are thought to have strongly influenced deep-time shifts in their distributions and relative abundance (Hill and Carpenter, 1991; Brodribb et al., 2005; Biffin et al., 2012; Brodribb et al., 2014). Because those conifer lineages are regarded, for well-understood physiological reasons, as drought intolerant today, they are presumed to have been so in the past (Brodribb and Hill, 1998, 1999; Brodribb, 2011; Brodribb et al., 2012; Wilf, 2012).

The survival of Gondwanan rainforest lineages is critically important to conservation in the modern world. Their history shows that they adapted to, or tracked, global climate change, were subjected to large-scale extirpation events, and continued to contribute to rainforest assembly across the Southern Hemisphere. Today, they remain important to the survival, diversity, and function of many rainforest areas, including montane parts of the modern Asian tropics (e.g., Kitayama, 1992). However, human activities are now exposing those survivors to significant and rapid global and local disturbances, including logging, clearing, and climate change (e.g., Laurance et al., 2014), that is unlike anything known from the fossil record. The rates of disturbance and change are widely thought to be too rapid for these lineages to adapt, or to track suitable habitat across large areas of unsuitable terrain.

In recent years, fossil discoveries at sites across the Southern Hemisphere have dramatically expanded our direct knowledge of paleorainforests on the former Gondwanan landmasses (Hill, 1994; Brodribb and Hill, 1999; Zamaloa et al., 2006; Barreda et al., 2012; Wilf et al., 2013). This increase in paleontological knowledge provides an exciting opportunity to use site-assemblage data to quantify the patterns of distribution and co-occurrence of southern lineages from deep time to the present.

We here present a large compendium of fossil rainforest sites and their constituent taxa from Patagonia, Antarctica, Australia, and New Zealand, and we compare the fossil assemblages to the extant distributions of the same lineages, using data from Australia, New Zealand, Patagonia, Papua New Guinea, New Caledonia, Fiji, and Mt. Kinabalu. We analyze these data to quantify and identify: (1) Gondwanan rainforest composition; (2) the signal of the ancient in modern assemblages; and (3) the floristic fidelity of Gondwanan rainforest assemblages through time and space. We use these analyses to test the ideas that floristic dissimilarity among regions increased with time, and that Gondwanan rainforest associations have persisted within regions. In addition, we ask whether the strengths of contribution by particular southern rainforest lineages shifted through time, and what influence those genera and families have on patterns of floral assembly.

MATERIALS AND METHODS

***Fossil data compilation*—**An ARC-NZ Vegetation Network Working Group meeting at Macquarie University allowed the initial gathering of the authors in Sydney, Australia, August 2010, to undertake: (1) a compilation of suitable Late Cretaceous to Pleistocene Gondwanan fossil sites and the well-identified components of their macrofloras and microfloras, plus geochronologic data (see Supplemental Data with the online version of this article; Appendices S1 and S2); (2) data assessment and cleaning; and (3) taxonomic resolution and updates.

Fossil rainforest sites were identified by comparing the constituent taxa of assemblages with an a priori list of primary Gondwanan rainforest indicator taxa. That list included certain co-occurring southern conifers and associated angiosperm taxa identified in the literature (e.g., Hill, 1994; Brodribb and Hill, 1999) and by the authors as the strongest indicators of rainforest (Table 1). Our focus was on the multiple and repeated co-occurrence of these rainforest indicator lineages, not rainforest structural definition sensu stricto, which is far more difficult to evaluate from fossil assemblages. The primary matrix includes separate fields for major fossil organ categories, including leaf, cuticle, reproductive (fruit, seed, flower), wood, and pollen (Table 2). The organ categories were merged for each taxon by region to genus (or family) level for the taxon-level analyses (Appendix S2). Species-level data, while noted in our compilation, were often not available, or comparisons between very similar fossil species were difficult to evaluate. Lists of woody taxa from extant rainforest floras in Australia, New Zealand, and Patagonia were compiled to compare extant taxon richness and taxonomic structure with fossil floras (Table 3a–d).

Our approach does not involve or assess the extensively discussed "vicariance versus dispersal" biogeographic scenarios or molecular "dating" techniques (e.g., Weston and Hill, 2013; Wilf and Escapa, 2014). Instead, we make

TABLE 1. Indicator taxa used to recognize fossil-rainforest sites of Late Cretaceous and younger age and their fossil occurrences in the four major regions studied.

	Aust	NZ	Pat	Ant
CONIFERS				
Agathis	1	1	1	0
Araucaria	1	0	1	1*
Dilwynites	1*	1*	1*	1*
Acmopyle	1	0	1	0
Dacrycarpus	1	1	1	1*
Dacrydium	1	1	1*	1*
Falcatifolium	1	0	0	0
Lagarostrobos	1	1*	1*	1*
Lepidothamnus	1	0	0	0
Microstrobos	1	0	0	0
Phyllocladus	1	1	1*	1*
Podocarpus	1	1	1	1*
Prumnopitys	1	1	0	0
Retrophyllum	1	0	1	0
Athrotaxis	1	0	0	0
Fitzroya	1	0	0	0
Libocedrus	1	1	0	0
Papuacedrus	1	0	1	0
ANGIOSPERMS				
Chloranthaceae	1*	1*	1*	1*
Gymnostoma	1	1	1	0
Nothofagus_Brassospora	1	1	1	1*
Nothofagus_Fuscospora	1	1*	1	1
Nothofagus_Lophozonia	1	1*	1	1*
Nothofagus_Nothofagus	1	0	1	1*
Trimeniaceae	1*	0	1*	0

Notes: Aust = Australia; NZ = New Zealand; Pat = Patagonia; Ant = Antarctica. *Athrotaxis* is known from older fossil deposits in Patagonia (Menéndez, 1966; Del Fueyo et al., 2008). *Papuacedrus* (and potentially other conifers on this list) is known from the Eocene of Antarctic Peninsula (Zhou and Li, 1994; Wilf et al., 2009), but not from a site that meets our vetting criteria. List includes extant southern conifer and associated primary indicator angiosperm lineages. For simplicity, palynotaxa thought to correlate to particular extant taxa (e.g., the pollen type *Dacrycarpites*, corresponding to the living genus *Dacrycarpus*) are simply reported under those taxa; see Appendices S1 and S2. *Dilwynites* is listed separately because of its affinities to both *Agathis* and *Wollemia* (Macphail and Carpenter, 2014). *Microstrobos* is synonymous with *Pherosphaera.* * Pollen record only.

direct use of the burgeoning primary data and examine empirically where lineages are actually known to have occurred through time and space, based on their fossil occurrences and their geochronologic constraints (Gradstein et al., 2012). Our extensively vetted compilation of sites and occurrences, as described below, is fully presented online (see Supplemental Data with the online version of this article) for those who wish to explore further using other approaches.

We compiled a matrix of 63 sites and 396 taxonomic occurrences, representing 154 families of vascular plants, from locations in Patagonia, Malvinas/Falkland Islands, Antarctica, New Zealand, and Australia (Table 3a). We provide one additional site in the compendium that is from eastern Antarctica (Appendix S2; Pross et al., 2012) but do not include it in quantitative analyses because it is the only deep-sea core. Extant and extinct taxa were selected and coded to allow filtering of the data. Data sources are provided in full in the supplemental materials to this article as a reference list linked to sites (see Appendix S1). As described above, sites were included in the compendium on the basis of rainforest floristic affinities, so the list of localities per region is not exhaustive. Occurrences for some of the individual lineages described here were also excluded because these were not clearly associated with rainforest fossil sites or had limited supporting information, especially regarding geologic age (e.g., *Papuacedrus* in Antarctica: Zhou and Li, 1994; *Lactoris* in Australia: Macphail et al., 1999). We vetted all fossil occurrences carefully to modern standards based on their preservation of diagnostic features, and we accordingly rejected many doubtful occurrences in the literature. Taxonomic assignments were done at two levels for subsequent analyses: genus and family. Most (61%) fossil taxonomic occurrences were identified to living genus by default. Where occurrences could be identified to family but not to genus (23%), we used the family name. The remainder represented mostly extinct genera (refer to Appendix S2). To simplify the text, we refer to taxa as "genera" throughout but acknowledge the inclusion of family-level data (described above). Also, several taxa that are strictly considered near equivalents of genera were analyzed as "genera." One example of this is the four sections of *Nothofagus* (recently proposed as separate genera by Heenan and Smissen, 2013), analyzed here under their historical section names.

TABLE 2. Summary of fossil datasets and bases for derived analyses.

Dataset	Derived from	Published
1. Macrofossil taxa records: 852	Primary, literature	Yes
2. Palynotaxa records: 1734	Primary, literature	Yes
3. Leaf component: 429	Dataset 1	Yes
4. Cuticle component: 319	Dataset 1	Yes
5. Reproductive organs: 83	Dataset 1	Yes
6. Wood: 22	Dataset 1	Yes
7. Fossil Locations: 63	Datasets 1, 2	Yes
8. Genera / Families (identified): 396	Datasets 1, 2	Yes
9. Conifers (all): 34	Datasets 1, 2	Yes
10. Conifers (indicator): 33	Datasets 1, 2	Yes
11. Angiosperms: 315	Datasets 1, 2	Yes
12. Ferns and lycopsids: 39	Datasets 1, 2	Yes
13. Cycads: 3	Datasets 1, 2	Yes
14. *Sphagnum*: 2	Datasets 1, 2	Yes
15. Hornworts: 1	Datasets 1, 2	Yes
16. Liverworts: 2	Datasets 1, 2	Yes
17. Extinct: 62 (total)	Datasets 1, 2	Yes
18. Extinct conifers: 8	Datasets 1, 2	Yes
19. Extinct angiosperms: 51	Datasets 1, 2	Yes
20. Extinct ferns: 2	Datasets 1, 2	Yes
21. Extinct Ginkgoaceae: 1/1	Datasets 1, 2	Yes

Notes: Associated literature and published sources are provided as a bibliography in the supplemental materials to this article (Appendix S1). Datasets (1) and (2), from which all the other datasets are derived, were merged into a single matrix (Appendix S2). In all cases, tallies represent identified fossil taxa by location(s) as records (occurrences), not total number of individual fossils. In most cases, and always for macrofossils, there is at least one museum specimen supporting the identification, usually of type, figured, and/or referenced material as listed in the source publications. This is not always the case for pollen.

The fossil rainforest compilation includes the most significant examples of the trans-Antarctic paleorainforest flora, in the broad sense, that is best known from the Late Cretaceous to late Eocene of the western Antarctic; Late Cretaceous to early Paleocene (Maastrichtian–Danian), early and middle Eocene, and early Miocene of Patagonia plus Malvinas/Falkland Islands; late Paleocene to late Pleistocene of Australia; and Paleocene and early Miocene of New Zealand. Details are provided in Appendix S2. Geochronology is based on Gradstein et al. (2012), as updated at http://www.stratigraphy.org/ICSchart/ChronostratChart2014-02.jpg.

Consistent with the known age of separation of the last Gondwanan landmasses from Antarctica during the Eocene and the associated global cooling events, we allocated sites to four broad time bins: K—Cretaceous; P–E—Paleocene and Eocene; Ne+O—Neogene plus Oligocene; and Pleistocene. We note that Australia and New Zealand had no Cretaceous rainforest fossil sites in our data, and only Australia had Pleistocene sites.

***Multivariate analyses*—**The multivariate analyses were based on three site-by-genus occurrence matrices, described in sequence below. All multivariate analyses were done using Primer version 6 (Clarke and Gorley, 2006). Sites in ordinations were labeled by geographic region (location) and age (see above; Figs. 1 and 2).

First, to compare all fossil assemblages in relation to age and region, we used the "full" matrix (Table 3a) based on the presence of genera (n = 396) at all identified fossil sites (n = 63; Fig. 1). Dissimilarity among sites was measured using Sorensen distances and nonmetric multidimensional scaling (NMDS) based on the underlying distance matrix. Lineage (genera) contributions

TABLE 3. Summary by region of number of known rainforest fossil taxa for three matrices used in multivariate analyses and for extant floras.

3a.	**Full fossil data**	Australia	New Zealand	Patagonia	Antarctica	Totals
	Number of families	125	66	93	45	154
	Number of genera	334	99	151	60	396
3b.	**Reduced fossil data**	Australia	New Zealand	Patagonia	Antarctica	Totals
	Number of families	62	59	80	40	95
	Number of genera	112	85	116	52	153
3c.	**Survivor woody genera**					
	Number of woody families	31	24	43	14	49
	Number of woody genera	68	39	63	23	87
3d.	**Extant woody data**	Australia	New Zealand	Patagonia	Antarctica	Totals
	Extant families	136	57	50	NA	162
	Extant genera	667	70	81	NA	759
	Extant woody species	2308	222	163	NA	2693

Notes: 3a. Full fossil data—families and genera in the full fossil data compendium (396 genera by 63 sites and 4 locations); 3b. Reduced fossil data—the 153 genera by 56 sites and 4 locations remaining after removal of: sites 1, 4, 5, 20, 13, 54, and 56; extinct lineages; and singleton taxa, by location (see text); 3c. Survivor woody genera—the 87 living woody genera representing known fossils; and 3d. Extant woody data—overview of the total extant woody rainforest floras from three regions (Australia, New Zealand, and Patagonia) for comparison to 3c.

to multivariate (Sorensen) similarity within, and dissimilarity among, groups of sites representing regions (Antarctica, Patagonia, Australia, and New Zealand) were quantified using the Simper routine (in Primer). This routine decomposes similarities within pairs of samples of a group (e.g., among samples of a single region at different times), and dissimilarities among groups (regions), into percentage contributions from each genus, and lists the taxa in decreasing order of contribution for every pairwise comparison.

Second, the same procedure was applied to a "reduced" matrix of 56 sites and 153 genera (Table 3b; Fig. 2). The data from the full matrix (Table 3a) were filtered to remove the following: Pleistocene locations in Australia, because these had no analogues in other regions; outlier sites without rainforest indicator conifers; one site (S56-Balcombe Bay) with only three genera recorded and described to date; extinct genera; and all taxa that occurred at only one site (singletons). The reduced matrix allowed us to (1) test the influence of outliers and singletons on the data analysis; (2) improve the basis for comparison among regions by aligning ages and removing the disproportionate amount of Pleistocene data from Australia; and (3) assess any shifts in site position in the ordinations in relation to pairwise comparisons and groupings with the reduced information. The Simper routine described above was repeated on the reduced matrix.

To measure the strength of influence of genera on the position (similarity) of assemblages in the ordination, we used the column-wise (site–region) aligned presence data (0–1) in the matrix to provide a binary ranking from which the standard product-moment correlation (Pearson) is computed. Because we used 0–1 presence data only, this defaults to a Spearman rank coefficient (Legendre and Legendre, 1998) that uses the taxa as variables. Values range from 0 to 1, where 0 = no influence and 1 = strongest possible influence. The results do not show causality, nor do they account for the problem of rare species interactions. However, they do highlight the complex relationships between genera and regions in a broad sense. We note that influence can include increasing or decreasing presence, and local extinction, across regions through time.

The third "age-by-region" matrix was used to compare the contributions of genera occurring as fossils to both fossil and modern assemblages. The matrix was produced by merging the fossil sites by the four regions (Australia, Patagonia, New Zealand, and Antarctica) into three age categories (bins), K, P–E, and Ne+O, and including only the woody genera occurring in the four locations. The rationale for excluding other life forms was that trees and vines represent the main structural features of any rainforest assemblage, and nonwoody plants are rarely and unevenly represented as fossils. We refer to the 87 woody fossil genera remaining in the matrix (Tables 3c and 4) as "survivor" taxa. This matrix included nine age-by-region fossil assemblages: P–E and Ne+O for Australia; K, P–E, and Ne+O for Patagonia; P–E and Ne+O for New Zealand; and K and P–E for Antarctica. We then added the extant distributions of the genera in the fossil matrix based on their occurrences in seven areas: Australia, New Zealand, Patagonia, Papua New Guinea, New Caledonia, Fiji, and Mt. Kinabalu. These included all fossiliferous regions in our dataset where rainforest is still extant (Australia, Patagonia, and New Zealand), and both old and relatively recent terrains. The additional regions included the northern uplift and older southern areas of New Guinea; Mt. Kinabalu, a recently uplifted granitic monolith associated with old Gondwanan fragments in South East Asia (Cottam et al., 2013); New Caledonia from the northern tip of Zealandia, the now largely submerged landmass that also included New Zealand (Schellart et al., 2006); and Fiji. Fiji represents an island group in the southwest Pacific associated with continental crust of possible Gondwanan origin that includes both older (late Eocene) island–arc volcanics and more recent (Miocene) plutonic intrusions (Neall and Trewick, 2008).

We note that applicable fossil sites for comparison are not yet available from these additional areas. However, there are palynological data that show relatively late (post-Eocene, particularly Neogene) penetration for most relevant southern lineages into areas north of Australia, and a corresponding lack of southern-derived taxa during the early Eocene and earlier Cenozoic (Muller, 1966; Khan, 1976; van der Kaars, 1991; Morley, 1998, 2002; Jin, 2009; Yao et al., 2009). For example, *Dacrydium* reached Southeast Asia by the Oligocene, and *Dacrycarpus* and *Phyllocladus* probably dispersed into New Guinea (from adjoining Australia) during uplift in the Miocene, then "island-hopped" to Borneo during the mid-Pliocene (Morley, 2011). By contrast, fossil pollen of *Podocarpus* and some other taxa first appear in Southeast Asia in the Eocene, either sourced from India as it docked with Asia or via long-distance dispersal from Australia (Morley, 1998, 2011).

The age-by-region matrix was the basis for the combined neo- and paleo-analyses, comparisons, and interpretations presented, including NMDS ordinations (Figs. 3 and 4) and measures of taxonomic structure (Fig. 5). This matrix allowed us to track the survivors across geographic regions through time (i.e., a "where did they begin" and "where are they now" analysis). To visualize the co-occurrences of genera and provide a directional measure of the strength of their influences on the position (similarity) of assemblages in the ordination, vectors representing the genera were added to the NMDS ordination using Pearson correlation (Fig. 4). The length of the vector axis of a genus is set by the circle (radius 0–1) and represents the strength of contribution to the ordination (Fig. 4). We preface the quantitative results with a qualitative synthesis, and also provide details of the broad-scale location of survivors in both fossil and extant rainforest floras in Table 4. Presence–survival in Australasia and eastern Antarctica was identified as E (= eastern); in West Antarctica and Patagonia as W (= western); and shared as EW (= both). Table 4 includes vector lengths (from the second and third matrices described above) as an overall measure of the strength of contribution by survivors to the multivariate relationship of regions in the ordinations. Actual percentage contributions by survivors to similarity (Simper routine) among regions are provided in the online Supplemental Materials (see Supplemental Data with the online version of this article; Appendix S3) for all three matrices. Appendix S3 allows detailed pairwise comparisons of taxon (including survivor) contributions across all combinations of regions, in relation to both the full and reduced datasets.

It was not our intention, nor was it feasible, to run comparative analyses for the full "living" tropical floras of Australia, Indo-Malesia including New Guinea, New Caledonia, and Oceania. Initial attempts to do so for Australia, New Zealand, and Patagonia (Table 3d) shed minimal light on analyses of surviving fossil lineages because most taxa lack fossil records.

***Taxonomic structure*—**To test whether, and how, taxonomic structures vary across sites and regions, we used average taxonomic distinctness (AvTD) to measure pairwise taxonomic distances between the lineages in a sample, to family and genus level (Clarke and Gorley, 2006). Average taxonomic distinctness is known to be orthogonal to richness and, importantly, is unaffected by either sample size or sampling effort. The measure (AvTD) describes the relatedness

Fig. 1. NMDS ordination of 63 fossil assemblages based on full floristics, representing all identified genera (n = 396) from all life forms for each of the four fossiliferous regions grouped by age: K = Cretaceous; P–E = Paleocene and Eocene; Ne+O = Neogene plus Oligocene; and Pleis = Pleistocene. Two Eocene Patagonian sites (larger squares; LH = Laguna del Hunco and RP = Río Pichileufú) nested with the Australian Paleocene to Eocene sites. Antarctica groups with Patagonia. The ordination used the Sorensen distance measure. Stress: 0.2.

of taxa (genera in this case) within a sample at a given richness and uses a simple taxonomic (relatedness) tree with equalized branch lengths, based on the background list of genera and families. Expected values at a given richness represent a null (no taxonomic structure) derived from 1000 random draws from the available pool. Lower values (outside the 95% confidence intervals [CIs] for average taxonomic distinctness in relation to random draws from the full pool) occur when genera have lower taxonomic breadth at a level of richness than expected under a null model (i.e., genera are more related or clustered). Higher values reflect greater taxonomic breadth at a given richness in relation to the null and equate with overdispersion or evenness (i.e., genera are less related).

To compare taxonomic structure across the paleo- and neo-representation of genera in regions, we focus on the age-by-region matrix described above, which included the survivor genera in nine age–location fossil assemblages and seven extant regional assemblages (Figs. 3 and 4). The pool of available taxa is based on the 87 survivors. Taxonomic structure results at site level from the full matrix (n = 63 sites; n = 396 genera) and the reduced matrix (n = 56 sites; n = 153 genera) are provided online (see Supplemental Data with the online version of this article; Appendix S4: Figs. S1 and S2).

***Continental phylogenetic structure*—**To quantify the contribution of the Gondwanan rainforest survivor taxa to continental community phylogenetic structure in Australia, we calculated net relatedness index (NRI; Webb et al., 2002) for a full continental dataset. This was done both with and without the survivor genera included (see Supplemental Data with the online version of this article; Appendix S5: Fig. S3 and Table S1), using the software program Biodiverse (Laffan et al., 2010). A correlation coefficient (r value) was generated to test the hypothesis of "no difference" in continental phylogenetic structure after removal of Gondwanan lineages. The dataset included the distribution records of all Australian woody rainforest taxa (freestanding and climbing plants) but excluded marginal taxa from wet sclerophyll, heath, and mangrove habitats (see Kooyman et al., 2013). We used Australia as a working example because there is access to full continental-scale distribution data previously allocated to 10 × 10 km grid cells (Kooyman et al., 2013); the continent provides a range of environmental gradients and filters across more than 30° of latitude; and, as reaffirmed here, its fossil record shows continuous occupation by classical Gondwanan lineages despite significant floristic exchange with Indo-Malesia (Sniderman and Jordan, 2011).

RESULTS

***Taxonomic patterns*—**We present the following qualitative synthesis of taxonomic patterns in our data as a framework for interpretation of the quantified measures that follow (Figs. 1–4;

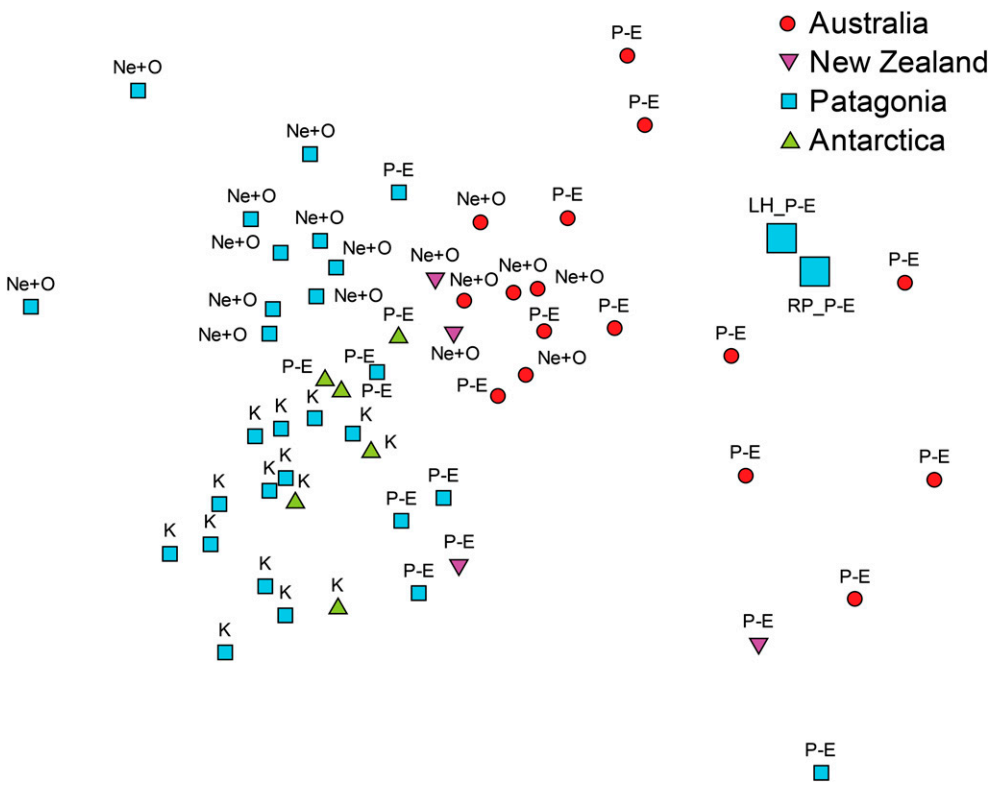

Fig. 2. NMDS ordination of 56 fossil assemblages (n = 153 genera) with sites 1, 4, 5, 20, 13, 54, and 56 removed (see text); plus extinct lineages and singleton taxa removed by location. Abbreviations and labeling as in Figure 1. The ordination used the Sorensen distance measure. Stress: 0.19.

Table 4). See Appendix S1 for the primary bibliography that supports this discussion.

Araucariaceae—Fossil Araucariaceae, including *Araucaria*, are known from all land areas in this compilation, and they occur across (and well before) the full temporal range covered here. *Araucaria* Section *Eutacta* occurred in Western and Eastern Gondwana, but it survives only in Australasia (eastern survival), whereas Section *Araucaria*, once present in Australasia and much earlier (Early Cretaceous) in Patagonia, is extant only in South America (western survival). *Agathis*, previously known from the fossil record only from Australia and New Zealand (Hill et al., 2008; Pole, 2008), is now known in Patagonia from early Paleocene and early and middle Eocene macrofossils of both vegetative and reproductive organs (Escapa et al., 2013; Wilf et al., 2014). The extant distribution of the genus is in New Zealand, Australia, Southeast Asia, and Oceania (eastern survival). It is present as fossils in Australia from at least the late Paleocene and in New Zealand since the early Miocene. Pollen assigned to *Dilwynites* can represent both *Agathis* and *Wollemia* (Macphail et al., 2013; Macphail and Carpenter, 2014). It appears in our data during the Eocene of Antarctica and Patagonia and the Paleocene to Pleistocene of Australia, where both *Agathis* and *Wollemia* remain extant (eastern survival).

Podocarpaceae—Records for Podocarpaceae in these data commence in the Late Cretaceous, in Antarctica and Patagonia. We acknowledge many earlier records of extinct podocarp genera, including from the Early Cretaceous of Patagonia (Archangelsky, 1966; Archangelsky and Del Fueyo, 1989; Del Fueyo et al., 1991), but these cannot be inferred to come from rainforest assemblages. Important genera that are extinct in Patagonia but extant in Australasia and Oceania (eastern survival) include *Microcachrys* (Carpenter et al., 2011), *Dacrycarpus*, *Lagarostrobos*, *Dacrydium*, *Phyllocladus*, and *Acmopyle*. *Lepidothamnus* is extant in New Zealand and South America; *Retrophyllum* is extant in both Oceania and northern South America and extinct in Australia; while *Falcatifolium* has no fossil record from southern South America or Antarctica and is extant in Oceania and Australasia. Similarly, *Halocarpus* occurs during the middle Eocene of central Australia and the early Miocene of New Zealand, where it is extant. Both *Dacrycarpus* and *Acmopyle* are noted for their drought intolerance and affinities with extremely wet habitats (Brodribb and Hill, 1998, 1999, 2004). *Dacrycarpus* survived in Australia until the early Pleistocene, while *Acmopyle* is present in these data from the early and middle Eocene of Patagonia and the late Paleocene to early Oligocene of Australia. It is extant today only in the Pacific, as one species each in Fiji and New Caledonia. In our data, *Microcachrys*, *Dacrycarpus*, *Dacrydium*, *Lagarostrobos*, and *Podocarpus* are present in Antarctica and Patagonia during the Late Cretaceous, and in Australia (and a little later in New Zealand) from the late Paleocene. *Prumnopitys* and *Phyllocladus* occur first during the late Paleocene of Australia. While both are known from the fossil record in New Zealand, *Phyllocladus* is not evident there until the early Miocene, whereas *Prumnopitys* is present from the late Paleocene. *Prumnopitys* is extant today in South America, Oceania, Australasia, and New Zealand. *Phyllocladus* is extant in New Zealand, Australia (Tasmania), and Malesia, but extinct in South America (eastern survival).

TABLE 4. Rainforest southern conifers, woody angiosperms, and ferns grouped by family and including survivor genera that occur in our fossil rainforest compendium (Appendix S1). Distributions of survivors in both fossil and extant rainforest floras: E = eastern; W = western (West Antarctica, Patagonia); EW = both. P1 and P2 represent the length (as strength of contribution by genera represented as positive values) of the Pearson correlation vectors from the reduced fossil matrix (n = 56 sites) and the age-by-region matrix (Fig. 4), respectively, in relation to the enclosing circle (0–1).

Family	Genus	Fossil	Extant	P1	P2
Conifers					
Araucariaceae	*Agathis*	EW	E	0.53	0.52
Araucariaceae	*Araucaria*	EW	EW	0.37	0.14
Araucariaceae	*Dilwynites*	EW	E	0.17	0.62
Araucariaceae		EW	EW	0.28	–
Podocarpaceae	*Acmopyle*	EW	E	0.40	0.29
Podocarpaceae	*Dacrycarpus*	EW	E	0.50	0.46
Podocarpaceae	*Dacrydium*	EW	E	0.31	0.41
Podocarpaceae	*Falcatifolium*	E	E	0.24	0.41
Podocarpaceae	*Lagarostrobos*	EW	E	0.49	0.58
Podocarpaceae	*Lepidothamnus*	E	EW	—	—
Podocarpaceae	*Phyllocladus*	EW	E	0.36	0.35
Podocarpaceae	*Microcachrys*	EW	E	0.52	0.60
Podocarpaceae	*Microstrobos*[a]	E	E	0.29	0.44
Podocarpaceae	*Halocarpus*	E	E	0.28	0.33
Podocarpaceae		EW	EW	0.13	—
Podocarpaceae	*Podocarpus*	EW	EW	0.36	0.69
Podocarpaceae	*Prumnopitys*	E	E	0.25	0.20
Podocarpaceae	*Retrophyllum*	EW	EW	0.46	0.24
Cupressaceae	*Athrotaxis*	E	E[b]	0.37	0.48
Cupressaceae	*Austrocedrus*	EW	W	0.15	0.43
Cupressaceae		EW	EW	0.26	—
Cupressaceae	*Callitris*	E	E	—	—
Cupressaceae	*Fitzroya*	EW	W	0.32	0.20
Cupressaceae	*Libocedrus*	E	E	0.39	0.34
Cupressaceae	*Papuacedrus*	EW	E	0.31	0.39
Ephedraceae	*Ephedra*	EW	W[c]	0.48	0.29
Cheirolepidiaceae	*Classopollis*	EW	—	—	—
Angiosperms					
Akaniaceae	*Akania*	W	E	0.34	0.16
Amaranthaceae		EW	EW	0.36	0.63
Anacardiaceae		EW	EW	0.06	0.61
Apocynaceae	*Alyxia*	E	E	0.11	0.67
Aquifoliaceae	*Ilex*	EW	E	0.18	0.68
Arecaceae	*Arecaceae*	EW	EW	0.39	0.40
Arecaceae	*Nypa*	EW	E	0.30	0.20
Atherospermataceae		EW	EW	0.18	0.38
Casuarinaceae	*Gymnostoma*	EW	E	0.55	0.51
Casuarinaceae	*Casuarina/Allocasuarina*	EW	E[d]	0.20	0.63
Chloranthaceae	Chloranthaceae	EW	E	0.24	0.47
Cochlospermaceae		W	E	0.34	0.41
Convolvulaceae		EW	EW	0.36	0.61
Cunoniaceae	Cunoniaceae	EW	EW	0.34	0.79
Cunoniaceae	*Eucryphia*	EW	EW	0.35	0.08
Cunoniaceae	*Ceratopetalum*	EW	E	0.39	0.36
Cunoniaceae	*Caldcluvia (Ackama)*	EW	EW	—	—
Cunoniaceae	*Callicoma*	E	E	0.18	0.48
Cunoniaceae	*Gillbeea*	E	E	0.09	0.48
Cunoniaceae	*Weinmannia*	EW	EW	0.13	0.62
Elaeocarpaceae	*Elaeocarpus*	E	EW	0.28	0.71
Elaeocarpaceae		E	EW	0.18	0.72
Ericaceae	Ericaceae	EW	EW	0.23	0.80
Ericaceae	*Richea*	E	E	0.20	0.47
Euphorbiaceae	Euphorbiaceae	EW	E	0.27	0.51
Fabaceae	Fabaceae	EW	EW	0.21	0.67
Fabaceae	Caesalpiniaceae	EW	EW	0.30	0.62
Fabaceae	*Acacia*	E	E	0.18	0.67
Goodeniaceae		EW	EW	0.15	0.58
Gyrostemonaceae		E	E	0.17	0.45
Juglandaceae	Juglandaceae	W	EW	0.09	0.20
Lactoridaceae	*Lactoris*	W[e]	W	0.20	0.25
Lauraceae	Lauraceae	EW	EW	0.67	0.50
Malpighiaceae		W	EW	0.08	0.56
Malvaceae	*Brachychiton*	E	E	0.39	0.48
Malvaceae	Malvaceae	EW	EW	0.35	0.81
Meliaceae	*Dysoxylum*	E	E	0.15	0.74

TABLE 4. Continued.

Family	Genus	Fossil	Extant	P1	P2
Menispermaceae	Menispermaceae	W[f]	E	0.12	0.49
Myricaceae	Myricaceae	W	EW	0.27	0.20
Myrtaceae	Myrtaceae	EW	EW	0.35	—
Myrtaceae	*Eucalyptus*	EW	E	0.21	0.46
Nothofagaceae	*Nothofagus*_Brassospora	EW	E	0.69	0.41
Nothofagaceae	*Nothofagus*_Fuscospora	EW	EW	0.45	0.58
Nothofagaceae	*Nothofagus*_Lophozonia	EW	EW	0.63	0.10
Nothofagaceae	*Nothofagus*_Nothofagus	EW	W	0.40	0.13
Olacaceae	*Anacalosa*	EW	E	0.32	0.32
Onagraceae	*Fuchsia*	EW	EW	0.25	0.55
Picrodendraceae	Picrodendraceae	E	E	0.20	0.61
Paracryphiaceae	*Quintinia*	EW	E	0.26	0.38
Paracryphiaceae	*Sphenostemon*	E	E	0.15	0.48
Polygalaceae		EW	EW	0.18	0.51
Proteaceae	*Beauprea*	EW	E	0.36	0.61
Proteaceae	Proteaceae	EW	EW	0.33	—
Proteaceae	*Banksia*	E	E	0.26	0.59
Proteaceae	*Embothrium*	EW	W	0.16	0.41
Proteaceae	*Lomatia*	EW	EW	0.17	0.27
Proteaceae	*Telopea*	E	E	0.13	0.47
Proteaceae	*Orites*	EW	EW	0.28	0.24
Rhamnaceae		EW	EW	0.34	0.68
Rosaceae		EW	EW	0.13	0.63
Rutaceae		EW	E	0.07	0.57
Sapindaceae	*Cupania* and others	EW	E	0.16	0.60
Sapindaceae	*Dodonaea*	E	E	0.11	0.58
Sapotaceae		E	E	0.13	0.71
Symplocaceae	*Symplocos*	W[g]	E	0.27	0.52
Trimeniaceae		EW	E	0.09	0.62
Ulmaceae	Ulmaceae	W[h]	E	0.16	0.55
Vitaceae	*Cissus*	EW	EW	0.06	0.75
Winteraceae	*Drimys*	W	W	0.27	0.59
Ferns and other					
Cyatheaceae	Cyatheaceae	EW	E	0.63	—
Lycopodiaceae	*Lycopodium*	EW	EW	0.49	—
Sphagnaceae	Sphagnaceae	EW	EW	0.15	—
Sphagnaceae	*Sphagnum*	EW	EW	0.46	—
Gleicheniaceae	Gleicheniaceae	EW	EW	0.48	—
Gleicheniaceae	*Gleichenia*	EW	E	0.18	—
Lophosoriaceae	*Lophosoria*	EW	W	0.50	—
Dicksoniaceae	Dicksoniaceae	EW	EW	0.32	—
Dicksoniaceae	Dicksonia	EW	EW	0.37	—
Blechnaceae	Blechnaceae	EW	EW	0.11	—
Osmundaceae	Osmundaceae	EW	E	—	—
Osmundaceae	*Todea*	W	E	0.30	—
Polypodiaceae	Polypodiaceae	EW	EW	0.28	—
Selaginellaceae	*Selaginella*	EW	EW	0.29	—
Schizaeaceae	*Lygodium*	EW	EW	0.36	—
Anthocerataceae	Anthocerataceae	EW	EW	0.14	—

[a] *Microstrobos* is synonymous with *Pherosphaera*.
[b] *Athrotaxis* is known from older fossil deposits in Patagonia.
[c] *Ephedra* occurs in both northern and southern hemispheres, but for the latter only in South America.
[d] *Casuarina littoralis* is pan-tropical.
[e,f,g,h] Known from the Australian fossil record but not from locations included in the final analyses (refer to full compendium in Supplemental Data). See additional taxonomic notes on Table 1.

Cupressaceae—In the Cupressaceae, *Libocedrus* is present as fossils from Australia and New Zealand during the late Paleocene to early Miocene, and it is extant in New Zealand and New Caledonia. *Austrocedrus* represents western survival in Patagonia of a genus that occurred in Tasmania during the Oligocene, and possibly in the Malvinas/Falkland Islands (grouped here with southern South America) during the middle to late Miocene. Similarly, *Fitzroya* is extant only in Patagonia (western survival) and occurs in these data in Tasmania during the early Oligocene and Miocene. *Papuacedrus* is present in Patagonia during the early and middle Eocene (Wilf et al., 2009) and in Tasmania (Australia) during the early to late Oligocene and early Miocene (Hill and Carpenter, 1989); it is extant in New Guinea and nearby in the Moluccas. *Athrotaxis* has its entire fossil record in the Southern Hemisphere, including Patagonia (Menéndez, 1966; Del Fueyo et al., 2008). However, in probable rainforest sites in our data, it occurs only during the early Oligocene of Tasmania, where it persists (eastern survival).

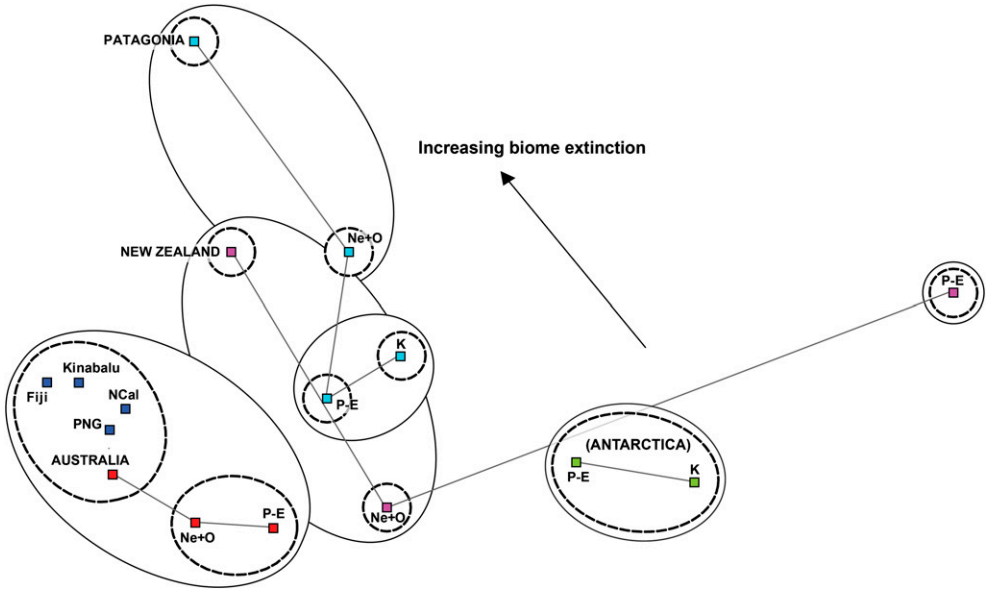

Fig. 3. NMDS ordination of 87 survivor genera (see text) from four fossiliferous and seven extant sample regions. Survivors represent woody fossil lineages that persisted through the long biogeographic history of the Gondwanan rainforest biome, and continue to contribute to biome persistence, lineage diversity, and community assembly. Age abbreviations for fossil samples as in Figure 1. Seven extant samples are from Australia (caps), New Zealand (caps), Patagonia (caps), Papua New Guinea (PNG), New Caledonia (NCal), Mt. Kinabalu, and Fiji. Antarctica is labeled in parentheses because it has no extant sample. Gray lines link the temporal sequence of each region. Gray ellipses/circles represent the groupings of age-regions with 55% similarity; broken black ellipses/circles show 65% similarity; black arrow shows the direction of increasing loss of the ancient rainforest biome.

Casuarinaceae—The family Casuarinaceae includes the wet-adapted lineage *Gymnostoma*, which is extant in the Australasian and Melanesian region. *Gymnostoma* macrofossils are present in these data from the Eocene of Patagonia, late Paleocene to Eocene of Australia, and the Miocene of New Zealand. Casuarinaceae pollen occurs from the Paleocene to Pleistocene of Australia, the Cretaceous to Eocene of Patagonia, and the Paleocene to Oligocene of Antarctica. We note that *Gymnostoma* cannot be differentiated from other Casuarinaceae solely on the basis of pollen morphology.

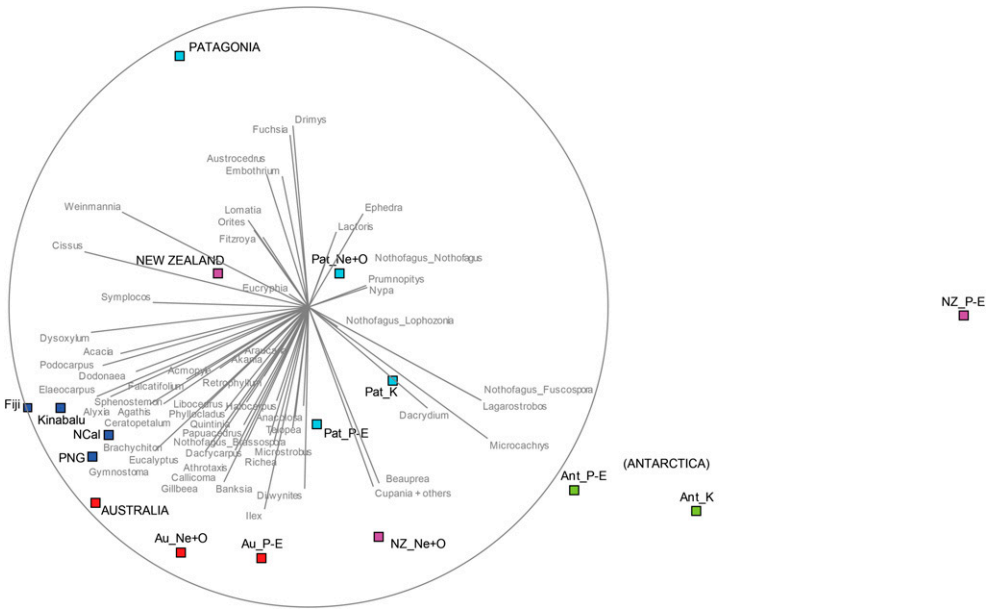

Fig. 4. NMDS ordination of 87 survivor genera from four fossiliferous and seven extant sample regions. Abbreviations and labeling as in Figure 3, plus labels for fossil samples: Au = Australia, NZ = New Zealand, Pat = Patagonia, and Ant = Antarctica. Gray vectors provide a directional measure of influence (strength) and co-occurrence of survivor genera on ordination of regions as Pearson Correlation values, where 0 = no influence and 1 = strongest possible influence. Enclosing gray vector circle is set at radius 1.0. Sorensen distance measure. Stress: 0.12.

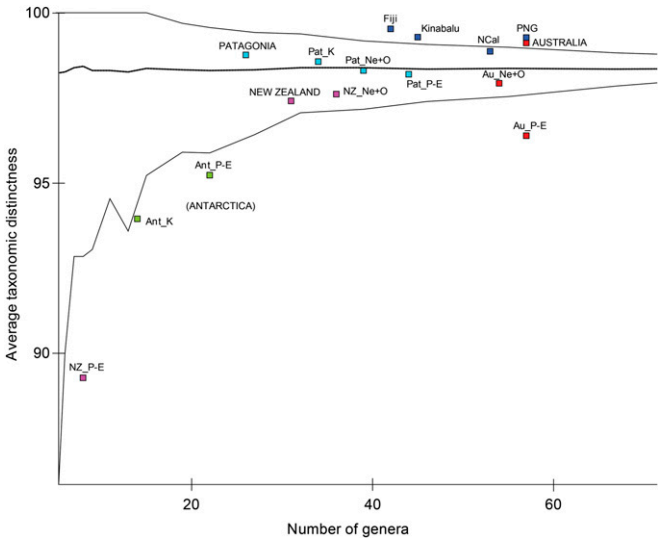

Fig. 5. Funnel plot of average taxonomic distinctness for 87 survivor genera representing four fossiliferous and seven extant sample regions. Abbreviations and labeling as in Figures 3 and 4. The funnel is bounded by 95% confidence intervals, and the central black line represents the expected position of regional samples in relation to average taxonomic distinctness at a given value of genus richness. Lower values than expected indicate less taxonomic breadth with genera more related than by chance, and higher values indicate more breadth and genera less related than by chance.

Proteaceae—The family Proteaceae is widespread but has a strong southern distribution of lineages that suggests Gondwanan origins (Johnson and Briggs, 1975; Weston, 2014). In these data, the rainforest members of the family show a continuous but surprisingly poorly differentiated record from the Cretaceous to Pleistocene (Sauquet et al., 2009), mostly from *Beauprea*-type and other, unattributed pollen. *Beauprea* itself is extant only in New Caledonia, representing eastern survival. *Embothrium* pollen is known from the Oligocene of Tasmania and Patagonia and the middle Miocene of the Malvinas/Falkland Islands. *Telopea* was recorded from the early Oligocene to Pleistocene of Australia, where it is extant (eastern survival). Records of *Telopea* from the Late Cretaceous of Patagonia were excluded from analyses because of ambiguity in relation to their assignment (Sauquet et al., 2009). Macrofossils of Proteaceae are best represented in these data from the Paleocene to Pleistocene of Australia (e.g., *Orites*, *Lomatia*, and *Banksia*), the Eocene of Patagonia (*Orites*; González et al., 2007), and the Oligo-Miocene of New Zealand (Carpenter et al., 2012).

Lauraceae and other Laurales—The family Lauraceae is globally widespread, but it differs from Proteaceae in being poorly represented in the palynological record (Macphail, 1980; Macphail et al., 2013). Macrofossils are present in our study from the Paleocene to Pleistocene in Australia, Cretaceous to Miocene in Patagonia, and the Paleocene in New Zealand. We note that older records for New Zealand are known (Cantrill et al., 2011; Bannister et al., 2012). The Laurales also include toothed-leaved genera in Atherospermataceae and Monimiaceae. Interestingly, recent fossil discoveries from the Eocene of Patagonia have strengthened the links between South American fossil Laurales and extant Australian genera, such as *Doryphora* and *Daphnandra* (Atherospermataceae) and *Wilkiea* (Monimiaceae) (Knight and Wilf, 2013).

Myrtaceae—Myrtaceae macrofossils in these data include *Eucalyptus* from the early Eocene of Patagonia, possibly sourced from volcanically disturbed areas adjacent to standing rainforest (Gandolfo et al., 2011; Hermsen et al., 2012). Other records include mostly undifferentiated taxa present from the Paleocene to Pleistocene in Australia, Late Cretaceous to Miocene of Patagonia, Late Cretaceous to late Eocene of Antarctica, and the Paleocene to early Miocene of New Zealand. Advances in systematic understanding of myrtaceous pollen promise improved biogeographic insights into this family (Thornhill and Macphail, 2012).

Nothofagaceae—The family Nothofagaceae is sister to all other Fagales and includes subgenera *Nothofagus*, *Fuscospora*, *Lophozonia*, and *Brassospora* (Hill, 1992; Hill and Jordan, 1993; Veblen et al., 1996). These distinctions are well supported by recent molecular systematic analyses (Sauquet et al., 2012; and see Heenan and Smissen, 2013) and allow relatively detailed exploration of the fossil record for this family. Juglandaceae (Fagales) is present in the record as pollen from the early Paleocene and Eocene of Patagonia, and Myricaceae (Fagales) is present from the Late Cretaceous to middle Eocene. Both families coexisted with *Nothofagus*. The first appearance of the Nothofagaceae in these data are from the Late Cretaceous of Patagonia, including pollen from both subgenera *Nothofagus* and *Fuscospora*, and from the western Antarctic, including subgenera *Lophozonia* and *Fuscospora*. By the Paleocene, all *Nothofagus* subgenera were present in western Antarctica at a single location (Seymour Island). Subgenera *Brassospora* and *Fuscospora* were present in Australia, and subgenus *Fuscospora* was present in New Zealand. During the middle to late Eocene, fossil assemblages from Patagonia included all *Nothofagus* subgenera. The late Eocene in Australia includes subgenera *Lophozonia*, *Brassospora*, and *Fuscospora*, and by the Oligocene also includes subgenus *Nothofagus*. Thereafter (in these data), all but subgenera *Lophozonia* and *Fuscospora* became extinct in Australia and New Zealand. Subgenus *Brassospora* is extant in New Guinea and New Caledonia (eastern survival), and subgenus *Nothofagus* is extant in South America (western survival) with subgenera *Lophozonia* and *Fuscospora*.

Cunoniaceae—The Cunoniaceae is another angiosperm family that is regarded as an important component of Gondwanan rainforest assemblages. Modern-day analogue vegetation types (notophyll vine forest or subtropical to warm temperate rainforest) that occur in Australia can be dominated by genera in Cunoniaceae such as *Ceratopetalum* and *Caldcluvia* (*Ackama*). These genera are evident in the record from the Eocene of Patagonia (Hermsen et al., 2010), and in Australia as *Ceratopetalum*- and *Weinmannia*-type pollen and macrofossils (Carpenter and Buchanan, 1993; Barnes et al., 2001). *Eucryphia* is extant in both South America and Australia. It is present in our compilation from the Paleocene to Pleistocene of Australia (Hill, 1991; Barnes and Jordan, 2000) and the Paleocene of Antarctica (Mirabelli et al., 2009).

Ferns and other life forms—Though not diagnostic for rainforest, *Lycopodium* (Lycopodiaceae) and *Sphagnum* (Sphagnaceae) are often associated with cool, moist habitats. In these data, they occur from the Cretaceous to late Eocene of Antarctica, the Cretaceous to Miocene of Patagonia, the Eocene to Pleistocene of Australia, and the Paleocene to Miocene of New Zealand.

Cyatheaceae, Gleicheniaceae (*Gleichenia*, *Sticherus*), Dicksoniaceae (*Dicksonia*), Polypodiaceae, and Blechnaceae (*Blechnum*) co-occur across the regions and throughout much of the temporal

record presented here. *Todea* (Osmundaceae) is extant in Australasia and South Africa, and it is known as macrofossils from the early Eocene of Patagonia (Carvalho et al., 2013). *Lophosoria* (Lophosoriaceae) is extant in Patagonia (western survival) and has fossil occurrences during the early Oligocene to Pleistocene of Australia, the Cretaceous to Miocene in Patagonia, and the Cretaceous to Paleocene of Antarctica (Hill et al., 2001). *Lygodium* (Schizaeaceae) is present here during the Eocene to Pleistocene of Australia, the Paleocene to Miocene of New Zealand, and the Cretaceous to late Oligocene of Patagonia.

***Multivariate patterns and interpretations*—**For the full dataset, the grouping of fossil sites in relation to floristics was most strongly influenced by geographic location (Fig. 1). Antarctica grouped with Patagonia, including the Malvinas/Falkland Islands, and New Zealand was positioned between Australia and Patagonia. Interestingly, but not surprisingly given recent discoveries there, the diverse Eocene sites from Patagonia, Laguna del Hunco and Río Pichileufú, grouped with the late Paleocene and Eocene sites in Australia (Figs. 1 and 2).

The second analysis (Fig. 2) used the reduced fossil matrix (n = 56 sites, and n = 153 genera) and, importantly, showed a very similar result to the full matrix analysis (Fig. 1). Laguna del Hunco and Río Pichileufú remained with the Australian late Paleocene and Eocene group. Of the 36 taxa used here from Laguna del Hunco, 27 are extant in Australia, four represent extinct lineages, and three are extant in proximity to Australia (eastern survival or shared).

The third analysis used the 87 survivors in the age-by-region matrix and combined neo- and paleo-distribution data. The resulting ordinations (Table 3c; Figs. 3 and 4) showed high similarity for Australian fossil age samples (P–E and Ne+O; 65% similarity). Cretaceous (K) and P–E Patagonia samples grouped at 55% similarity but were isolated from Ne+O and extant Patagonia. Cretaceous (K) and P–E Antarctica grouped at 65% similarity. New Zealand P–E and Ne+O were highly dissimilar to each other. Australian extant and fossil samples grouped at 55% similarity. Extant New Zealand grouped with K and P–E Patagonia, and New Zealand Ne+O, at 55% similarity. Extant sample locations, including Papua New Guinea, New Caledonia, Mt. Kinabalu, and Fiji, grouped with extant Australia at 65% similarity, and with P–E and Ne+O Australia at 55% similarity. Figure 4 includes the survivors as vectors based on Pearson correlation values.

***Taxonomic structure*—**We detected lower-than-expected estimates of taxonomic distinctness at four fossil age-locations in the combined analysis of 16 survivor samples. This result reflects phylogenetic clustering, or higher relatedness, among the genera in those four instances (Fig. 5). These included Cretaceous and Paleocene to Eocene Antarctica; and the Paleocene to Eocene of New Zealand and Australia. Higher-than-expected taxonomic distinctness, reflecting overdispersion or evenness and less relatedness of taxa within regions, was detected at four extant locations, including Australia, Papua New Guinea, Mt. Kinabalu, and Fiji. The remaining fossil and living floras showed expected levels of taxonomic distinctness in relation to richness (i.e., they occurred within the funnel bounded by 95% CIs). In terms of richness and taxonomic structure, the modern tropical floras adjacent to northern Australia were more similar to each other and to Australia itself than to modern New Zealand and Patagonia.

All fossil regions (Antarctica, Patagonia, Australia, and New Zealand) had some assemblages outside and lower than expectations defined by 95% CIs for taxonomic distinctness. This result was consistent at different levels of generic richness for fossil sites from the full (n = 63) and reduced (n = 56) data matrices (see Appendix S4: Figs. S1 and S2).

***Continental phylogenetic structure*—**The correlation between NRI values for the Australian rainforest, both with and without the Gondwanan survivor genera identified in our compendium included, was $r = 0.43$, $P = 0.001$. A value of $r = 1.0$ equates with no difference following removal. Lower values (as here) suggest a measure of difference after removal, with (in this case) the retention of a strong positive relationship (see Appendix S5: Fig. S3).

DISCUSSION

***Data compilation*—**The data compilation allowed us to track Gondwanan rainforest composition through time (Appendix S2; Figs. 1–4), identify the strength of the signal of the ancient in modern assemblages (Fig. 4; Table 4), and determine the stability of Gondwanan rainforest assemblages in regions (Figs. 1–4; Table 4).

***Floristic patterns*—**The floristic analyses confirmed that dissimilarity within and among regions generally increased with time. However, despite major spatial movements, Gondwanan rainforest lineages apparently co-occurred continuously, both before and after final Gondwanan breakup. In addition, the direction of change, from ancient to modern, followed a similar trajectory among most of the regions, reflecting loss of diversity and local extinction (Fig. 3). However, the extent of floristic dissimilarity, reflecting change through time, differed markedly among the regions (Fig. 3).

***Assembly through time*—**The strengths of contributions by genera in the survivor pool, to co-occurrence in regional assemblages, shifted most significantly in relation to regional extirpations and movement into newly emerging habitat. The results confirm that lineages continued to co-occur, but generally at locations far removed from their origins. Although the strength of contribution by some southern rainforest lineages shifted through time, for others it remained stable but included extirpation in different locations (Fig. 4 and Table 4). Despite the variation in assemblage composition among regions, it is clear that Gondwanan rainforest survivors continued to form assemblages reflecting ancient combinations.

In terms of contribution to modern floras, the correlation of continental phylogenetic structure values (NRI) for Australian rainforests (in grid cells) before and after removal of "survivor" genera showed a significant difference. However, the values remained positive, suggesting underlying similarity based on continuing contributions to rainforest assembly by other lineages, many of which lack fossil records (Sniderman and Jordan, 2011; Kooyman et al., 2013; see Appendix S5). Most notably, the NRI analysis showed that the fossil record is now sufficiently robust to record a statistically significant fraction of the lineages that influence the phylogenetic structure of living Australian rainforests.

By merging sites in regions, we identified the regional patterns of loss (extinction) of survivor genera, and we were able to quantify their continuing contribution to community assemblage

across the regions through time (Table 4). At the continental scale, Australia retained more of its ancient rainforest flora than Patagonia or New Zealand, despite losing vast areas of the biome to aridification. Loss of the biome was most severe in the south and west, whereas retention was highest in the east and northeast of the continent. Assemblage shifts in fossil locations through time, and the co-occurrences of survivors in modern floras (Figs. 3 and 4; Table 4), showed that genera extirpated from Australia because of the loss of cool–wet habitats survived by shifting into newly emerging highland, and other compatible habitats, in the nearby tropics (e.g., Papua New Guinea and New Caledonia). By contrast, Patagonia showed initial and increasing convergence (similarity) with Antarctica (K, P–E) and Australia (P–E), and then increasing extinction and loss of the ancient biome because of the transition from greenhouse to icehouse conditions and subsequent lineage filtering (from P–E to Ne+O to modern). Ancient Antarctica (K and P–E) showed only minor change, then lost the rainforest biome completely during the subsequent icehouse. Ancient New Zealand (P–E) was quite dissimilar from other land areas, though most similar to ancient (K) Antarctica (see Pole, 2014). New Zealand (Ne+O) was more similar to (P–E) Patagonia, Antarctica, and Australia (Fig. 3). The New Zealand trajectory then showed substantial extinction and loss of the accumulated elements of the ancient biome (Ne+O) followed by increasing similarity (into the present) with extant Patagonia.

The compositional similarity, taxonomic structure, and relatively high richness of samples from the extant Old World tropics confirmed that survivor genera from different lineages are well represented in those regions. These included *Agathis* and Podocarpaceae in Australia, New Guinea, Fiji, and Indo-Malesia (Wilf et al., 2013), and numerous other angiosperm lineages that occur in Australia and New Guinea (Sniderman and Jordan, 2011). At higher latitudes, the floristically simple cool–moist *Nothofagus* forest, with conifers and consistently co-occurring angiosperm lineages, remains a feature of southern Australia, Patagonia, and New Zealand (Veblen et al., 1996).

Regional extinction phases, and lineage movements, have previously been described and associated with major plate movements, volcanism, uplifts, subsidence, and shifts in climate (Crisp and Cook, 2013; Wilf et al., 2013; Lawver et al., 2014). A feature of those large-scale patterns is their close alignment with the movements of particular lineages (e.g., *Dacrycarpus* and *Acmopyle*) that are known to have greater sensitivity to factors such as water balance and freezing (Brodribb and Hill, 1998, 2004; Brodribb and Feild, 2010; Brodribb et al., 2012; Wilf, 2012). The loss of mesic lineages from Patagonia–Antarctica and their persistence in Australia and Papua–Asia highlight the role of shifting distributions and increasing dissimilarity among locations through time.

The striking differences between the Paleocene–Eocene rainforest floras of New Zealand and their Oligocene to recent "replacements" reflect climate change and the catastrophic Oligocene inundation of most of Zealandia. This event was followed by the subsequent recolonization of reemergent New Zealand during the Neogene by long-distance dispersers, mostly from Australia (Campbell and Hutchings, 2007). The Neogene recolonization of New Zealand resulted in rainforests that were quite dissimilar from those in Australia and nearby regions, and from the ancestral associations, even though they do include a number of important ancient taxa (e.g., *Agathis* and many Podocarpaceae).

By contrast, the similarity of the Patagonian Eocene floras of Laguna del Hunco and Río Pichileufú to Australian fossil floras quantified in this study (Figs. 1 and 2) highlights a period of floristic similarity between these now much more distant locations. This is thought to have been made possible by Eocene warmth that allowed the required trans-Antarctic distributions and a lack of significant oceanic barriers to biotic interchange. The floristic similarity between these fossil floras and the living floras of Australasia continues to grow with the inclusion of recently described and shared genera. Several of these taxa are not yet known as fossils in Australia (e.g., *Todea*, *Wilkiea*, *Daphnandra*, and *Akania*) but contribute substantially to modern Australian floras.

Conclusions—This study highlights the complex journey of survival of southern rainforest lineages and confirms their continuing co-occurrences in widely dispersed assemblages far from their fossil sources. The endurance, survival, and persistence of these rainforest lineages provide one of the earth's greatest biological and evolutionary success stories. These assemblages from deep time remain ecologically important today. Their conservation will require targeted research to quantify the evolutionary, phylogenetic, ecological, and functional contributions of the ancient southern flora to global vegetation diversity and ongoing rainforest community assembly.

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