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The roots of Finnish avian ecology: from topographic studies to quantitative bird censuses

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Ornithological research classified as topographic shared certain characteristics, including location type descriptions, full species lists of breeding birds for each location type, and usually at least a relative estimate of each species' abundance. Bird topographic research was inspired by the Finnish plant topographers, most notably J. P. Norrlin, and was presented as an explicit research programme by J. A. Palmén in 1885. We investigated the structure of and concepts used by 30 bird topographic studies published before 1930. The first clearly bird topographic study was published in 1886 (C. Brander), and since the 1920s topographic studies were gradually replaced by modern-type quantitative bird censuses. Terminology used in topographic studies varied. A commonly used concept was *ståndort*. In our material, the term "biotope" was first used in 1928. The term "topography" was occasionally used by Finnish ornithologists until the 1960s. The topographic approach improved the quality of faunistic reports, inspired later quantitative field censuses of birds, and even contributed to the study of habitat selection by birds.

Introduction

It is well-known that animal ecology developed later than plant ecology, and for a long time followed the approaches developed by plant ecologists rather closely (Palmgren 1930, Elton 1933, Renkonen 1938). In Finland, plant ecological research, that at the time was called topographic, was launched by the pioneering works of Johan Petter Norrlin (1842–1917) on the flora of south-eastern Tavastia (Norrlin 1870; Table 1) and the Lake Onega district in eastern Karelia (Norrlin 1871; Norrlin's doctoral thesis; *see* also Renvall 1897, Cajander 1921, Collander 1965). The term plant topography was probably first used in 1867 by the Swedish botanist Hampus Adolf von Post (Palmgren 1928, Tuomikoski 1941). In its most simple form, plant topography was the listing of plant species that occurred in particular localities (Collander 1965). The first biological doctoral thesis written in Finnish (by E. A. Vainio) had a plant topographic focus (Renvall 1897, Linkola 1929).

Formal definitions of plant topography varied. Cajander (1921) defined plant topography broadly as the study of relations between vegetation and location type (*Standort* in German), which also covered the study of growing sites (*Standortslehre*) and the study of plant vegetation formations (*Formationslehre*). Hus-

tich (1939) emphasized the concept of location type (*ståndort* in Swedish) as the starting point of plant topography, and considered plant topography a mediator between plant sociology and ecology. Tuomikoski (1941) defined plant topography as the study of how plant species are located within topographic entities in a particular environment. Plant sociology, instead, focused on plant communities or vegetation (Hustich 1939, Tuomikoski 1941). Since the early 1900s, the concepts of plant sociology, and later plant ecology, have largely replaced the older term "plant topography", although the exact relations of these terms always remained ambiguous (Tuomikoski 1941). Already Kalliola (1942) considered the entire field of plant topography outdated.

Also in Finland advances in botany inspired early animal ecology. Birds were from the very beginning important study objects. Avian topography was until the late 1920s or early 1930s an umbrella concept for a major part of bird ecological research in Finland. First introduced by Johan Axel Palmén in 1885, the topographic approach focused on listing bird species in particular location types, usually with scale-based estimates of species abundance (Palmén 1885, 1908). Such research can be called ecological as far as ecology is defined as the study of the distribution and abundance of organisms (Elton 1933, Andrewartha & Birch 1954, Krebs 1972). At the time, these studies were called faunistic bird reports (Palmgren 1972).

In this paper, we review the history of avian topography in Finland and its importance for the later development of Finnish avian ecology. It will be shown that topographic approaches influenced and preceded both quantitative bird censuses and studies of habitat selection.

Material and methods

In the selection of study material, the first task was to decide which studies should be considered topographic in their approach. Two main criteria were used. Firstly, we used criteria listed in Palmén's original paper (Palmén 1885)

Table 1. Topographic location types of Norrlin (1870) and Palmén (1885, 1908). *See* text for details.

Norrlin (1870)	Palmén (1885, 1908)
Pine forests	Aquatic locations
Spruce forests	Seawater locations
Deciduous forests	Pelagic islands
Groves	Seashores (outer and continental)
Heathlands	Outer archipelago
Dry and open hillsides	Inner archipelago
Hillsides	Freshwater locations
Dry and moist meadows	Lakeshores
Agricultural fields	Rivers, brooks and rapids
Built-up areas (with associated grasslands)	Lakes and ponds
Pine-growing mires	Swamps
Open mires	Terrestrial locations
Open mires with small ponds	Open and treeless locations
Lakes	Fields and heaths
Lakeshores	Dry meadows
Wetlands	Cultivated fields
Wetland shores	Human settlements
Small ponds	Bushy areas and forests
	Scrublands
	Groves
	Mixed forests
	Deciduous forests
	Coniferous forests
	Mountains

where he explicitly listed the characteristics of a topographic study: it should include location type-specific lists of observed bird species, and estimates of bird abundance based at least on some relative scale. Secondly, we used the lists of published topographic studies presented by Palmgren (1930: p. 58) and Soveri (1940: p. 8). A particular study was included in our analysis if at least one of these criteria was fulfilled. A single study mentioned by Soveri was omitted due to its geographical focus (Norway). We used Palmgren's (1972) comprehensive list of faunistic bird studies in Finland that did not distinguish between topographic and other types of faunistic studies, for checking the coverage of our data.

We included six publications not listed by Palmgren (1930) or Soveri (1940). Three were field studies (Lindforss 1886, Suomalainen 1915, Hildén 1920), and review papers or books (Renvall 1910, 1916, Levander 1914). These studies were found either in the reference lists of other topographic studies, or in Palmgren (1972).

This left us with 30 bird topographic studies, of which all but four were faunistic reports. All studies included in the material were analysed for their structure (with respect to Palmén's criteria), geographical focus, measures of abundance used, and terminology.

For a theoretical and methodological background of bird topographic and early ecological research, our main sources were Palmgren (1928, 1930), Kalela (1938), Renkonen (1938), Soveri (1940), and Merikallio (1946).

Research agenda of Palmén (1885) and its influence

Johan Axel Palmén (1845–1919) was "the ornithologist" in Anto Leikola's *History of Zoology in Finland 1828–1918*, and clearly the dominant figure in Finnish zoology at the turn of the 19th and 20th centuries (Leikola 2011). Originally more interested in entomology, he turned early in his career to ornithology, primarily because as a young assistant at the zoological museum, he was given the task to edit the manuscript of the second volume of Magnus von Wright's *Finlands Foglar*. Von Wright had died in 1868 before completion of his pioneering monograph on the birds of Finland. This work was completed in 1873 (von Wright & Palmén 1873), and by that time Palmén had nearly finished his doctoral dissertation on the migratory routes of birds, which appeared in 1874. His important later ornithological works included a study of Siberian coastal birds based on the Vega Expedition, and establishment of the so-called Palmén archive (a collection of local bird reports), as well as the launching of bird ringing activities in Finland (Leikola 2011).

Palmén introduced avian topography into Finnish zoology as an explicit research programme that was published twice with practically identical content (Palmén 1885, 1908). His central role as the founder of bird topographic research in Finland was emphasized by many authors (e.g. Hildén 1920, Palmgren 1930, Soveri 1940, Merikallio 1946), although it is possible that some were primarily influenced by Norrlin (Renvall 1897). Palmén was concerned about the low quality of local faunistic reports (*see* also von Wright & Palmén 1873). Not surprisingly, he started with a reference to the Finnish plant topography, which he as a friend of J. P. Norrlin knew well. According to him, in the analysis of the Finnish flora, quality demands had increased from the level where a simple species list was enough to the level where topographic data on occurrence of species was required; i.e. what plant species occurred together at particular growing sites or locations, and also, how these location types were distributed in the study area. The ultimate objectives of such studies were, according to Palmén, an overall picture of the Finnish flora, and floristic comparisons between Finland and other floristic areas. A comparative approach had been apparent already in Norrlin's works (1870, 1871).

Palmén claimed that the fauna could be studied in a similar manner. He emphasized the collection of basic biological data of bird species from several location types within the range of the species. Otherwise one might generalize on the biology of the species based only on observations made in a small portion of the species' range. A proper topographic analysis requires, according to Palmén (1885, 1908), not only knowledge on what species live in a particular area, but also information on location types

suitable for different species' occurrences. The boundaries between different types of locations are not sharp, and for instance birds living in an isolated patch of spruce forest embedded within a non-forested area may not be generally representative for spruce forest birds. Palmén recognized that isolated patches of spruce forest may differ from large forests in their species composition. This observation is consistent with the much later ideas of island biogeography (MacArthur & Wilson 1963).

Palmén then proceeded to analysing typical bird species for each location type. He divided the locations broadly into aquatic and terrestrial ones (Table 1). Each location type may have its local variants, and intermediate types abound. A prevalent location type, such as a large mire, may also influence other location types in the area, e.g. by affecting their humidity or temperatures. In such areas, birds representing the dominant location type may also frequently be observed at non-typical sites. Palmén also noted that in different location types, factors influencing a particular species' occurrence may be different. For instance, swifts in built-up areas nest in high towers and buildings, but in wilderness areas in holes of tall pine trees. Location preferences thus vary also within species.

A proper topographic analysis in a study area would, according to Palmén, also require field studies in different location types in all seasons, as well as some estimates of abundance for each species. The abundances of bird species should be expressed either numerically (number of individuals per unit area) or with a commonly used relative scale (rare, uncommon, common, abundant, irregular). It is very common for birds to have different location preferences during the breeding season, migration and in winter. For instance many waders breed in swamps, but prefer coastal areas during their migration. Palmén considered the study of migration localities especially important as it could help in mapping a species' migration routes.

Palmén's successor at the University of Helsinki, K. M. Levander (1867–1943), also took some interest in topographic studies, and was later keen on getting recognition for his role (Levander 1917). In the meeting of the *Societas pro Fauna et Flora Fennica* on 7 February 1914, he spoke about the use of topography in the study of mires. His main interest was, however, entomological. The talk was later published in the proceedings of the Society (Levander 1914). Levander (1914) was familiar with the classical works of V. E. Shelford on ecological succession, and those of Eugen Warming, the founder of plant ecology. Levander considered topographic-faunistic and animal ecological approaches separate but close fields, and recommended the use of both in mire research. For him, topography meant location type-specific species lists, while ecology was the study of relations between animals and their natural environment. Finnilä (1915) explicitly mentioned Levander's paper as an inspiration for his study.

Although Palmén is supposed to have inspired or influenced nearly all local bird faunas (Merikallio 1946, Palmgren 1972, Väisänen *et al.* 1998), his papers were directly cited by only three of the 15 topographic faunistic papers published before 1914 (i.e., Krank 1898, Suomalainen 1908, Palmgren 1913). In some cases, Palmén's influence was however straightforward. Elias W. Suomalainen (1883–1931) was a student of Palmén, and his Master's thesis supervised by Palmén was a topographic study of the bird fauna of the Kallavesi area in the Savonia province (Ekman 1932). Suomalainen (1908) was also the first local faunistic study on birds published in Finnish (Kauppinen & Ruokolainen 1999: p. 29). Some who applied the topographic approach, such as Thorsten Renvall, referred to both Norrlin (Renvall 1897) and Palmén (Renvall 1910). Finnilä (1915), in turn, referred to both Palmén and Levander.

The structure of topographic studies changed over time. The earliest study that included both a list of location types and the breeding birds for each location type was by Brander (1886; Table 2). The first study that included both a list of location types, and location type-specific bird species lists with relative estimates of species abundance was by Sandman (1892). After Sandman's study, the basic structure of topographic studies remained more or less the same until the 1920s, when quantitative estimates of abundance gradually gained dominance (Table 2). There was naturally great variability in the length and amount of detail in faunistic studies. Following

Palmén's guidelines, the majority of faunistic studies also reported migration phenology and species residence outside the breeding season.

Geography and terminology of topographic studies

The geographic locations of the 26 bird topographic field studies are shown in Fig. 1. The specific terms used in the Finnish bird topographic literature for location types are summarized in Table 3. In the period studied by us, a great part of the biological literature in Finland was published in Swedish. The term *ståndort* (*Standort* in German), used already by Norrlin (1870), and considered by Hustich (1939) the central term in plant topography, was the most widely used term also in bird topographic studies. All but two Swedish-speaking authors used this term (Table 3); the exceptions were Enwald (1886) and Renvall (1910). Krank (1898) used a derivative term *häckningsståndort* (i.e., breeding location type). Suomalainen (1908: p. 7) and Hildén (1920: p. 140) explicitly named *ståndort* as the Swedish language synonym of the Finnish term *paikanlaatu*, which was the most widely used Finnish term for topographic location types (Table 3). Merikallio (1917), however, used this Finnish term as a synonym of the botanical term "plant community".

Some authors used a more specific terminology based on bird behaviour. Already Palmén (1885) had made a distinction between the nesting location and the larger "wandering location" of birds during the breeding season. The rather simple topographic classifications used in plant topography did not suffice for ornithological

Table 2. Characteristics of bird topographic faunistic studies in Finland from 1885 to 1930. Y = Yes, N = No, (Y) = no direct list, but information available, None = list of abundance categories not presented. Topographic locations correspond to habitats, biotopes or ecosystems in modern terminology.

Reference	Study area	Topographic locations listed	Breeding birds listed	Measures of abundance (R = relative, A = absolute)
Backman (1886)	N of Ladoga	N	N	None
von Bonsdorff (1886)	N of Ladoga (Salmi)	N	N	None
Brander (1886)	Pirkanmaa (Parkano)	Y	Y	None
Enwald (1886)	Lapland	N	N	None
Hollmerus (1886)	Sotkamo, Kuhmo	N	N	None
Lindforss (1886)	Sulkava	N	N	None
Walléen (1889)	Karelian Isthmus	N	N	None
Sandman (1892)	Hailuoto	Y	Y	R (7-step scale)
Krank (1898)	S Ostrobothnia	Y	Y	R (6-step scale)
Nordling (1898)	Lapland (Inari)	Y	Y	R (6-step scale)
Suomalainen (1908)	Savonia	Y	Y	None
Munsterhjelm (1910)	W Lapland	Y	Y	None
Munsterhjelm (1911)	Lapland (Enontekiö)	Y	Y	None
Finnilä (1913)	Lapland (Sodankylä)	N	N	None
Palmgren (1913)	Helsinki region	Y	Y	R (7-step scale)
Finnilä (1914a)	Lapland (Salla)	(Y)	N	None
Finnilä (1914b)	N Tavastia (Ätsäri)	N	N	None
Palmgren (1915)	Satakunta (Pori region)	Y	Y	R (6-step scale)
Finnilä (1915)	Lapland (Salla)	Y	(Y)	A (number of breeding pairs)
Suomalainen (1915)	Pori region	Y	Y	Not mentioned
Montell (1917)	Lapland (Muonio)	Y	Y	R (10-step scale)
Hildén (1920)	Tavastia, Karelian Isthmus	Y	Y	R (10-step scale)
Hortling (1921)	S Finland	Y	Y	R (3-step scale)
Merikallio (1921)	Salla, Kuusamo	Y	Y	R (5-step scale) based on A
Sundström (1927)	Tammisaari archipelago	Y	Y	A
Suomalainen (1927)	Kokemäenjoki area	Y	Y	R (5-step scale)

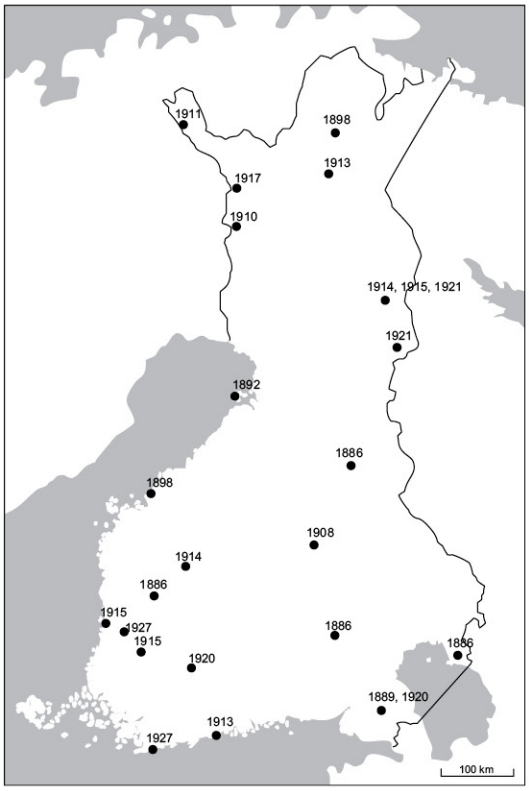

Fig. 1. Locations of bird topographic field studies in Finland. The Finnish national borders are those of the years 1920–1940. Year is the year of publication, not of the actual study. Only studies that could be rather precisely located are included.

studies due to the greater mobility of birds (Renvall 1910, Merikallio 1917).

Biologist and schoolteacher Thorsten Renvall (1868–1927), who was always careful with terminology (Renvall 1897, 1916), presented an interesting hierarchical terminology for bird topographic units (Renvall 1910, 1916, Vuorisalo *et al*. 2014; Table 4). He distinguished between (i) locations where birds are commonly observed during the breeding season (general location), (ii) their actual foraging locations, (iii) breeding locations, and finally (iv) the nest sites. Renvall provided several examples. For instance, song thrushes (*Turdus philomelos*) are commonly seen in spruce forests (general location) during the breeding season, while they actually forage on ground (foraging location; Renvall 1910). On the other hand, the European kestrel (*Falco tinnunculus*) breeds in forest margins (breeding location), but builds its nests between tree branches (nest site; Renvall 1910).

Forest scientist and future prime minister of Finland, A. K. Cajander (1879–1943), one of Norrlin's students, had presented a forest type theory based on ground-layer vegetation (Cajander 1909). The first ornithologist to use Cajander's terminology in bird topographic research was I. Hildén (1920; for the pioneering status of this work *see* Palmgren 1930, Kalela 1938, Soveri 1940). In the 1920s, forest type terminology, although for a long time considered controversial (Renkonen 1938), was quickly adopted by pioneers of quantitative bird studies (Merikallio 1921, Palmgren 1928).

In our research material, Palmgren (1928) was the earliest who used the term "biotope". Kalela (1938) synonymized bird topographic studies, based on Palmén's agenda, with comparative biotope research (*vergleichende Biotopforschung* in German).

Classifications of location types

Topographic units, irrespective of the term used, were separated in the field and later classified on the basis of local geography or vegetation. The geographic variability of conditions made classifications highly diverse (Table 4). Obviously, a classification of topographic units made for Helsinki coastal areas (Palmgren 1913) would be of little use in a study performed in the primeval forests of eastern Finland (Merikallio 1921). Renvall (1910, 1916) proposed a general classification of topographic units that would apply anywhere in northern Europe (Table 4). Unfortunately, nobody else seemed to have used his classification. Neither Merikallio (1921) nor Suomalainen (1927) referred to it, although Renvall's book (Renvall 1916) must have been known to them. It is known that Suomalainen and Renvall had rather polemic personal relations (Suomalainen 1926).

From relative to absolute measures of bird abundance

Although already Palmén (1885) had put for-

ward the possibility that abundances of birds could be expressed in absolute terms (number of individuals per unit area), relative scales dominated the field for decades. Levander (1907) specifically recommended the collection of quantitative information (number of breeding pairs) in studies of lake birds.

Merikallio (1917) was unhappy with the lack of clearly defined abundance scaling, which complicated comparisons between study areas. He thus shared Palmén's (1885) original concern. Norrlin (1870) had used a relative four-step scale from abundant to rare (in Swedish *ymniga*, *spridda*, *sparsamma*, *sällsynta*). Mela (1882) introduced a rather complex relative-scale classification of abundance for vertebrates that took seasonal differences into account. Palmén (1885, 1908) considered a five-step scale from abundant to rare as commonplace. A variety of scales was used in bird topographic field studies (Table 2). In our material, one author used a three-step scale, two authors a five-step scale, three authors a six-step scale, two authors a seven-step scale, and two authors a ten-step scale. Montell (1917) took into account the possibility that bird abundances may vary spatially. He therefore expressed the range of variation in relative bird abundances in his large study area, for instance, by 3–6, or 5–8 (Montell 1917: p. 17).

Einari Merikallio (1888–1961) became the great pioneer of quantitative bird censuses in Finland (Merikallio 1946; for his career *see*

Table 3. Terminology of topographic units (until 1930). Works that did not use specific terms are not included.

Reference	Term(s) in		
	Swedish	Finnish	German
Norrlin (1870)	ståndort		
Palmén (1885, 1908)	ståndort, vistelseort	asuinpaikka, esiytymispaikka	
Enwald (1886)	lokal		
Sandman (1892)	ståndort		
Krank (1898)	häckningsståndort, lokal		
Nordling (1898)	ståndort		
Suomalainen (1908)	ståndort	paikanlaatu, oleskelupaikka, pesimispaikka	
Munsterhjelm (1910, 1911)	ståndort, lokal		
Renvall (1910)	naturlig lokal (uppehållslokal, näringslokal, häckningslokal, boplats)		
Palmgren (1913, 1915)	ståndort, lokal (näringslokal, häckningslokal)		
Finnilä (1915)		kasviyhdistymä	
Renvall (1916)		oleskelupaikka, ravinnonsaantipaikka, pesimispaikka, pesäpaikka	
Merikallio (1917)		kasviyhdyskunta, paikanlaatu	
Montell (1917)	ståndort, lokal		
Hildén (1920)	ståndort	asuinpaikka, paikanlaatu	
Hortling (1921)			Brutlokal
Merikallio (1921)		paikanlaatu	
Sundström (1927)			Standort, Lokal
Suomalainen (1927)		paikanlaatu	
Palmgren (1930)			Standort, Standortstyp, Biotop, Biotoptyp

Väisänen 1988). He was early on fascinated by the possibilities and problems posed by the topographic and regional diversity of native breeding birds in Finland (Anonymous 1958, Väisänen 1988). In his 1917 study, Merikallio introduced a quantitative basis for the widely used five-step scale in bird topography. "Very abundant" were birds with more than 50 pairs per km^2, "abundant" birds with 10–50 pairs per km^2, "relatively abundant" those with 3–9 pairs per km^2, "rare" were the birds with 0.5 to 2 pairs per km^2, and "very rare" were bird species with fewer than 0.5 pairs per km^2 (i.e., fewer than 5 pairs per 10 km^2). As methods for measuring breeding bird population densities, he recommended mapping, or a simple form of line-transect method (Merikallio 1917).

Merikallio had since 1915 experimented with quantitative bird censuses in different parts of Finland (Väisänen 1988). Merikallio used the scaling of his 1917 paper in a topographic field study in eastern Finland, performed already in 1917, but perhaps due to the Finnish Civil War not published until 1921 (Merikallio 1921). This study was not only Merikallio's first extensive scientific paper (Väisänen 1988), but also one of the first, and at the time the most extensive in Finland, that systematically applied a quantitative approach (Merikallio 1946). There had been a couple of earlier attempts (Merikallio 1917), including the study by Finnilä in the Salla region in Lapland (1915, not cited by Merikallio 1917). It is clear that topographic approaches preceded genuinely quantitative bird surveys in Finland, and to some extent served as a model to them.

Discussion

Topography as a field of ornithology is probably unfamiliar to most of today's ornithologists. In the contemporary Finnish ornithological literature we only know of two references to the concept (Kauppinen & Ruokolainen 1999: p. 29, Vuorisalo *et al.* 2014). Interestingly, ornithologist Torsten Stjernberg was still in the late 1950s inspired by Palmén's (1908) paper while censusing birds as a schoolboy in the Porkkala region (Björklund 2014). The historical importance of the topographic approach primarily was in

Table 4. Examples of classifications of bird topographic localities during the nesting period.

Renvall (1910)	Palmgren (1913)	Suomalainen (1927)
I Forests (3 subtypes)	A. Water-dominated localities	Islands: small, outer archipelago
II Bushlands (3 subtypes)	I Marine localities (2 subtypes)	Islands: small, inner archipelago
III Open terrain (2 subtypes)	II Freshwater localities (3 subtypes)	Islands: large, southern archipelago
IV Wetlands/Mires (4 subtypes)	B. Wetlands	Human environments (settlements, fields)
V Shore areas (3 subtypes)	I Tree-growing mires (2 subtypes)	Islands: large, northern archipelago
VI Aquatic areas (2 subtypes)	II Open mires (2 subtypes)	Continental seashores
VII Air (4 subtypes)	C. Terrestrial localities	Small ponds
VIII Inhabited areas (2 subtypes)	I Open localities exposed to sun	Forests (6 subtypes)
	II Bushlands	Agricultural field margins
	III Forests (several types)	Rocky areas
		Small mires
		Drained mires and wetlands
		Large meadows
		Cultivated fields
		Forest patches in agricultural landscape
		Gardens and parks
		Manor houses
		Lakes (4 subtypes)
		Kokemäenjoki River delta
		Urban area (of the city of Pori, 14 subtypes)

the introduction of systematic data collection to Finnish ornithological field studies. It is clear that the topographic methodology gradually improved the scientific quality of Finnish faunistic studies, as Palmén (1885, 1908) had hoped. Research classified as topographic shared certain characteristics, most notably detailed location type (i.e., habitat) descriptions, compilations of full species lists (at least for the breeding season) for each location type, and at least relative estimates of species abundance (Table 2). These had not been totally lacking before, but the topographic approach made them a standard.

The terminology of topographic studies differed markedly from that of today. It is now commonplace to discuss bird communities of certain biotopes, habitats, habitat types or ecosystems. At the turn of the 19th and 20th centuries, none of these terms were used in the Finnish ornithological literature, although the terms habitat and biotope already existed. For instance, Warming (1909) used the term habitat, and Dahl (1908) the term biotope. The concept of ecosystem was first used in print by Tansley (1935). It is therefore not surprising to find a wide array of terms used for topographic units in the early bird topographic literature. In addition to terms listed in Table 3, terms such as *näkymätyyppi* (type of visual scenery; Seppä 1927) and *eloalue* (living area; Anonymous 1927) were used in the Finnish zoological literature. Of the modern terms listed above, biotope was the first to be adopted in Finland. In our research material it was first used by Palmgren (1928). Interestingly, it took a long time before the use of biotope became more widespread. While some ornithologists adopted it early (e.g. Siivonen 1936), the more traditional terms *ståndort* or *Standort* were still used by some authors at the turn of the 1930s and 1940s (Grenquist 1938, Hortling 1941).

A more profound transition than the terminological one was the shift from simple topographic species classifications to an early version of "ecosystem thinking". Pontus Palmgren (1907–1993) advocated this approach in his landmark article entitled *Zur Synthese Pflanzen- und Tierökologische Untersuchungen* (Towards a synthesis of plant and animal ecological studies; Palmgren 1928). The 21-year old author referred to Palmén's two bird topographic papers already in the preface of his study. The main point of his paper was to replace topographic studies by a more holistic or "biocoenotic" approach that would effectively combine plant and animal ecological research. Palmgren thought that Americans had been more successful than Europeans in synthesizing these two fields. A synthesis could be achieved, argued Palmgren, by adopting a production biological approach. This had already been done in hydrobiology/limnology and in Cajander's forest type theory. In his own field work, mainly in the Åland archipelago, Palmgren was able to produce data on total bird densities (pairs per km^2) in the different forest types that also represented different productivity levels. A production biological perspective necessarily requires quantitative data on breeding bird densities, which was not provided by most topographic bird studies.

It is interesting to compare the influence of Norrlin on Palmén with that of Cajander on Palmgren. In both cases, a promising new methodology was adopted from botanical to zoological studies. In the former, the transfer proved successful very quickly. In the latter, success was not immediate. Palmgren's idea of combining productivity data with quantitative bird censuses was ahead of its time, and to our knowledge was not applied by anyone either in Finland or elsewhere. It was not until the 1950s and 1960s when productivity levels were more widely applied in ecological research (Odum 1963). Also, the personal links between individuals are interesting. Norrlin and Palmén were close friends since their student years (Leikola 2011). Cajander was a student of Norrlin, and one of the key persons in the Finnish school of plant topography. Palmgren was too young to be a student of Palmén (he was a schoolboy at the time of Palmén's death), but was strongly influenced by his writings.

There was another interesting attempt to combine bird topographic data gathered from different parts of the country with Cajander's forest type theory. Päiviö Kuusisto proposed a classification of bird community types, partially based on Cajander's forest types (Kuusisto 1939). He tentatively distinguished five biogeographical regions in Finland based on species composition of bird communities. The typical

species compositions were derived from his own field studies and faunistic reports. Sadly, Kuusisto's untimely death in the Finnish Winter War in March 1940 stopped further development of this idea.

Although criticized by proponents of quantitative bird censuses (Merikallio 1917, Palmgren 1928), topographic surveys still have longstanding value as historical reference studies. In the Helsinki region, Palmgren (1913) is still considered a classical study on the local (Solonen *et al*. 2010). Palmgren's study was much more detailed than the first study on the birds of Helsinki and its surroundings that had been mainly a list of species without much reference to habitat preferences (von Wright 1848). In the province of Satakunta, the works of Suomalainen (1915, 1927) were "the most visible achievement of the province's ornithology for several decades to the future" (Soikkeli 1984). Also R. Palmgren's 1915 study in Huittinen was highly regarded by Soikkeli (1984).

Elias W. Suomalainen was also one of the great pioneers of ornithology in the province of Savonia. His 1908 topographic paper was discussed in detail in a monograph on birds of Northern Savonia, with the following commentary: "What would the bird faunistics of Northern Savonia or even the whole country be without E. W. Suomalainen, who was a forerunner, and is still a source of inspiration for us" (Kauppinen & Ruokolainen1999: p. 29).

Avian topography influenced the early phase of quantitative field ornithology in Finland. Merikallio's pioneering work in quantitative bird censuses in Finland seems to have stemmed from a purely bird topographic approach. Merikallio knew Palmén's two papers (Merikallio 1946), and wished to improve the quantitative basis of topographic studies (Merikallio 1917). His paper on the bird fauna of eastern Finland (Merikallio 1921) was a very typical (although exceptionally well written) bird topographic study with the exception of the use of a relative five-step scale of species abundance that was, for the first time, based on numerical analyses of bird populations. Such relative scales of species abundances were still used in the 1950s (Merikallio 1955).

Finally, the topographic approach has an obvious link with the study of bird behaviour. Especially Renvall (1910, 1916) understood that observed topographic patterns in the field result from the birds' behaviour while they select for breeding, foraging or nesting locations. Using modern terminology, topographic patterns or species distributions in nature are in part results of habitat selection by birds. This link between old bird topographic studies and habitat selection was explicitly observed by Olavi Hildén (1958, 1965). Hildén (1958) wrote in his paper on choice of breeding habitats by birds, that studies of the "topographic" distribution of birds have shown that several factors together limit the range of possible breeding habitats. Hildén (1965) made a clear distinction between the concepts. According to him, habitat selection takes place first, and affects the topographic distribution of species. Topographic distributions observed in nature are, in turn, influenced by both intraspecific and interspecific competition.

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