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MARK BRINSON REVIEW

J.G. Watson, Inundation Classes, and their Influence on Paradigms in Mangrove Forest Ecology

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Abstract The influence of tidal inundation on mangrove vegetation species distribution is a key concept in mangrove ecology, and is especially important when considering the vulnerability of mangroves to predicted future sea level rise. While the tidal inundation-vegetation relationship defines a huge number of studies in mangrove science, it is not a new concept, but was mapped in the 1920s by scientists such as James Gilbert Watson, a forester with the colonial Forestry Department in Malaysia. Watson is particularly famous for his description of "Inundation Classes", which described the flooding frequency at which different mangrove vegetation species could be found. It is interesting to consider how current paradigms and management practices (e.g. mangrove restoration) are shaped by the historical research that contributed to them. This article introduces JG Watson as a key figure in mangrove ecology, describes his seminal work on mangrove species distribution in peninsular Malaysia, and charts his legacy and contribution to current scientific debates surrounding physical controls on mangrove ecology. Importantly, research on tidal inundation and species distribution by Watson and others must be used correctly, including an acknowledgement that vegetation-inundation linkages are not universally applicable, and that species distribution is multi-factorial, and not dependent on inundation alone.

Keywords Flooding · Malay Peninsula · Restoration · Sea level rise · Species distribution · Tolerance · Zonation, 1928

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Introduction

Historically, the field of ecology emerged from natural history, out of a desire to explore and explain the processes, order and balance of natural systems (Fieldler et al. 1997). Studying the early history and development of ecological paradigms allows us to show the influence of observational hypotheses on later process-based ecological thinking and the development of overarching paradigms (representation of the current state of scientific understanding of specific models, sensu Graham and Dayton 2002). Ecological thinking is inherently interdisciplinary, requiring knowledge of botany, physiology, geography, and more recently, molecular and genetic sciences. Mangrove forests are potentially a model ecosystem to investigate paradigms that relate to interdisciplinary physical-ecological processes and linkages, due to their relatively simple ecological structure, and the variety of physical processes they experience. Mangrove ecology also has a rich history, from which a timeline of physical-ecological paradigms can be traced.

A key paradigm in mangrove ecology is the role of tidal inundation as an important influence on mangrove species establishment and distribution (Lewis 2005; Krauss et al. 2008; Feller et al. 2010) due to species-specific physiological thresholds to flooding (Ball 1988; Friess et al. 2012). This paradigm influences a large part of the field of mangrove ecology, including studies related to vegetation establishment (Cardona-Olatre et al. 2006; Chen et al. 2013; Balke et al. 2015), distribution (Satyanarayana et al. 2010; da Cruz et al. 2013), vulnerability to sea level rise (Gilman et al. 2008; Lovelock et al. 2015; Sasmito et al. 2016), and the restoration of degraded mangrove systems (Lewis 2005). However, it is a paradigm with a long history, most famously shown in the work of the British forester James Gilbert Watson in his 1928 book *Mangrove Forests of the Malay Peninsula*

(Watson 1928a). It is important to reflect upon historical contributions such as this, during a time where scientific literature is expanding rapidly, and contemporary research specialization in ecology threatens to erase historical developments (Graham and Dayton 2002).

This article aims to highlight the key role that early researchers such as Watson played in the development of contemporary ecological paradigms in mangrove science. This article has three specific objectives: (1) to introduce Watson and provide a historical account of his mangrove research that defined the Watson Inundation Classes; (2) understand the role of Watson's work in contemporary discussions regarding mangrove species distribution, "land building" and mangrove restoration; and (3) discuss the correct use of Watson's Inundation Class paradigm. Ultimately, this article seeks to increase the accessibility of Watson's work, to introduce him to a new generation of coastal wetland researchers, and to ensure that his seminal work is used appropriately.

A Brief Biography of J.G. Watson

The life of James Gilbert Watson (Fig. 1) is described in detail by Wong (1987) and Desmond (1994). Born in 1889 into a horticultural family (his father William Watson was a curator of the Royal Botanic Gardens at Kew, United Kingdom) Watson studied forestry at Eberswalde University, Germany. Watson arrived in Singapore on the 7 March 1913 on the P&O Steamer "India" (Straits Times 1913). Watson then travelled to Malaya (now Malaysia) to begin a position as an Assistant Superintendent of Government Plantations, and became a government forest economist in 1926. Though seemingly a humble man who in his writings was quick to promote his staff's efforts before his own, Watson played a leading role in establishing what is now the Forest Research Institute Malaysia (FRIM), a world famous tropical forestry research institution and statutory body of the Malaysian Government. This included the creation of an important arboretum in Kepong (near Kuala Lumpur) in 1929, which now holds more than 350 species across 149 genera (FRIM 2014). Perhaps because of this experience, in the 1930s Watson repeatedly advocated for the creation of a Science Bureau in the Forest Department, recognizing the need to bring together multiple science disciplines (botany, physiology, mycology, meterology and geology) for sustainable forest management (Kathirithamby-Wells 2005). Watson eventually rose to the position of Director of the Malaya Forestry Department in 1940, before retiring in 1947 and returning to Bedfordshire, United Kingdom.

Fig. 1 A photograph of James Gilbert Watson, year unknown. Source: Wong (1987)

Watson was based in Malaya during a turbulent phase in Southeast Asia's history, as British colonial power declined and the Japanese Imperial Army controlled much of the region during World War II. In a memorial article published in the *Empire Forestry Journal* about foresters interned during World War II, Watson (1945) stoically describes his own experience during the British retreat from Malaya in late 1941 and early 1942. Watson evacuated Kuala Lumpur, Malaya, on the 9th of January 1942, moving to Johor in southern peninsular Malaya, and eventually to Singapore with the retreating Allied armed forces. In his description of the retreat, Watson exhibits the stereotypical British stiff upper lip, carrying on "as best as we could", with evacuation "sounding like a bit of a rout, but actually it was reasonably orderly considering the black-out and narrowness of the road" (Watson 1945). Once in Singapore, Watson describes moving the Forest Department Office to a lower floor in the Fullerton Building, so that they could continue working during air raids. After the surrender of Allied forces to the Japanese Imperial Army, Watson and others were interned on the 17 February 1942, eventually being held in Changi Prison (prisoner ID 5292, www.changimuseum.sg). Watson (1945) describes the conditions at Changi, and later Sime Road Prison, where up to 4000 internees were held. In his writings (e.g., Watson 1945) Watson seemed particularly concerned about the welfare of interned foresters and that their sacrifice and dedication should not be forgotten. Watson blithely observed that "there was not much scope for forestry in internment", though he and four other interned foresters continued to plan for forestry supplies after the war, and lectured on silivculture to fellow internees until their release in August 1945. World War II significantly hampered regional forestry operations, though soon after release Watson fully expected that most forestry officers would be "fit to return to duty after a few months' leave" (Watson 1945).

Seminal Work on Mangrove Species Distribution

The majority of Watson's research was conducted on terrestrial tropical forest systems, in keeping with the main mission of a colonial forestry department. Though most of his work was focused on forestry aspects, Watson was a keen botanist, and was responsible for the collation of an important compendium of *Malayan Plant Names* (Watson 1928b). His influence on tropical forestry and botany is clear, and includes a number of species named after him (e.g., *Eugenia watsoniana* (M.R. Hend) and *Phyllantus watsonii* (A. Shaw)). A number of his publications and datasets may never have been published due to the interruption and loss of records during World War II (Watson 1946).

Despite his predominantly terrestrial forestry remit, Watson maintained a strong interest in botanical aspects of mangroves, including the collection of herbarium specimens (Fig. 2). Watson was also keen on their conservation, fighting calls for mangrove areas to be put into private hands for

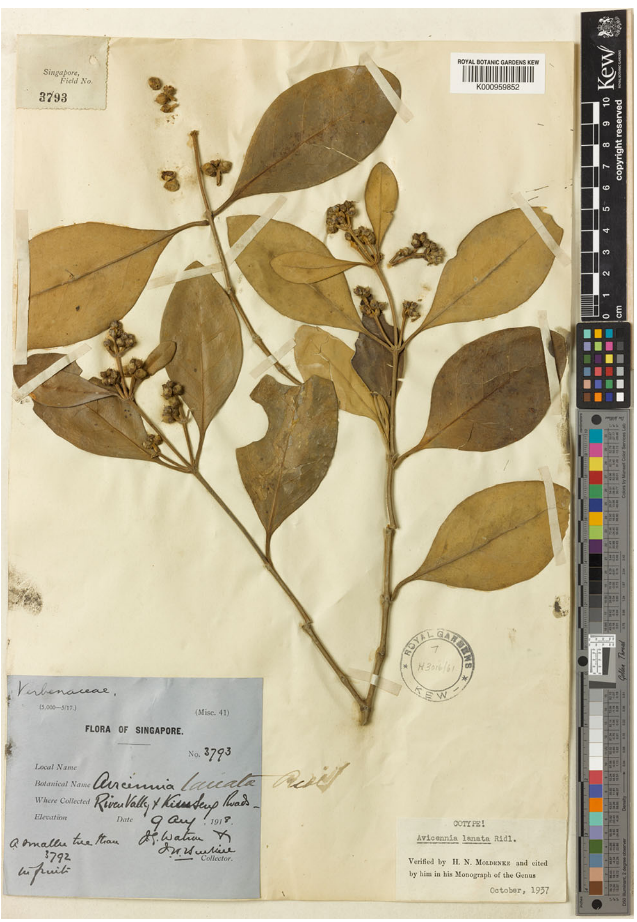

Fig. 2 A herbarium specimen for *Avicennia lanata* or *rumphiana* (specimen number K000959852), collected on the 9th of August 1918 along River Valley Road, Singapore. This location was subsequently reclaimed and is now a residential and commercial area. Source: Royal Botanic Gardens at Kew, United Kingdom. © the Board of Trustees of the Royal Botanic Gardens, Kew. Reproduced with the consent of the Royal Botanic Gardens, Kew

economic purposes (Kathirithamby-Wells 2005). Watson's main body of mangrove work was the publication *Mangrove Forests of the Malay Peninsula* (Watson 1928a). This book was the culmination of at least a decade (delayed by the onset of World War I) of observations and data collected by several Malaya Forestry Department staff, including JP Mead and GE Cubitt. Though we refer to this work as authored by Watson, he humbly considered himself "its editor rather than its author" (Watson 1928a), describing how a rough manuscript was left with him as JP Mead left Malaya for France during World War I (Straits Times 1929). *Mangrove Forests of the Malay Peninsula* represented a substantial treatise on the mangroves of Malaya, covering floral characteristics, silviculture, management, and utilization and exploitation. The focus on human uses reflected the mission of colonial Forestry Departments in promoting and overseeing commercial and sustainable forestry practices (Kathirithamby-Wells 2005).

While not the main aim of this publication, Chapter 4 (entitled '*Silviculture*') started with a small section that considered linkages between physical processes and vegetation distribution. A key aspect of this section was a table that divided various mangrove species into one of four vegetated Inundation Classes, determined by the frequency of flooding per month (Table 1). Watson's Inundation Classes were based on preliminary work undertaken by AB Boswell, who presented them at a local conference in 1926 (Watson 1928a). These classes separated the mangrove ecosystem into several geomorphological classes, related to their surface elevation relative to the (location-specific) tidal frame. Importantly, Watson assigned species to particular inundation classes based on their ability to reproduce in that geomorphological setting, not merely to persist (Watson 1928a, p130; FAO 1994). This was in contrast to similar studies occurring around this period, that defined mangrove zones primarily by their dominant species, as opposed to dominant physical processes (e.g., Walter and Steiner 1936). While they did not specifically research species adaptations to tidal inundation, Boswell, and later Watson were observing and describing the outcome of species-specific thresholds to tidal inundation, especially the difference between pioneer and non-pioneer species (c.f. Friess et al. 2012).

Watson further described the Inundation Classification spatially through a map of mangrove species distribution (Fig. 3). The veracity of information contained within this map is unknown. The text in the proceeding pages of the book describe the details in Fig. 3 as "entirely imaginary" (Watson, p130), as the map is meant to act as a diagrammatic indication of species distribution across the 4 vegetated Inundation Classes. However, the map does not correspond neatly to the Inundation Classes outlined in Table 1. Furthermore, while clear boundaries can exist between different species assemblages (Fig. 4), we may not always expect such clearly defined

Table 1 Watson's Inundation Classes, based on the predicted regular diurnal tidal regime at Port Swettenham (now Port Klang, Selangor), Peninsula Malaysia for the year 1927

Inundation Class	Flooded by	Species present	Height above Admiralty datum (ft)		Number of times flooded per month	
			From	To	From	To
1	All high tides	*Rhizophora mucronata* (river banks only) No species present on the seaward edge.	-	8	56	62
2	Medium high tides	*Avicennia alba* *Avicennia intermedia*[1] *Avicennia lanata* *Rhizophora mucronata* (river banks only) *Sonneratia griffithii*[2]	8	11	45	59
3	Normal high tides	*Acrostichum aureum* *Aegiceras majus*[3] *Avicennia intermedia*[1] *Avicennia lanata* *Avicennia officinalis* *Bruguiera gymnorhiza* *Bruguiera eriopetala*[4] *Bruguiera parviflora* *Carapa obovata*[5] *Ceriops candolleana*[6] *Rhizophora conjugata*[7] *Rhizophora mucronata* *Nipah fruticans* *Scyphiphora hydrophyllacea*[8] *Sonneratia alba*[9] *Sonneratia griffithii*	11	13	20	45
4	Spring high tides	*Acrostichum aureum* *Aegiceras majus*[3] *Avicennia officinalis* *Brownlowia lanceolata*[10] *Bruguiera eriopetala*[4] *Bruguiera caryophylloides*[11] *Bruguiera gymnorhiza* *Bruguiera parviflora* *Bruguiera eriopetala*[4] *Carapa obovata*[5] *Carapa moluccensis*[12] *Cerbera lactaria*[13] *Ceriops candolleana*[6] *Derris uliginosa*[14] *Excoecaria agallocha* *Kandelia rheedii*[15] *Lumnitzera coccinea*[16] *Lumnitzera racemosa* *Nipah fruticans* *Rhizophora conjugata*[7] *Scyphiphora hydrophyllacea*[8] *Sonneratia alba* *Sonneratia acida*[17] *Thespesia populnea*	13	15	2	20
5	Abnormal or equinoctial tides	*Acrostichum aureum* *Bruguiera gymnorhiza* *Brownlowia riedelii*[18] *Rhizophora conjugata*[6] *Carapa moluccensis*[10] *Carapa obovata*[5] *Cerbera lactaria*[13] *Cerbera odollam* *Cycas rumphii* *Daemonorops leptopus* *Derris uliginosa*[14]	15	-	-	2

Table 1 (continued)

Inundation Class	Flooded by	Species present	Height above Admiralty datum (ft)		Number of times flooded per month	
			From	To	From	To
		Excoecaria agallocha *Heritiera littoralis* *Hibiscus tiliaceus*[19] *Intsia retusa*[20] *Lumnitzera coccinea*[16] *Lumnitzera racemosa* *Oncosperma filamentosa* *Nipah fruticans* *Pluchea indica* *Podocarpus polystachyus* *Sonneratia acida*[17]				

[1] Probably *Avicennia marina var. intermedia*; [2] misclassified, should be *Sonneratia alba* (Chapman 1976); [3] probably *Aegiceras corniculatum*; [4] now *Bruguiera sexangula*; [5] now *Xylocarpus granatum*; [6] now *Ceriops tagal*; [7] now *Bruguiera gymnorhiza*; [8] now *Scyphiphora hydrophylacea*; [9] misclassified, should be *Sonneratia ovata* (Chapman 1976); [10] now *Brownlowia tersa*; [11] now *Bruguiera cylindrica*; [12] now *Xylocarpus moluccensis*; [13] now *Cerbera manghas* or *Cerbera odollam*; [14] now *Derris trifoliata*; [15] unresolved, potentially *Kandelia candel*; [16] now *Lumnitzera littorea*; [17] now *Sonneratia caseolaris*; [18] now *Brownlowia argentata*; [19] now *Talipariti tiliaceum*; [20] now *Intsia bijuga*

bands to exist (though some of the classification zones in Fig. 3 do show multiple species co-existing).

It is clear that the observation of geomorphological processes in Malaya strongly shaped Watson's thinking about mangroves. Even though the main focus of this book was on forestry practices and commercial exploitation, Watson devotes most of the Introduction chapter to a discussion on geomorphological processes and their control on mangrove distribution at the national and local scales. For example, Watson posits silt supply and geomorphological position (e.g. estuaries) as a key explanation for mangrove presence, rather than physiological controls that were strongly believed at that time (Watson 1928a, p1), and quickly highlights the role of tidal inundation and surface elevation in controlling the seaward distribution of pioneer genera such as *Avicennia* and *Sonneratia* (Watson 1928a, p2–3).

Parallel Research in Coastal Saltmarsh Ecosystems

When discussing Watson's research on physical-ecological linkages, it is also pertinent to consider parallel advances in other coastal ecosystems. Pioneering research on the role of tidal flooding in determining the vigour and density of the pioneer saltmarsh species *Salicornia europaea* was conducted by Wiehe (1935). In contrast to Watson's semi-quantitative observational approach, Wiehe (1935) took a quantitative and experimental approach to investigating the role of tidal inundation on intertidal vegetation. Five transects were established along an elevational gradient from the mudflat (north) to the upper limit of *S. europaea* (south) on a saltmarsh in the Dovey Estuary, Wales. Vegetation density decreased from ~72 % to ~1 % towards the seaward edge of *S. europaea's* distribution, and seedling mortality increased from ~34 % to ~97 % along the same distance. While focusing on one species only, Wiehe (1935) highlighted the strong influence of tidal inundation on determining vegetation presence, health and distribution which, similar to the impact of Watson's work in mangroves (discussed below), has become an important paradigm discussed in temperate saltmarsh science (e.g., Brinson 1993).

As they occurred in different ecosystems in very different locations, and because both authors had very different professions (forester versus academic), it is assumed that neither Watson or Wiehe were aware of each other's work. However, both were important early studies in defining this important physical-ecological relationship in coastal wetlands.

Recognition of Watson's Contribution

Originally priced at \$3, the *Mangrove Forests of the Malay Peninsula* was available to the public, and received positive reviews in the national press as a book that could change the negative image of mangroves in the public's mind, while advertising the tireless and unseen work conducted by the Malaya Forest Department (Straits Times 1929). Academically, Watson's work was quickly regarded by other researchers as an important ecological work, being "the most complete work on the mangrove forests of the eastern region, or indeed of any region" (Troup 1929). The importance of Watson's work linking inundation and species distribution was particularly noted, with an "interesting diagrammatic map showing the typical distribution of the most important mangrove species" (Troup 1929) and another reviewer noting that "the ecological account of the forests is particularly

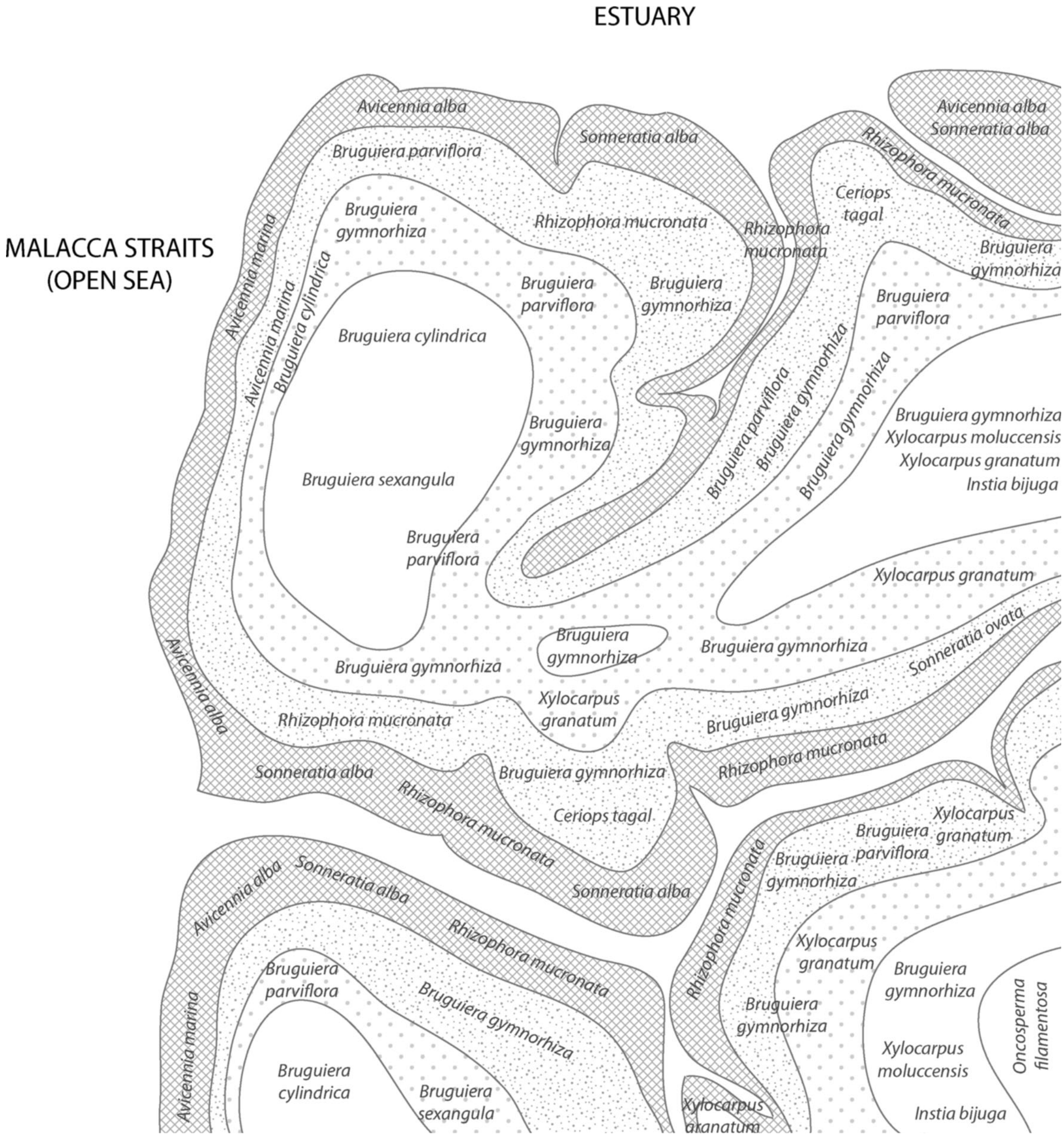

Fig. 3 "A diagram to illustrate the typical, but by no means inevitable distribution of the more important mangrove species". This diagram was originally drawn by the Federated Malay States Survey Department. This version has been updated with current species names. Note that the shading does not completely correspond to the Inundation Classes described in Table 1. Redrawn from Watson (1928a)

interesting, dealing as it does with the distribution of the species and the effects of inundation" (LN 1930).

Other researchers immediately built upon Watson's work (Table 2). In 1931, the Dutch botanist J.H. De Haan incorporated observations of salinity into Inundation Classes at sites in Indonesia (Knight et al. 2008). Other researchers also investigated inundation-vegetation relationships after the publication of Watson's book, though it is unclear to what extent these researchers were influenced by Watson's publication. Walter and Steiner (1936) based their mangrove classification in East Africa primarily on the dominant vegetation observed (later expanded by Macnae 1968), and while they made brief and casual observations of broad inundation frequencies for particular mangrove species, any focus on physical-ecological linkages was on water balance and transpiration.

Perhaps best known among Neotropical mangrove ecologists is Chapman's (sensu Chapman 1944) application of Watson's inundation classification to his "New World" mangrove Inundation Classification (Chapman 1976). VJ Chapman was strongly influenced by Watson's "Old World" research, and attempted to broaden the geographic scope of both classifications by bringing them together (Table 2).

While Watson (1928a) was immediately recognized by other mangrove scientists after its publication, his work has

Fig. 4 Example of distinct boundaries in species assemblage across an intertidal gradient, from the mudflat, to an *Avicennia alba*-dominated mangrove fringe, to a *Rhizophora mucronata*-dominated back mangrove zone in Palian, Trang Province, southwest Thailand. For transect elevation information see Horstman et al. (2013). Photo by author

continued to influence contemporary thinking in mangrove ecology; in November 2015, Google Scholar ascribed 434 citations to *Mangrove Forests of the Malay Peninsula*, though this is likely to be a gross underestimation due to issues surrounding tracing citations to older articles. Due to the low availability of hard copies of Watson (1928a), it is unlikely that all of these citations have referred back to an original copy (as opposed to citing from other review articles), though it shows the continuing relevance of Watson's observations to contemporary debates in mangrove science.

Influence on Paradigms in Mangrove Ecology

Watson's Contribution to Debates around Mangrove Zonation

Watson's early observations of species distribution in peninsular Malaysia have also been observed in other mangrove systems across the tropics, leading to spirited debates over many decades as to whether the (generally) clear distribution of mangrove species represents zonation and/or ecological succession. This discussion is summarized in depth by many authors (e.g., Snedaker 1982; Smith 1992), so is only summarized briefly here. Similar to terrestrial forested systems, many authors have considered species-rich back mangrove communities to be a mature climax forest type in a process of ecological succession from a species-poor pioneer community (Chapman 1976; Snedaker 1982).

Ecological succession is often defined in part by the modification of the physical environment by an ecological community (autogenic), so succession is a predominantly community-controlled process (Odum 1969; Lugo 1980). Watson (1928a)'s emphasis on the reverse – the predominant role of physical processes in controlling species distribution – forms the foundation for arguments against strict succession in mangroves. Zonation can be apparent but does not necessarily indicate succession, and could instead reflect species tolerances along an environmental gradient of stress (Woodroffe 1992), with the distinct-preference hypothesis suggesting that each species has its own optimum across an environmental gradient, resulting in separate species distributions (Smith 1992).

Watson's Contribution to Debates around Mangroves as "Land Builders"

A discussion on mangrove zonation and succession leads to another linked debate in mangrove science, whether mangroves are land builders (creating their own suitable elevations), or colonize and stabilize existing suitable elevations. This can essentially be summarized as ecological processes controlling physical patterns, or physical processes controlling ecological patterns. Lee et al. (2014) provide an extensive history and critique of the "mangroves as land builders" paradigm. The paradigm was recorded as early as 1888, in a letter to the horticultural magazine *Forest and Garden*, where it was suggested that organic material from mangroves in Florida were consolidated in order to create islands that will eventually merge with the mainland (Curtiss 1888). This was further hypothesised for other mangroves in Florida (Davis 1940) and Jamaica, where the accumulation of peat material determined biogenic mangroves as direct agents of land formation (Chapman 1940). The work of Davis (1940) in particular was a key influence in promoting the land building hypothesis, and this case study was almost universally adopted for several decades (Lugo 1980).

In contrast to these views, through his observations that led to his 1928 book, Watson considered that, in peninsular Malaysia, the Inundation Class was the ultimate control on vegetation establishment, so that physical processes drove ecological patterns, such that "mangroves follow silting rather than cause it" (Watson 1928a, p5). This is a view that was not supported until some decades later, when Egler (1952)

Table 2 Comparison of various Inundation Class schemes for "old world" and "new world" mangrove systems. Adapted from: Chapman 1976

Old world Classifications			New world classification	
Watson (1928)	De Haan (1931)	Dominant Species	Chapman (1944)	Dominant Species
	A. Brackish to saline. Sal at H.T., 1–3 %			
1. All high tides	A1. Areas flooded 1–2 times daily for min. 20 days per month	*Sonneratia alba* *Sonneratia apetala* *Avicennia marina*	530 to 700 submersions per annum	*Rhizophora mangle*
2. Medium high tides	A2. Areas flooded 10–19 days per month	*Rhizophora* spp.		
3. Normal high tides		*Bruguiera* spp.	400 to 530 submersions per annum	*Avicennia germinans*
	A3. Flooded 9 days per month	*Xylocarpus granatum*		
4. Spring high tides	A4. Flooded only a few days per month	*Lumnitzera littorea*, *Bruguiera sexangula*	150 to 250 submersions per annum	*Avicennia germinans* *Laguncularia racemosa*
5. Abnormal or equinotial tides		Halophytes or salt flats	4 to 100 submersions per annum	*Avicennia germinans* *Laguncularia racemosa* *Cornocarpus erectus*
	B. Fresh to brackish water, sal 0–1.0 %			
	B1. More or less under tidal influence	*Nypa fruticans*		

considered the role of rising sea level, viewing the accumulation of autochthonous and allochthonous material as retaining its relative position in the tidal frame, as opposed to building new land suitable for seaward expansion. This view of mangroves as land stabilizers, as opposed to land builders, began to dominate (Chapman 1976), and it is now widely recognize that mangroves respond to large-scale geomorphological processes, as opposed to driving large-scale geomorphological changes (Smith 1992). Our view of mangrove geomorphology has changed to such an extent that the original land building hypothesis is now not considered to be "based on solid evidence, and is not generally applicable to all settings" (Lee et al. 2014).

The difference in opinion between Watson on the one hand, and Curtiss, Davis and Chapman on the other, and indeed the early dominance of the land building hypothesis, could be explained by considering the geomorphological settings in which both groups were considering this question. There is a clear geomorphological distribution of mangrove types globally (Balke and Friess 2016), with "land building" biogenic mangroves found in North America and the Caribbean (where Curtiss, Chapman and Davis were based), and "land colonizing" minerogenic mangroves throughout much of Southeast Asia, upon which Watson based his observations. Interestingly, a review of the land building paradigm in the 1970s (Carlton 1974) did not include a discussion of Watson's seminal observations in minerogenic systems, but instead focused mostly on studies from Florida (USA) and the Caribbean. This could potentially have been due to a perceived lack of comparability, for example not seeing the relevance of applying hypotheses from a species-rich Indo-Pacific region to a species-poor neotropical region. However, a focus on North American and Caribbean case studies is more likely due to poor access to the Indo-Pacific literature (especially older literature) at that time, or a researcher bias towards systems local to them or within their region (sensu Stocks et al. 2008). Indeed, Carlton (1974) concedes that the neotropical focus of his Review is due to the availability of literature. Carlton suggests that "most of the ideas discussed here should be applicable to other mangrove areas around the world", making a broad (and incorrect) assumption that Indo-Pacific systems are similarly biogenic and of low species diversity. Thus, poor consideration and understanding of minerogenic, species-diverse Indo-Pacific systems, such as those described by Watson, could have contributed to the prominence of biogenic, land building hypotheses in the literature (based on key works such as Davis 1940) until recent decades.

Influence on Mangrove Restoration Knowledge

The role of inundation in controlling natural vegetation species distribution in mangroves means that hydrological processes are also important when restoring or rehabilitating a degraded wetland (Lewis 2005). Mangrove rehabilitation is notoriously unsuccessful across much of the tropics, in part because of a disregard for hydrological processes, such as the planting of non-pioneer species (e.g. *Rhizophora* spp.) on low-elevation seagrass beds or mudflats outside the elevation envelope of most mangrove species (e.g., Samson and Rollon 2008).

Watson's Inundation Classes are often presented in mangrove restoration planning documents and manuals (e.g., Hamilton and Snedaker 1984; FAO 1994; Lewis 2005; Brown 2007; Global Nature Fund 2007; Marchand 2008; Chan and Baba 2009; Ong 2012; Ong and Gong 2013; Lewis and Brown 2014). This is in part due to the ease with which the Inundation Classes can be measured, requiring at a minimum only an elevation survey (using water hoses, Abney levels or a theodolite) linked to a local tidal datum. Thus, elevation may be viewed as a simple predictive tool for potential species establishment (Snedaker 1982). Inundation Classes may also be used in restoration because they are straightforward to communicate to engineers, managers and communities. By showing a defined link between surface elevation and the type of mangrove species expected, it clearly shows the importance of manipulating physical processes for successful restoration, and clarifies complex physical-ecological linkages (including tidal inundation, salinity, nutrients and oxygen content) into a simple relationship that can be understood by all stakeholders.

Using Watson's Inundation Classification correctly

The Generality of Inundation Classes

Watson's Inundation Classes represent a simplified model of a shallow-sloping, open coast fringing mangrove forest experiencing a regular diurnal tidal regime. Further studies have shown how the Watson inundation classification can be insufficient in mangrove areas that experience an irregular tidal regime or have variable intertidal topography (Van Loon et al. 2007). This includes its use in restoration sites, where hydrological constrictions can cause substantial tidal asymmetry (sensu Symonds and Collins 2007 for saltmarsh restoration). Instead, it has been suggested that classifying sites by their average duration of inundation, instead of their frequency of inundation (as per Watson's Inundation Classes), may be more suitable in such situations (Van Loon et al. 2007).

Poor applicability of Watson's inundation classification for particular sites is not surprising: this conceptual classification was based on a simplified shallow-sloping site in southern Peninsular Malaysia, though mangrove forests show huge variation in species diversity, topography, geomorphological setting and tidal regime at multiple scales (from the local scale to the regional scale). In addition, Watson observed species spanning multiple Inundation Classes, those using Watson's classification may not fully take into account the broad elevation envelopes that mangrove species can occupy (e.g., Chapman 1976).

Watson himself noted that "there can be no doubt, however, that there is considerable variation in the distribution of the species, not only in different countries but within local limits. The remarks that follow [his observations on Inundation Classes] can therefore, only be accepted as generally true for Malaya" (Watson 1928a, p126). In effect, Watson probably never meant his classification to be applied universally, though it has been used in this manner subsequently by researchers and restoration practitioners because of its relative ease and simple requirements for data collection. This is especially important in tropical developing nations where many mangrove restoration projects are based, and where simple and cost-effective assessment techniques are required to guide restoration activities. Thus, while Watson's Inundation Classes can be useful as a broad guide to describe mangrove-inundation linkages, we must always communicate that specific inundation frequencies are based on a single site and are a general guide only.

Species Distribution Is Multi-Factorial

Despite our rich knowledge of species tolerances and adaptations to tidal inundation, and strong observations of zonation along tidal gradients, such as those made by Watson, proving a statistical link between species distribution and inundation has often proved elusive (Ellison et al. 2000; Feller et al. 2010). This may be in part due to the range of other processes involved in ultimately determining species distribution (e.g., Twilley and Rivera-Monroy 2005; Castañeda-Moya et al. 2006), some of which are co-correlated with tidal inundation. Indeed, correlations between species distribution and inundation defy broad scaling between sites precisely because of the effect of direct and indirect intermediate factors such as soil saturation, nutrient availability and salinity (Ball 1988; Ellison 2002). The combined role of multiple factors has long been appreciated, at least since De Haan (1931) incorporated salinity into his expanded set of inundation classes, though their interactions are non-linear and difficult to predict. Thus, while tidal inundation may be an "ideal proxy for the wide variety of plant conditions that affect plant growth" (Ellison 2002), the multiple processes controlling mangrove distribution make projections of species distribution based on tidal inundation alone fraught with challenges (Alongi 2008, 2009; Clarke 2014).

Conclusions

The role of surface elevation and tidal inundation in controlling mangrove species distribution is an established tenet in mangrove science, as it is in other wetland systems. Watson and colleagues contributed substantially to the early development of the relationship between physical geography and ecology in mangrove forests that we now take for granted. The early work of Watson and others, while subsequently refined, has generally been found to have broad applicability, and has "stood the test of time"- two key aspects of a prevailing paradigm (Graham and Dayton 2002). Importantly, the hypotheses posited by Watson have stood the test of time even as we gain a better understanding of the multi-factorial nature of mangrove species distribution, and the multitude of physical and ecological processes involved.

Perhaps more broadly, Watson's most important contribution to mangrove science was his devotion to the research process. While moving increasingly into administrative positions during his career, Watson was still acutely aware of the importance of research in forestry, and the issues of maintaining and funding long-term research plans (Watson 1934); issues which still remain in ecological research today. A botanical, ecological and geographical research focus, perhaps unexpected from a forester in an economics-driven colonial natural resource department, ensured that early ecological observations were recorded, assembled and reported in such a way that they could contribute to contemporary thinking in mangrove ecology. It is interesting to speculate where Watson thought his observations on physical-ecological linkages in mangroves would lead. Certainly, it is not a hypothesis that he pursued further to any great degree in subsequent published works, though it has become a key foundation upon which much of our knowledge of mangrove geomorphology and ecology is now based. The burden is on mangrove researchers to support the virtues of historical perspectives (Graham and Dayton 2002) to ensure that we continue to build upon and advance, instead of replicate Watson's strong ecological foundation.

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